FURTHER STUDIES ON THE BREEDING BIOLOGY OF REDSHANK (*Tringa totanus L.*)

by

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ABSTRACT

Redshank breeding biology is examined and reviewed in relation to other sandpiper studies.

• Primarily, general aspects are described. The mean clutch size was 3.82 eggs. Fourth eggs laid were significantly smaller and more likely to hatch last. Nest hatching success varied annually from 30-74%, with tidal flooding the main cause of nest failure. In successful nests, hatch success was less variable. Chick size at hatch was positively correlated with egg size. Pre-fledging mortality is discussed in relation to overall fledging success.

Surviving adults generally remained mate faithful.

Experienced birds were found to nest earlier in the season and to produce larger eggs. In all years, female age correlated positively with egg volume. Inexperienced birds laid smaller eggs later in the season. Older birds were more successful at hatching eggs.

Experienced breeders were more likely to return to their former breeding grounds than were younger birds, particularly when they were successful the previous year. Birds unsuccessful in the previous year were more likely to divorce. Divorced females were less site faithful than males and were more likely to disperse.

Natal philopatry is discussed in relation to pre and post-fledging mortality. Philopatry is non sex biased and is estimated at being very high.

Chick growth and development is considered and an age determining formula devised for ageing chicks from their weight and bill length. Growth rates were constant between and within years.

Annual adult survival (0.75), life expectancy (3.48 years), and study area population are calculated. An estimated 175 pairs breed in the restricted area (168 pairs/km^2) and approximately 500 pairs on the Nature Reserve.

A model of population dynamics estimates pre-fledging mortality at between 66-74%.

Timing of breeding in other waders and a comparison with the related Greenshank are reviewed in the Appendices.

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Chapter 1

Redshank Breeding Biology - A General Review

General Introduction

The Redshank Tringa totanus is a member of the order Charadriiformes, Family Scolopacidae (sandpipers).

Redshanks are to be found breeding in continental middle latitudes, mainly in temperate and steppe, but overlapping into boreal and Mediterranean zones. Within oceanic regions they extend into subarctic and marginally into low arctic areas.

In the non breeding season Redshank are generally coastal. During the breeding season they are dependent on a high water table and local saturation of soil. Habitat types satisfying such requirements are coastal saltings, damp but not wet marshland, grassy fields subject to partial flooding, water meadows, rushy fields and wet pastures; occasionally they may be found on low lying damp moorland.

The Ribble Marshes study of Redshank started in 1973. Since then Redshank have been intensively studied. Data have been gathered on a number of general topics, especially courtship, incubation, chick rearing, migration and winter distribution. More specialised studies have been undertaken on breeding site fidelity, natal philopatry, chick growth, female quality, and the timing of breeding.

The initial aim of this research project was to attempt to gain a fuller understanding of the biology of Redshank. With the accumulation of basic data, it soon became possible to study some aspects of breeding biology in more detail. In particular, the study focussed on breeding dispersal, natal philopatry, female quality and growth rates in young Redshank. Comparisons between this study, and those carried out on other wader species, particularly other sandpipers, are essential if we are to understand more about relatedness, quality of individuals, geographical differences in productivity both within and between species, and mortality. Only long term studies can provide the detailed in-depth information essential for such a complete understanding.

Many short studies do provide useful material, but they often neglect the variables that lead to important seasonal variation. Only in recent years have studies of wader breeding biology begun to gather the data required for a fuller understanding of breeding biology, and in particular population dynamics. Classic works, such as Witherby *et al* (1941), Bannerman and Lodge(1961), Glutz et al (1977) and Cramp and Simmons (1983) provide a wealth of good information on breeding, distribution, plumage, migration and other aspects of biology.

More specialised studies have been carried out by Byrkjedal (1978a,b 1980), Gratto *et al* (1985), Grosskopf (1958a,b, 1959, 1963, 1970), Hilden (1975, 1978, 1979), Holmes (1966, 1970, 1971, 1972), Miller (1979, 1983), Nethersole-Thompson (1951, 1973), Nethersole-Thompson & Nethersole-Thompson (1979), Oring *et al* (1982, 1983), Soikkeli (1967, 1970) and Pienkowski (1983, 1984a,b). These studies have been concerned with individual species for at least 3 years. Such long term intensive studies have added greatly to our understanding of breeding biology and populations. For example see Coulson's recent review of Kittiwake *Rissa tridactyla* studies (Coulson and Thomas 1985).

Other workers have concentrated on more specific problems rather than on individual species. Major reviews have appeared on population dynamics, timing of laying, courtship and mating systems by Burger and Olla (1984), Erckmann (1983), Goss-Custard (1978/79), Greenwood (1980, 1982), Green, Greenwood and Lloyd (1977), Jenni (1974), Miller (1979 a,b., 1983 a,b.), Perrins (1970), Vaisanen (1977), and Vaisanen et al (1972).

At an International Workshop on the Ecology of Shorebirds, held in Cardiff in September 1983, the selection of papers presented indicated that wader research was very much on the increase. However, the majority of research has been on feeding ecology of wintering waders. One of the aims of the Symposium was to attempt to promote more research on breeding waders (W.S.G.B. December 1983). It is hoped that the current upsurge in breeding studies will continue, as our knowledge is still very sparse. This international upsurge is also reflected in wader studies in Britain. At a recent Wader Workshop, held in Durham in December 1985, the participants were involved in both single species studies and more general wader problems. One obvious gap is the lack of long term research. Studies of 2-3 years duration by post-graduate students are often then discontinued.

It is noteworthy that the Ribble Redshank project has involved five 3-year postgraduate students and three research technicians. The entire project has been over-viewed by Professor W.G. Hale, thus allowing for a long term project which is constantly reviewing the status of research, with the aim of maintaining the continuity whilst minimising repetition. The long term nature of the study makes it possible to assess annual variations and provides a fuller picture of the biology of the Redshank than would be possible from a short term study.

My own contribution, following on from the work of Greenhalgh, Ashcroft, Selman and Yates, is intended to demonstrate age related differences in breeding time, egg size and reproductive output; and in the main to determine what role birds of differing age groups play in the population.

Studies of age related reproductive differences in waders have, so far, received little attention: Anderson (1948, 1951), Gratto et al (1983, 1985), Grosskopf (1970), Hilden (1979), Thompson et al (1986) and Tuck (1972). Other studies have made passing reference to possible age-related reproductive differences.

Research on other groups have highlighted age related variability, in particular Ankney and Macinnes (1978), Coulson and White (1958, 1960), Coulson (1966), Coulson and Horobin (1976), Coulson and Porter (1985), Crawford (1980), Davis (1975), Greenwood et al (1979), Mills (1979), Nelson (1978), Ollason and Dunnet (1978), Perrins and Moss (1974) and Thomas (1983).

Aims

The initial priority was to determine if birds of different ages performed differently within the population and if so to examine what aspects of breeding biology were affected. Such analysis could only be undertaken with the detailed background histories that exist for many of the Ribble birds. Secondary aims were to study breeding site tenacity and natal philopatry and to assess young Redshank growth and survival.

Study area

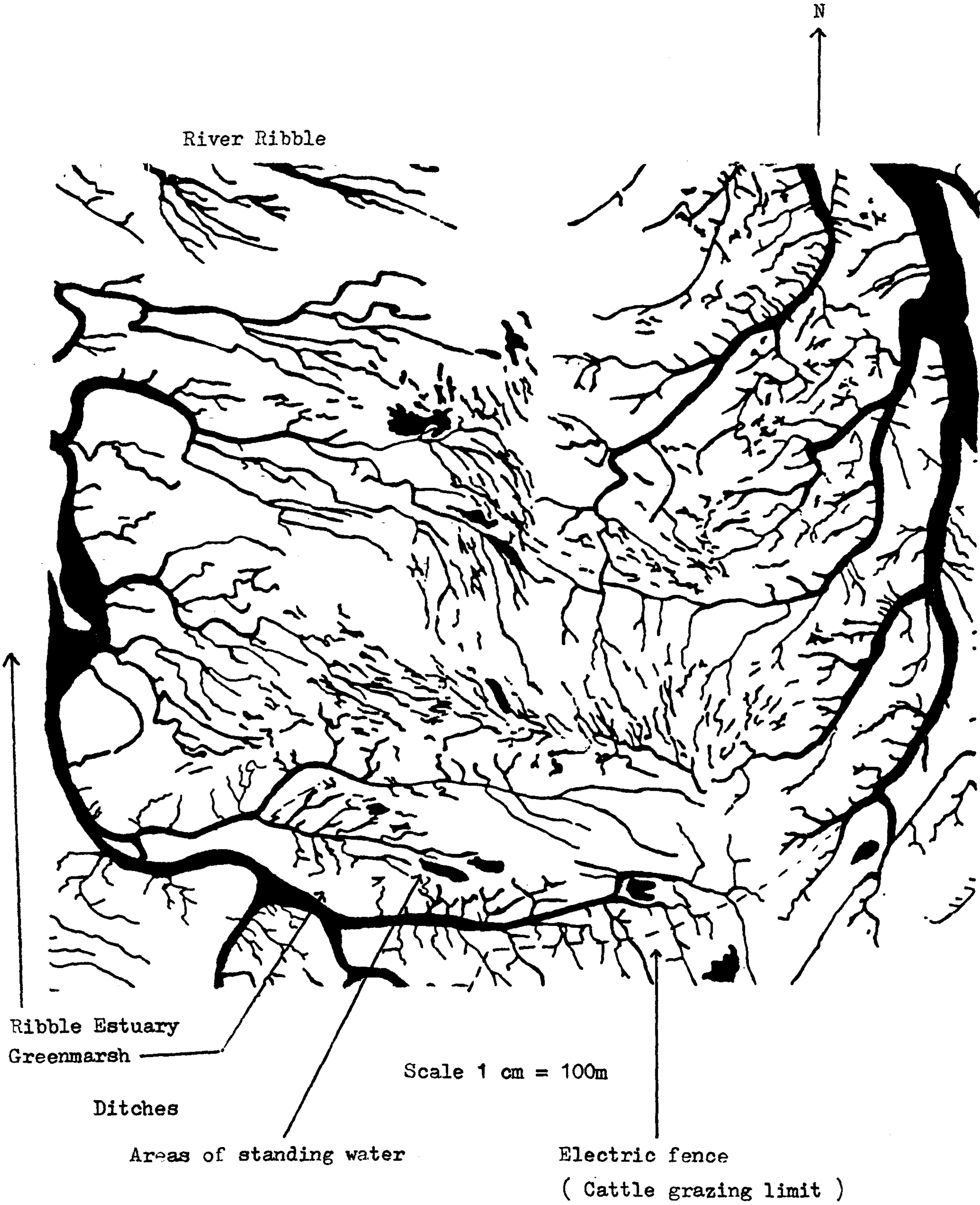
This study was carried out on Banks Marsh 53°42' N, 02°55'W, an integral part of the Ribble Marshes National Nature Reserve, Lancashire, N.W. England.

This NNR covers 2302 hectares of saltmarsh and intertidal flats on the south side of the River Ribble. The Nature Conservancy Council purchased 2182 hectares of Banks and Crossens Marsh in 1979 to prevent it from being embanked and converted to arable land. A further 120 hectares (Hesketh Out Marsh) were added to the Reserve as part of an agreement with the owners. Approximately half of the area is vegetated saltmarsh and half is mudflats and sandbanks.

The Reserve is of international importance for birds, supporting one of the largest wintering and passage populations of wading birds in Britain. During the autumn/winter months the saltmarsh is grazed by a large number of wildfowl. The mudflats and sandbanks also accommodate high numbers of passage and wintering waders.

During late spring and summer the green marsh is grazed by some 850-900 cattle. Grazing begins at the end of April and continues well into autumn. Between 1974 and 1980 all of the study area was continuously grazed throughout the summer. Since 1980 the study area has been fenced off from the rest of the marsh by an electrified fence for a period of some ten weeks. Cattle grazing has therefore been controlled during the birds breeding season (see Fig. 1). The study area is the main part of a Sanctuary Zone to which entry by unauthorised persons is prohibited. It is therefore relatively free from any form of disturbance other than that caused by the research team.

Fig.1. The Banks Marsh study area.



Old Hollow Meadows.
Area approx. 1 Km. S.E. from sanctuary area.

The research area (2 km^2) is dissected by an extensive network of channels which fill and empty to a varying degree, depending on the state of the tide. There are also large areas of standing water in the form of scrapes and smaller pools. During early spring the marsh surface is saturated and the vegetation cover very short, as a result of air temperature, day-length, soil saturation and grazing wildfowl. During the following weeks the soil dries out gradually but may be saturated periodically by the spring tides. Vegetation growth once begun is rapid; and soon the marsh surface, and in particular the channel edges, have a luxuriant growth of grasses. Areas away from the channel edges are lower and subsequently vegetation growth is slower due to the higher levels of soil saturation. By mid-June the entire marsh is well vegetated.

All year round the marsh is subject to varying degrees of flooding at the time of spring tides. These frequently cover the whole marsh, depositing all sorts of debris on the surface. When the channel edges are flooded, material is deposited, leading to the edges being higher than the surrounding marsh. These higher, drier channel edges are very important to breeding Redshank.

Since the construction of the sea wall from Southport to Hesketh Bank, the saltmarsh on the westward (seaward) side has matured, rapidly spreading northwards and westwards. This rapid spread and maturation has been greatly harnessed by the pioneer _Spartina anglica_. Maturation of the surface marsh has been so rapid that channels which were uncrossable in 1973 are now easily crossed (W.G. Hale _pers. comm_). On the landward side of the sea wall there are some fine examples of reclaimed marsh. Some of this land has ditches, seasonally wet depressions, pools or generally wet grassland areas.

One such area, next to Old Hallow Farm, is worked as a minor study area and is normally grazed throughout the breeding season.

The typical saltmarsh plant communities are represented on Banks Marsh. The major grasses are Festuca rubra, on the higher drier areas, and Puccinellia maritima. The hybrid cord grass S. anglica is the dominant pioneer but in some areas, notably pool edges, the first pioneer is Salicornia spp. Additionally, there are large growths of Cochlearia danica on some channel edges, Attriplex littoralis and Aster tripolium on poorly vegetated areas and Glaux maritima and Armeria maritima on the more open areas of marsh. In many of the channels there are large growths of Halimione portulacoides, giving much cover for sandhoppers Gammarus spp. when the tide is out.

Banks Marsh supports a large number of breeding birds. In particular there is a very large colony of Black-headed Gulls Larus ridibundus, smaller colonies of Herring Gulls L. argentatus, and Lesser Black-backed Gulls L. fuscus. There is a large colony of Common Terns Sterna hirundo and also a small number of Arctic Terns S. paradisaea. Wading birds are poorly represented, with only Oystercatcher Haematopus ostralegus and Redshank breeding regularly. Redshank densities in some areas are amongst the highest ever recorded for the species (Hale 1980). Breeding wildfowl include Shelduck Tadorna tadorna, Mallard Anas platyrhynchos and, very occasionally, Teal A. crecca. The only regular breeding passerines are Meadow Pipits Anthus pratensis and Skylarks Alauda arvensis. For additional details see Greenhalgh (1971).

Methods

Fieldwork began on the 20th, 17th and 12th of April and was terminated on 28th, 31st and 30th July in 1983, 1984 and 1985 respectively. A normal working day was from 9.00 to 18.00. A maximum of 4 days were missed over the three year period.

Nest finding

The whole study depended on a large number of nests being found. Nests were found in a variety of ways, every effort being made to find them at the laying stage.

(a) Cold searching: Channel edges and edges of standing water were searched on a 4-day (sometimes 3-day) rota. Areas between ditches and more open green marsh were also meticulously checked. Initially, searching was relatively easy and quick, as nesting habitat (tussocks) were in short supply. Later in the season searching was slowed up due to the length and preponderance of suitable nesting areas. Where possible, almost every area of the study site was searched every four days. Searching involved walking, while looking from side to side at the ground. Where necessary, a stick was used to separate vegetation in tussocks. A 'search image' for nests and preferred habitat was quickly formed each year and greatly facilitated nest finding.

Searching of this type begun prior to egg laying, allowing the searchers to "get their eye in" and also to identify areas of activity due to the number of nest scrapes. Nesting did not tend to begin at the same time everywhere; small groups began to lay in isolated areas.

(b) Flushing incubating birds: Occasionally whilst searching, but more often when walking across the marsh to set or empty nest traps, a bird would be flushed from an area of vegetation. A quick search usually then revealed a nest, normally with a full clutch.

(c) Watching: Nests were sometimes found whilst sitting down to have lunch. Normally birds returned quickly and could be seen running back to eggs. Depending on the state of incubation, the return rate may be rapid.

Watching back was by means of 8x30 binoculars and a telescope, but not many nests were found in this manner. On rare occasions a nest was found with a bird actually incubating.

Nest marking

Once found, nests were marked and numbered with a bamboo cane. The canes were pushed well into the mud, 10 paces from the nest, in order that they would not betray the location. Nests were plotted on a detailed map of the study area.

From the moment of finding each numbered nest was allocated a Nest Data Sheet (Appendix 1).

Nest visits

At the laying stage nests were visited daily to determine, where possible, laying times and laying intervals. Once the clutch was complete, visits were no longer on a regular basis. Nests were visited to measure eggs, to trap the adults, and also to check for signs of hatching. Nests were visited during the hatch to ring and measure chicks. Great care was taken not to wear a path to the nest. Whilst setting traps it was important not to flatten the surrounding vegetation. Normally, once the trap was removed any disturbed areas were tidied up.

Eggs

Nests found during the laying stage had their eggs numbered with an indellible marker. Eggs were numbered 1 to 4 in accordance with their order of laying, the first egg being labelled 1. If found after the clutch was complete, the eggs were labelled A-D.

The date of clutch completion was recorded for those nests found during laying. In completed clutches the date of clutch completion (or days incubated) was determined by:

(a) counting back 25-26 days (incubation period) from the date of hatch;

(b) estimating the angle of floatation of eggs in a cylinder of fresh water (for details see Yates 1982, unpubl.). Generally there was good agreement between the two methods. It was essential to know when the eggs were going to hatch to maximise the number of chicks ringed in the nest.

At all nests, eggs were measured with vernier calipers:

Egg length - to nearest 0.05 mm (L)

Egg breadth - to nearest 0.05 mm (B)

From these measurements a calculation for egg volume was made using the formula of Vaisanen <u>et al</u> (1972).

Egg volume = $L \times B^2 \times 0.37698 + 3.283$ (cm^3).

Vaisanen arrived at this formula by filling 50 redshank eggs of known length and breadth with a measured amount of water.

Laying intervals

Where a nest was known to contain a fresh egg, the interval between this time and the time the next egg appeared could be used as an indication of laying interval.

Incubation time

This has been calculated from the completion of the clutch to the hatching of the first egg.

Trapping

Birds were trapped at the nest using a walk in funnel shaped trap made from wire mesh (10 x 25 mm), with a plastic netlon roof. In 1984, 85 we also used traps made of plastic mesh with a plastic netlon roof. These caused less injury to the trapped birds.

The funnel shaped doorway was placed at the entrance to the nest with the main body of the trap placed over the eggs and then firmly pegged to the ground. On a few occasions each year, birds were caught without using a trap.

Trapping tended to be carried out in two separate areas within the study area. Each trapping area was discrete with no more than 10 traps being set in each. Once all the traps were set the study area was left for 2 hours. No nest was trapped on consecutive days if, on the previous day, a bird had been caught. No nest was trapped until incubation had been in progress for six days. At all nests the aim was to catch both adults. In 1983 trapping ended on 5 July; in 1984 on 30 June; and in 1985 on 29 June.

Towards the end of June the brooding drive was greatly reduced and trapping was normally ended prematurely, even though some nests were still present. This reduced the desertion rate.

At the time of trapping all nests were emptied at once (in separate discrete areas). Emptying normally took 15 minutes. Once trapped, each bird was removed and placed in a separate bird bag. This had the effect of pacifying the adults.

Mist netting

In addition to trapping at the nest, some birds were caught in mist nets. This part of the study was mainly concerned with capture of fledged Redshank. The ringing and measuring of birds was carried out all at once. Birds were checked for BTO ring and if ringed (control), the ring number was recorded. Each bird was assigned a separate data sheet (Appendix 2). Nest number, date and ring number were all recorded.

The following measurements were also recorded on the data sheets:
Weight (1 g); wing measurement (1 mm); bill to feathers (0.5 mm); tail length (0.5 mm); tarsus length (0.5 mm); tarsus width (0.01 mm). Weight was measured using a Salter 200 g spring balance. Other measurements were made using dividers, 30 cm stopped ruler, and a micrometer for tarsus width.

The number of summer plumage feathers on the breast, mantle, scapulars and secondaries were also recorded on data sheets (breast and mantle scores were counted in a 2.5 cm square). In 1984 and 1985 the colour of the legs, the bill, and the presence or absence of juvenile inner median coverts, was scored for all birds (the technique was standardised by colour chart). The last criterion is an ageing technique for first summer Redshank discovered by W.G. Hale and first published in the BTO Wader guide (Prater, Marchant and Vuorinen 1977, this study).

Birds trapped without rings (from here on called unrings) were ringed with an individually numbered BTO ring and recorded on a bird data sheet. Once the unring was ringed, similar data was recorded as was gathered on ringed birds.

Yates (Unpubl. 1982) highlighted the problems of sexing

Redshank. Several techniques were used.

(a) The cloaca method: the width and shape of the cloacal protuberance was examined. After egg laying, females have a fleshy distended cloaca, the male cloaca appears small and lacks the fleshy outer membrane.

(b) The overall size of the bird: The weight, bill measurement, wing measurement and tarsus length were considered and compared with previous years data, if the bird had previously been captured. Museum specimens indicate females are larger than males (Hale 1971).

(c) Pair complex method: A bird's case history was examined at the end of each season. If bird 'A' was caught with 'B' in one year and with 'C' and 'D' in previous years, then B, C and D must all be of one sex. Such groups, many of them very large (one contained 67 birds), allowed for the accurate grouping of birds of like sexes. All data gathered since 1974 were stored on computer using the 1022 Database management system. This facilitated access to and analysis of pair complexes.

In accordance with Hale (1971) groups with consistently larger birds and fleshy cloaca were considered to be females; larger groups therefore gave rise to a greater degree of accuracy. At the end of the season each bird's data sheet and its previous capture and mate history were examined. There was good agreement between all three techniques.

Hatching:

Nests were visited regularly in the days before the hatch and the time recorded from the first chipping of the eggshell to the hatch. All hatched chicks were measured and ringed with BTO numbered rings and where a specific chick was known to have hatched from a specific egg a note was made on the nest data sheet.

Chicks were aged in the nest; wet, tired chicks were obviously last to hatch, whilst dry lively chicks had been hatched for some hours. At an asynchronous hatch, chicks could often be aged from 1-4 (first to last). Where possible, hatch order was related to chick measurements and chick size to egg size.

In cold weather, ringing chicks took preference over measuring chicks. Chick measurements were made by a 150 mm stopped rule and dividers and a 50 g Salter spring balance.

Weight	(0.5 g)
Tarsus	(0.5 mm)
Bill tip to feathers	(0.5 mm)
Bill tip to rear nares	(0. 5 mm)
Bill tip to front nares	(0.5 mm)

The ring allowed chicks subsequently re-captured to be aged accurately.

Nest assessment:

Nests were visited regularly to assess the clutch size and towards the end of their incubation period nests were checked for signs of hatching. Nests were also checked to assess that incubation was in progress. This was important at the laying stage to assess if incubation had begun before clutch completion and continued after trapping had occurred.(In some cases an adult continued to incubate when its mate had deserted).

An attempt was made to follow all nests through to hatching or disappearance. In this manner all nests were classified according to their outcome. Regular visits allowed for a more accurate assessment of nest and egg losses.

After a flood, nests were said to have been 'lost to flood' if all eggs were gone when they were previously known to be present. If a nest was close to hatching, the flooded nest was examined for signs of shell fragments.

Nests were adjudged as predated if egg fragments or yolk fragments were found in or near by the nest.

Eggs were considered as addled/infertile if they failed to hatch, even though they had been fully incubated.

Details on chick capture are given at the start of Chapter 4.

Redshank Breeding Biology - A General Review

Introduction

This chapter outlines and presents the wealth of basic information collated on breeding Redshank. All data were gathered in the 3-years study on the Ribble Marshes.

Without an understanding and knowledge of the basic facts of breeding biology one cannot undertake more specialised studies.

The breeding behaviour and biology of Redshank has been studied in detail by Grosskopf (1958 a,b, 1959, 1963, 1970) in Wangerooge, Germany. More recent studies have been conducted on the Ribble Marshes by Ashcroft (unpubl. thesis 1978), Hale and Ashcroft (1982, 1983) and Yates (Unpubl. thesis 1982). The latter more specialised studies have added greatly to our understanding of the Redshank and its way of life.

Generally, our understanding of wader biology is very poor with the exception of a few notable studies. In particular our knowledge of breeding sandpipers (Scolopacidae) is poor and in many cases even the most basic of information, such as laying dates, incubation period and fledging period, is lacking or totally inadequate. Our understanding of some Tringine sandpipers such as the Greenshank T. nebularia, Common Sandpiper Actitis hypoleucos and Spotted Sandpiper A. macularia has been greatly enhanced by long term studies. The Greenshank has been studied by the Nethersole-Thompsons in two different regions of Scotland (Nethersole-Thompson 1951; Nethersole-Thompson and Nethersole-Thompson 1979; Thompson et al 1986; and Nethersole-Thompson and Nethersole-Thompson 1986). Common sandpipers have been studied in the Peak district (N. England) over a number of years (Holland et al 1982 a,b; and Yalden 1984, 1986).

The Spotted Sandpiper has been studied in two different areas in North America (Hays 1972; Lank *et al* 1985; Oring and Knudson 1972; Oring and Lank 1982, 1985; Oring and Maxson 1978 and Oring *et al* 1983).

Published data on other tringine sandpipers such as the North American Greater Yellowlegs *T. melanoleuca*, Lesser Yellowlegs *T. flavipes* and the Spotted Redshank *T. erythropus* are of a much lower standard. In addition to the lack of studies on the 'shanks', other Tringine sandpipers such as the Wood Sandpiper *T. glareola* and Green Sandpiper *T. ochropus* have been studied in little detail.

In contrast, many Calidritine sandpipers have been studied in much greater detail. Thorough research has been undertaken on the Sanderling *Calidris alba* (Parmelee 1970 and Parmelee and Payne 1973), Semipalmated Sandpiper *C. pusilla* (Ashkenazie and Safriel 1979 a,b), Western Sandpiper *C. mauri* (Holmes 1971b,1972, 1973), Temminck's Stint *C. temminckii* (Hilden 1975, 1978, 1979), Least Sandpiper *C. minutilla* (Miller 1979 a,b, 1983 a,b), White-rumped Sandpiper *C. fuscicollis* (Parmelee 1968), Purple Sandpiper *C. maritima* (Bengtson 1970, 1975) and the Dunlin *C. alpina* (Holmes 1966 a,b, 1970, 1971a and Soikkeli 1967, 1970 a,b and 1974). These studies concentrated initially on the gathering of basic information. In many cases the data gathered were then subjected to detailed analysis allowing for a fuller understanding of the breeding biology.

For my own part, the following chapter is a general review of Redshank breeding biology on the Ribble marshes. These findings are integrated and compared with other studies of Redshank in the Discussion and, where relevant, comparisons are made with other sandpipers. It must be emphasised that the basic information gathered is an important part of any study as all subsequent analyses are normally based on the data gathered. By documenting much of this basic information, future workers on the species will be saved a great deal of work and will be able to start research at a higher level. It is also of note that several aspects, such as egg and clutch size, hatching success and laying dates may well be used as an indicator of breeding potential and success. Researchers carrying out work in later years can then examine these results in the light of their own findings, and perhaps make meaningful comparisons.

Results

Arrival

Redshank begin to arrive back at the breeding grounds from mid-February onwards. Birds have been sighted locally as early as 6 February (DR36492 sighted 6.2.83 at Marshside, Southport). In contrast, birds have been sighted on the south coast of England as late as 8 March. These birds subsequently bred in the first nesting wave of that year.

The earliest recording of Redshank (marked individual) on the breeding grounds is 17 March. Birds are present on the breeding grounds prior to this, but a number will not yet have returned.

There is indirect evidence to suggest that younger birds returning to breed for the first time do so later than older, more experienced birds. However, it is very difficult to prove this without an active catching programme.

A further two individuals were sighted on 11 and 14 March on the Plym and Severn Estuaries. These were not exact sightings as the identity of individuals remained unknown (the wing tag symbols were not clearly seen).

Courtship and display

At no time were quantitative data gathered on this aspect of biology. For full details see Ashcroft (1978) and Hale and Ashcroft (1982, 1983).

The first and earliest song flight was recorded on 10 March 1985. This was a full song flight, lasting at least 5 minutes, on a warm spring day with clear blue skies.

The earliest copulation observed occurred beside a pool on 31 March 1985. Throughout the three years study, copulations were rarely observed on the marsh. In contrast, copulations were seen fairly regularly at the meadow site by Old Hollow Farm. Early copulations were almost certainly unsuccessful.

By the end of March, beginning of April, Redshank song flights were observed more frequently. In particular there appeared to be a peak in singing activity in the late afternoon and early evening.

Scraping

The first definite signs of nest scraping give a good indication of how breeding behaviour is progressing. In 1983 the first nest scrapes were found on 4 April; by 16 April many scrapes were in evidence. In 1984 the first scrapes were not found until 7 April. On 7 April 1985 only a few scrapes were located on the breeding grounds, but by 12 April there were many more in some areas. In other parts of the marsh, however, there was less activity.

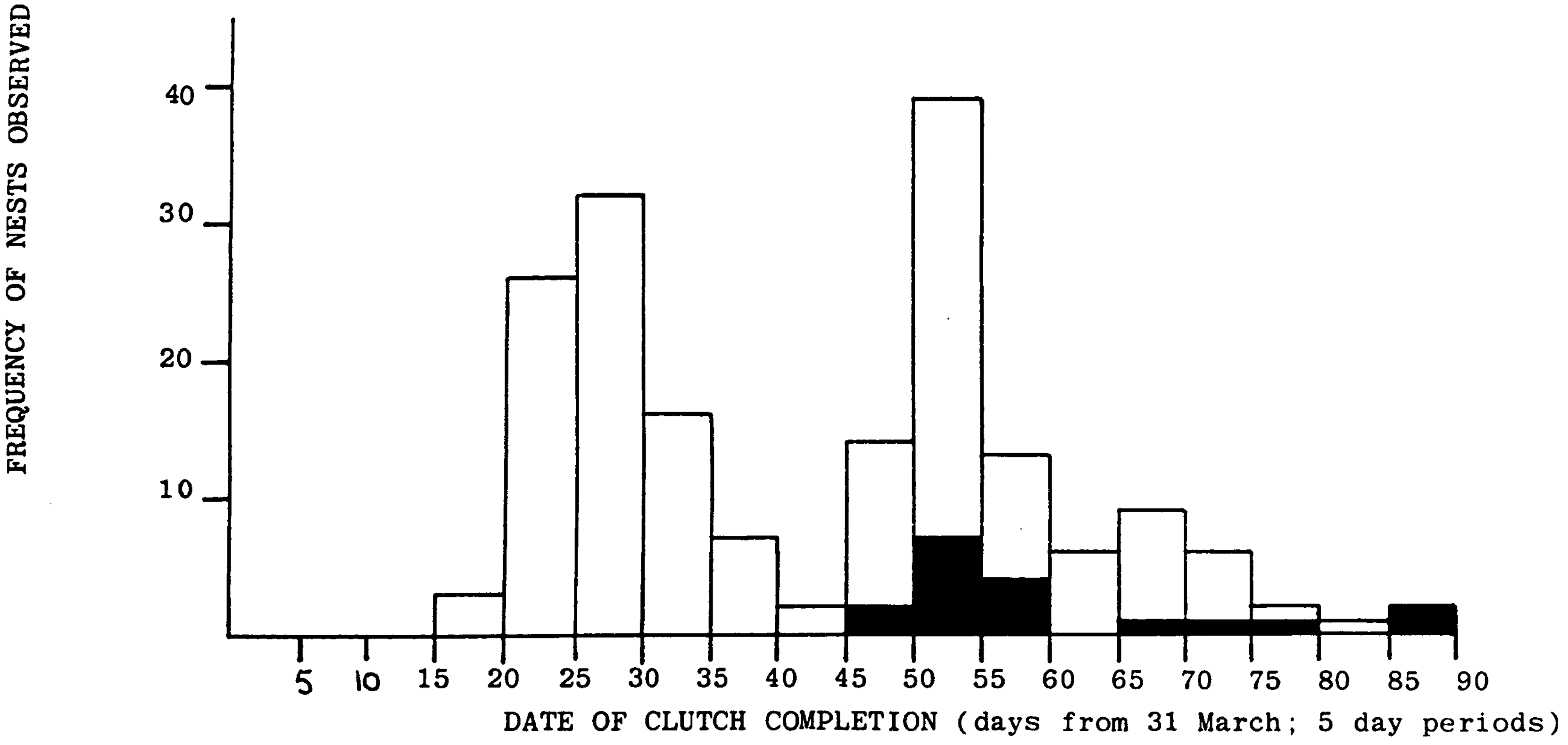
Once the final scrape was selected, laying commenced. Normally the first egg was laid in a bare scrape. Lining was added whilst the remaining eggs were laid. Further details of scraping behaviour and displays were not recorded as this was previously studied in great detail by Ashcroft (1978 unpubl. thesis), and Hale and Ashcroft (1982, 1983).

Timing of Laying

Figures 2-4 show the dates of clutch completion (where known) of all nests found on the marsh during this study. In these figures the number of nests found during each 5-day period are plotted as histogram columns.

In an attempt to explain the timing of laying in relation to tidal pattern, the predicted tidal heights are shown for the Ribble over the same period. These data are shown in figures 2a-4a.

Fig. 2a. The date of clutch completion of all nests found (where known). 1983.



Solid shading denotes relay (n=19).
48% of nests were found at time of laying.

Fig. 2b. The highest predicted daily tide heights. 1983

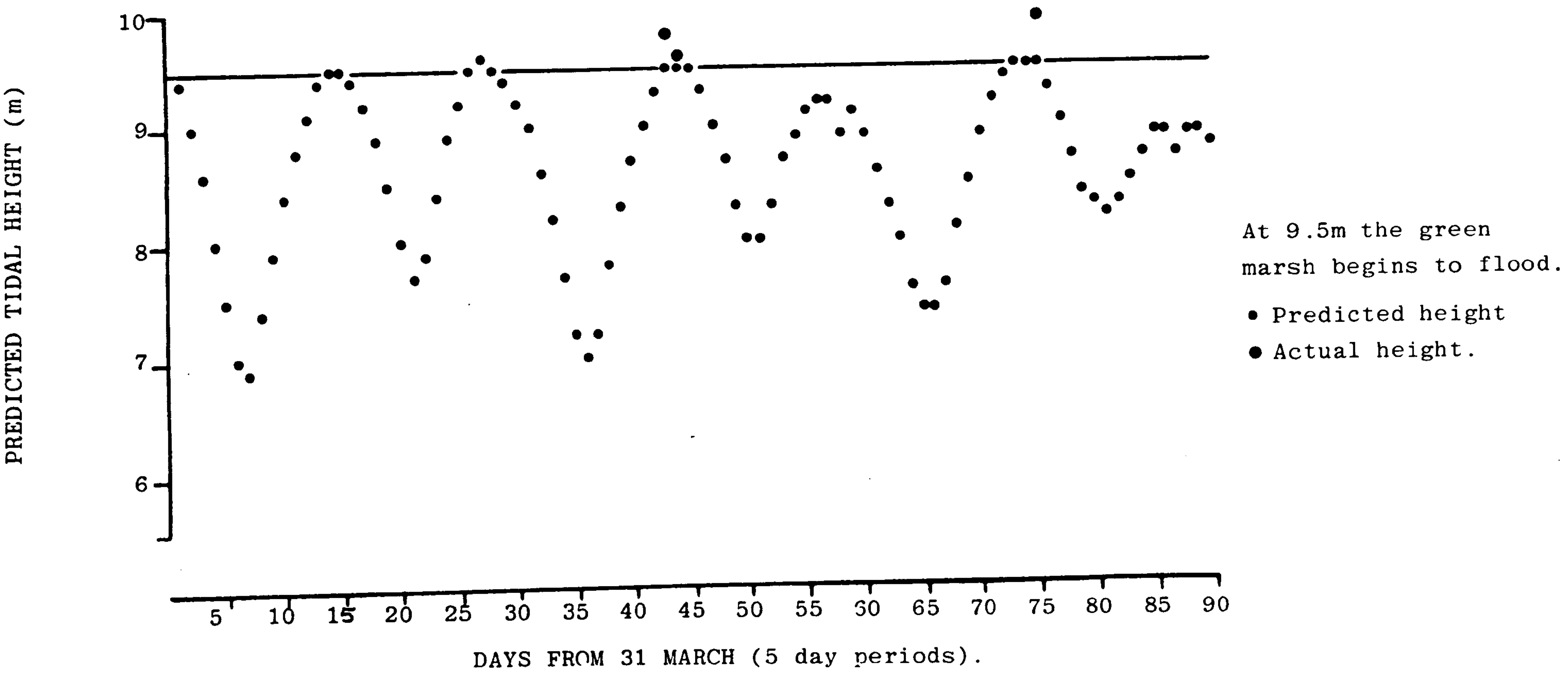
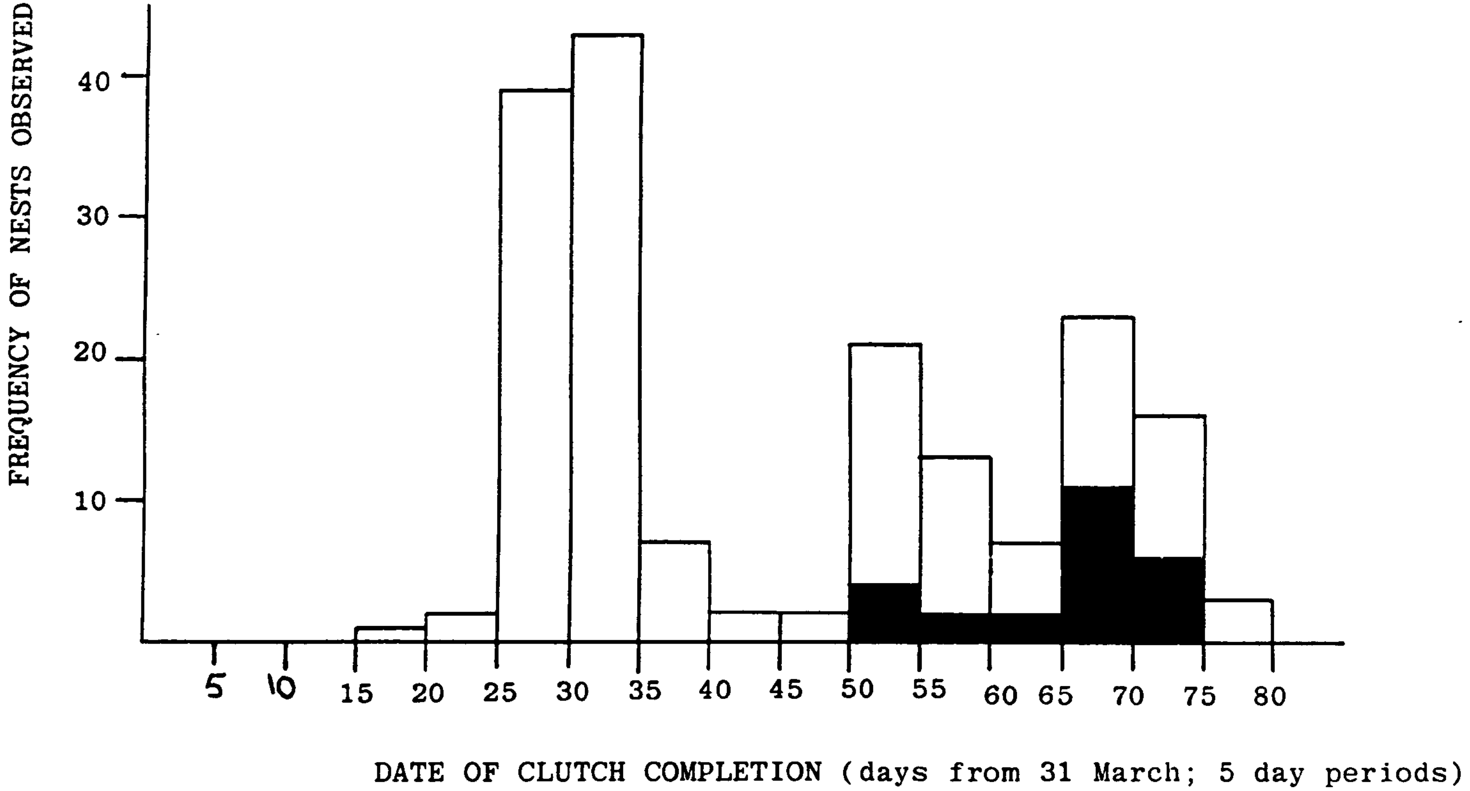


Fig.3a. The date of clutch completion of all nests found (where known). 1984



Solid shading denotes relays (n=25)
54% of nests were found at time of laying.

Fig.3b. The highest predicted daily tide heights. 1984

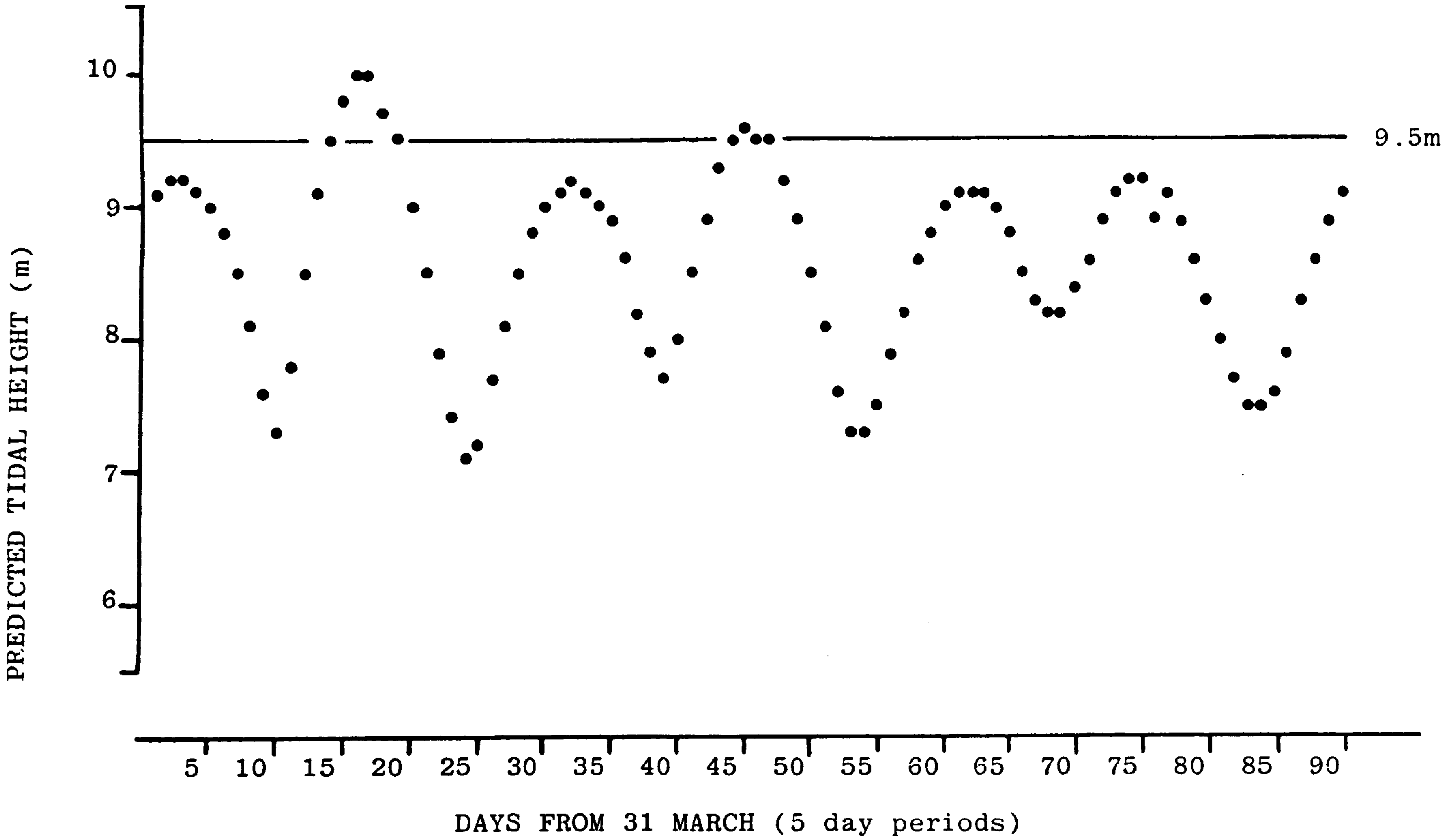
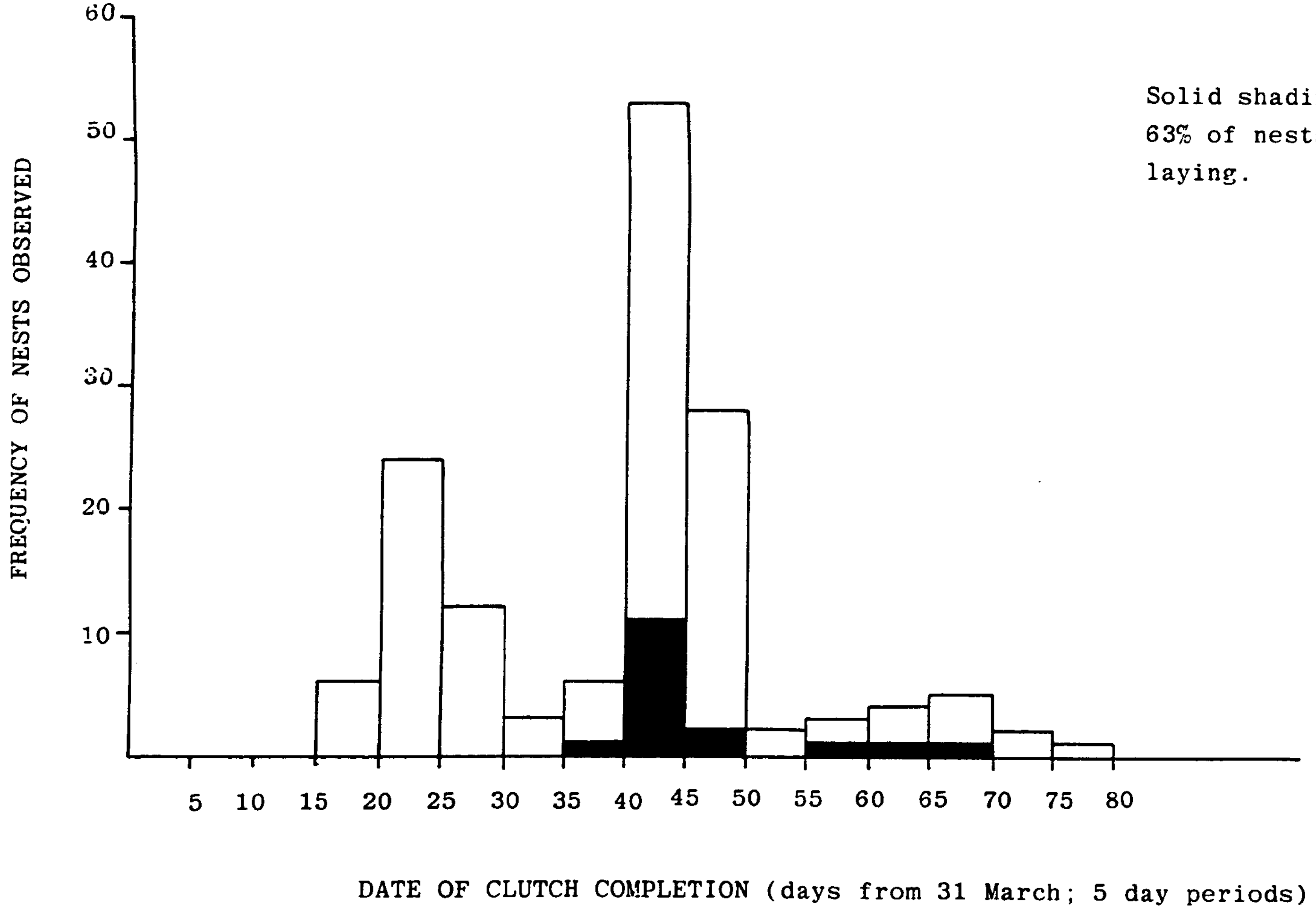
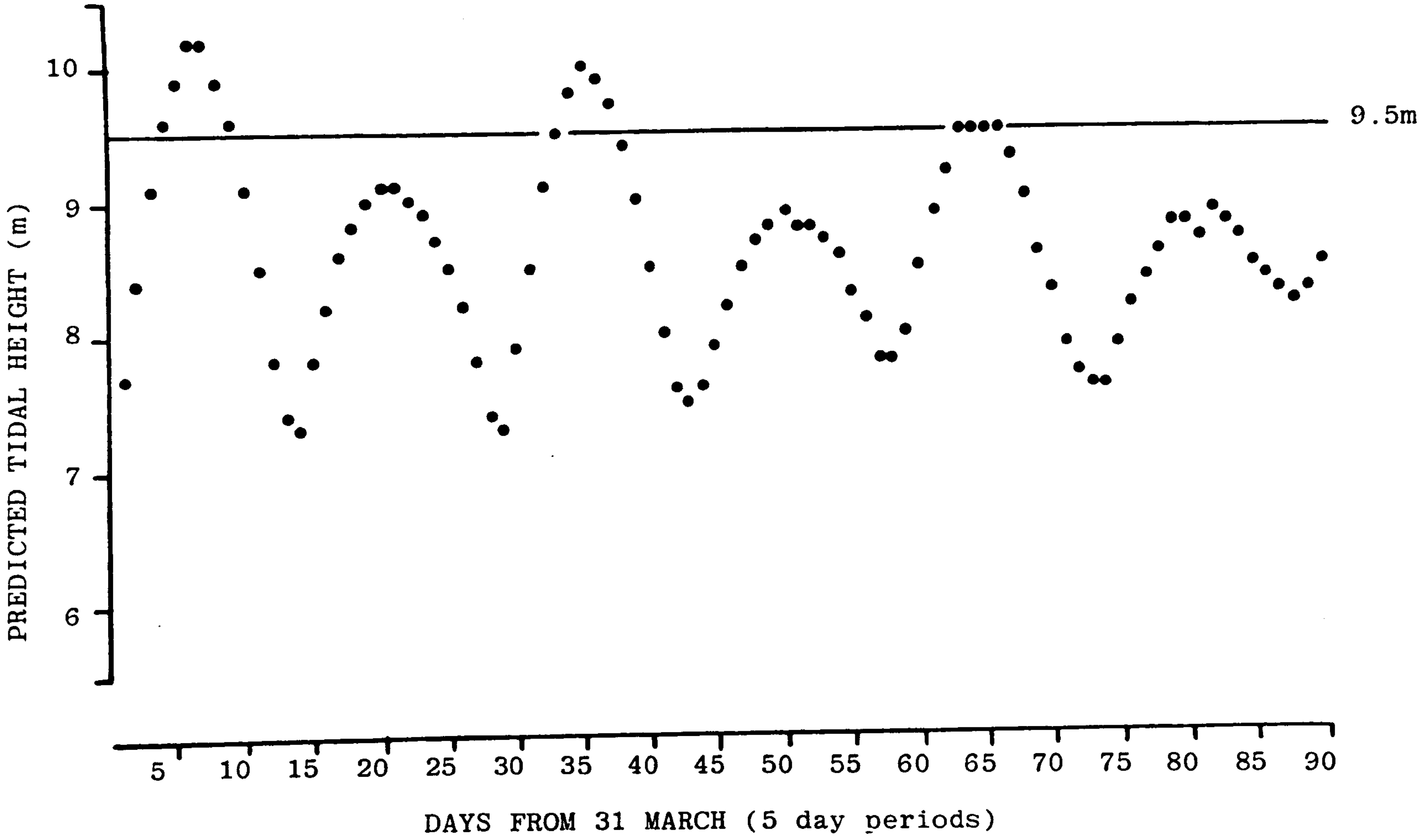


Fig.4a. The date of clutch completion of all nests found (where known). 1985



Solid shading denotes relay (n=17)
63% of nests were found at time of laying.

Fig.4b. The highest predicted daily tide heights .1985



Dates of clutch completion were known where a nest was found during laying or where a nest hatched enabling the date of clutch completion to be calculated (counting back 25-26 days). For a very few nests, date of clutch completion was estimated by observing the degree of egg floatation in a cylinder of fresh water. Over the three years, 48, 54 and 63% of all nests were found during the laying period.

In each year, egg laying occurred in two distinct peaks. In 1983 the first clutches were completed between the 15-20 April. After this period, the number of clutches completed on a 5-day basis began to increase, peaking between 25-30 April. In 1984, the season got off to a much slower start but the majority of laying took place over a shorter period. In this case most clutches were completed between 1 and 5 May. The 1985 season was different; many birds appeared to delay laying until after the beginning of May. As a consequence, the first observed peak was much smaller than in 1983 and 1984.

In 1983 and 1984 the first peak of laying occurred after a spring tide of 9.5 m and 10 m respectively. In 1985 the second peak of laying occurred after a late series of spring tides peaking at 10.0 m. In all years a large amount of re-laying occurred after each spring tide over 9.5 m. In 1983 there were two very high series of tides peaking at 9.8 m (13 May) and 9.9 m (14 June). As a result of these tides, there was very heavy nest losses resulting in a considerable amount of relaying. In 1984 the lack of tidal innundation resulted in only a few nests being lost. The majority of relays which were recorded arose as a result of Redshank losing their chicks at an early stage of development. In 1985 the huge tide which occurred on 5 May (10 m) resulted in the loss of almost all nests which were in existence at that time. As a result of this tide, some nests which were lost were replaced.

In 1983 the last clutches found were completed in the last week of June. In 1984 and 1985, a year of no late season flooding, the last nests were completed in the third week of June.

In areas of the marsh outside the study area, laying was found to be even more protracted due to nest destruction by cattle.

In any one year, birds were subjected to the same environmental conditions. It was therefore of great interest to examine laying dates in an attempt to determine why some birds laid early and others late.

Egg laying times

Once the scrape has been selected and the female is ready to lay, egg laying commences. Prior to the actual laying of the egg she remains quiet, close to the nest. Very often the male is also present at this time.

On one occasion a female, obviously about to lay, was watched back to an empty scrape. She walked very slowly and it was noted that the underside of the bird in the areaof the cloaca was greatly distended. This scrape was checked three hours later and found to contain a fresh egg. Neither adult was then present.

On another occasion a female Redshank was lifted from a nest with four eggs. One of the eggs was wet and sticky on the shell and was presumably just laid (see Methods). The female appeared lack-lustre and the cloaca was greatly distended and also contained mucoid material around it. Generally such observations are rare. However, it has been possible to estimate timing of laying of some eggs due to the presence of sticky mucoid material on the eggshell.

On one occasion an egg was known to be laid between 4 a.m. and 8 a.m. Twenty one eggs were laid between 8 a.m. and 12 noon and another twenty six between noon and 4 p.m. Over the study period seven eggs were laid between 4 p.m. and 8 p.m.

These egg laying times are not wholly representative as the study area was normally only worked between 9 a.m. and 6 p.m. Eggs laid before or after this period would not be detected as regularly. Because of the bias in field work, little else can be concluded from these data.

Laying intervals

The egg laying intervals calculated represent minimum times that the nest contents remained the same (the interval between the laying of eggs was a minimum of x hours).

Table 1.1 Egg laying intervals: the minimum time recorded between the laying of one egg.

Minimum time nest contents remained the same (hours)	Frequency observed	Mean	s.d.
24-28	40	25.5	1.42
28.01 - 32	11	29.5	1.08
32.01 - 36	1		
36.01 - 40			
40.01 - 44	4	40.9	0.629
44.01 - 48	2	47	
48.01 - 52			
52.01 - 56			
56.01 - 60			
60.01 - 64			
64.01 - 68	1		

In two nests the contents remained the same for a mean of 69.5 hours (s.d. = 1.5) and in one further nest the contents did not change for 98 hours. In all cases, at least one egg was laid after the recorded interval.

Some additional data have been gathered on the period for laying two or more eggs. In this case the nest contents have changed by at least two eggs between visits. Where the time difference between the first and second visit was short, a more accurate estimate of laying period was achieved.

Table 1.2 The change of nest contents over a known period of time.

No. of eggs laid since last visit	Period between nest visits (hours)
2	42*
2	48*
2	48*
2	115
2	117
2	126
2	144
3	72*
3	73*
3	97

* in these cases egg laying intervals can be more accurately determined.

Additional findings: 1 egg was laid in less than 27 hours 40 minutes. Finally, a nest with a very fresh egg contained three eggs, one of which was fresh 73 hours 30 minutes later. The average laying interval was therefore 36 hours 45 minutes.

Calculations of a mean laying period between eggs is difficult without exact observations. However, several points can be made:

(a) the laying interval between eggs may extend over 40 hours (10 instances).

(b) In two instances, where 3 eggs were laid within a given period, the average laying interval could not be more than 36 - 36.5 hours.

(c) In one case two eggs were laid in a period of almost 73 hours 30 minutes. As in (b) this averages out at 36-37 hours between the laying of eggs.

Finally, the shortest known laying interval (27 hours 40 minutes) clearly demonstrates that eggs may be laid within 30 hours of each other.

Over the period of study, nest contents were carefully checked and documented. At the end of each season the main clutch size was calculated for nests found on the study sanctuary and for nests found outside the sanctuary.

Clutch size

Table 1.3a Clutch size. The frequency observed of clutches of different and unknown size. Data are shown for all years. (study sanctuary zone)

Year	c/1	c/2	c/3	c/4	c/5	c/6	unknown
1983	7	3	14	164	1*	1†	8
1984	7	1	7	169	2*	-	11
1985	8	1	5	143	-	-	8

Table 1.3b The mean clutch size for all nests of known clutch size found on Banks Marsh.

Year	No. of nests of known clutch size	No. of eggs laid	Mean clutch	s.e.
1983	190	722	3.80	0.049
1984	186	716	3.85	0.046
1985	157	597	3.80	0.055
1983-85	533	2035	3.82	0.029

Notes: † The c/6 arose after one egg was broken by a dog at the laying stage.

* The c/5 in 1983 and one c/5 in 1984 arose when an egg was dumped in a nest by a 'foreign' female after incubation had begun.

There was no statistical difference in mean clutch size between all three years.

Table 1.4a <u>Clutch size: the frequency observed of clutches of different and unknown size.</u> Data are shown for all years (Old Hollow meadows).

Year	c/1	c/2	c/3	c/4	unknown
1983	-	-	2	8	1
1984	-	-	1	6	-
1985	-	-	-	9	3

Table 1. 4b <u>The mean clutch size for all nests of known clutch size found on Old Hollow meadows.</u>

Year	No. of nests of known clutch size	No. of eggs laid	Mean clutch	s.e.
1983	10	38	3.80	0.133
1984	7	27	3.86	0.143
1985	9	36	4.0	0.000
1983-85	26	101	3.88	0.064

Egg size

Every year an effort was made to measure as many eggs as possible. Egg measuring was carried out for several reasons:

(a) by measuring length and breadth an estimate of egg volume may be calculated.

(b) egg size could be related to female size and age.

(c) egg size could be related to chick size.

(d) egg size could be examined in relation to laying order.

A total of 1349 eggs were measured, of which only some were of known laying order.

Table 1.5 examines the relationship between egg laying order and egg length, breadth and volume.

Table 1.5 The mean size of eggs (Length, Breadth and Volume) in relation to their laying order.

		1983			1984			1985		
		Mean	s.d.	(n)	Mean	s.d.	(n)	Mean	s.d.	(n)
Egg 1	L.	4.487	0.17	61	4.526	0.19	91	4.515	0.128	53
	B	3.187	0.096	61	3.186	0.079	91	3.160	0.079	53
	Vol.	20.49	1.44	61	20.61	1.10	91	20.25	1.023	53
Egg 2	L.	4.493	0.15	53	4.511	0.148	89	4.526	0.153	50
	B.	3.199	0.08	53	3.207	0.086	89	3.179	0.066	50
	Vol.	20.64	1.26	53	20.79	1.22	89	20.54	1.051	50
Egg 3	L.	4.508	0.18	53	4.523	0.151	91	4.535	0.117	50
	B	3.205	0.086	53	3.206	0.086	91	3.182	0.068	50
	Vol.	20.76	1.37	53	20.77	1.113	91	20.62	1.002	50
Egg 4	L.	4.558	0.17	69	4.534	0.186	90	4.528	0.188	49
	B.	3.17	0.06	69	3.159	0.081	90	3.121	0.083	49
	Vol.	20.56	1.07	69	20.37	1.29	90	19.95	1.352	49

L = Length
B = Breadth
Vol= Estimated Volume

The most obvious result to emerge is that the fourth egg is always smaller than the second and third eggs. The first egg is also small, but normally not as small as the fourth. The implications of egg size in relation to laying order are discussed later.

The results in Table 1.6 highlight the variation that was found to exist in egg length, breadth and volume.

Table 1.6 The annual variation in egg size over three field seasons.

Year	no. of eggs measured			
1983	557	Max L	5.075 x 3.26	23.61
		B	4.55 x 3.435	23.52
		Vol	4.915 x 3.3625	24.23
		Min L	3.95 x 3.33	19.79
		B	4.27 x 2.8225	16.11
		Vol	4.27 x 2.8225	16.11
1984	583	Max L	5.645 x 2.895	21.11
		B	4.44 x 3.60	24.97
		Vol	4.44 x 3.60	24.97
		Min L	3.95 x 3.28	19.30
		B	4.185 x 2.825	15.87
		Vol	4.00 x 2.88	15.79
1985	249	Max L	4.945 x 3.19	22.25
		B	4.48 x 3.345	22.18
		Vol	4.785 x 3.335	23.34
		Min L	3.765 x 2.715	13.74
		B	3.765 x 2.715	13.74
		Vol	3.765 x 2.715	13.74

As a general comment, the smallest eggs tended to be fourth eggs. Large eggs were normally much larger than others in the clutch. Clutches of large eggs were found to be produced by the same female on consecutive years.

It was strongly suspected that egg size (length, breadth and volume) varied in accordance with the order of laying (Table 1.5). To test this idea, a series of paired t-tests were carried out. The mean egg lengths of all known first eggs were compared with the mean length of second, third and fourth eggs. Second eggs were compared with third and fourth eggs and third eggs with fourth eggs. Similar analysis were conducted on mean egg breadths and volume.

The 1984 data set was used because it was the largest single set of data.

The statistical comparison of eggs of known laying order are shown in Tables 1.7, 1.8 and 1.9.

Table 1.7 Between clutch comparisons of egg lengths of known laying order, 1984 data.

Variable	No	Mean	s.d.	s.e.	t	Deg. of freedom	P
Egg Length 1	78	4.5056	0.152	0.017	0.16	77	0.872
2		4.5034	0.150	0.017			
1	78	4.5056	0.152	0.017	-1.08	77	0.285
3		4.5206	0.153	0.017			
1	77	4.5047	0.153	0.017	-1.15	76	0.256
4		4.5253	0.194	0.022			
Length 2	78	4.5034	0.150	0.017	-1.28	77	0.206
3		4.5206	0.153	0.017			
2	77	4.5007	0.149	0.017	-1.48	76	0.142
4		4.5253	0.194	0.022			
Length 3	77	4.5220	0.153	0.017	-0.22	76	0.824
4		4.5253	0.194	0.022			

Table 1.8 Between clutch comparisons of egg breadths of known laying order, 1984 data.

Variable	No.	Mean	s.d.	s.e.	t	Deg. of freedom	P
Egg Breadth 1	78	3.1873	0.074	0.008	-2.23	77	0.029
2		3.2017	0.089	0.010			
1	78	3.1873	0.074	0.008	-1.29	77	0.201
3		3.1956	0.073	0.008			
1	77	3.1879	0.075	0.009	4.37	76	0.000
4		3.1565	0.083	0.009			
Breadth 2	78	3.2017	0.089	0.010	0.95	77	0.343
3		3.1956	0.073	0.008			
2	77	3.2024	0.090	0.010	5.78	76	0.001
4		3.1565	0.083	0.009			
Breadth 3	77	3.1966	0.073	0.008	5.61	76	0.001
4		3.1565	0.083	0.009			

Table 1.9 Between clutch comparisons of egg volumes of known laying order, 1984 data.

Variable	No.	Mean	s.d.	s.e.	t	Deg. of freedom	P
Egg volume 1	78	20.5672	1.127	0.128	-1.62	77	0.110
2		20.7071	1.266	0.143			
1	78	20.5672	1.127	0.128	-1.46	77	0.149
3		20.7033	1.138	0.129			
1	77	20.5708	1.134	0.129	2.25	76	0.027
4		20.3088	1.360	0.155			
volume 2	78	20.7071	1.266	0.143	0.04	77	0.967
3		20.7033	1.138	0.129			
2	77	20.7045	1.274	0.145	3.34	76	0.001
4		20.3088	1.360	0.155			
volume 3	77	20.7194	1.136	0.130	4.03	76	0.001
4		20.3088	1.360	0.155			

There is no statistical difference in egg lengths of different laying order. Fourth eggs are of significantly smaller breadth than first, second and third eggs. First eggs are of smaller breadth than second eggs.

The effect of egg breadth carries through to egg volume. Fourth eggs are of significantly smaller volume than eggs laid first, second and third. Thus, egg size is at least partially determined by order of laying.

For clutches where all eggs were measured, a mean egg length, breadth and estimated volume were calculated. This allowed for the mean egg size of one clutch laid by a female to be compared with the mean egg size of a second clutch laid by the same female.

It was felt that mean egg size might vary between a first and repeat clutch. Secondly, if an age effect was involved in egg size, mean egg size may vary (for one female) from one season to the next. A series of paired t-tests were carried out to compare the mean egg length, breadth and volume of a first and repeat clutch.

Table 1.10 A comparison of mean egg size of eggs laid in a first and repeat clutch. (The eggs from first and repeat clutches were known to be laid by the same females).

		Mean	s.d.	s.e.	t	Deg. of freedom	P
Mean egg L.	C_1	4.4683	0.126	0.024	-2.43	26	0.022
	C_2	4.5023	0.131	0.025			
Mean egg B.	C_1	3.1843	0.076	0.015	-0.39	26	0.697
	C_2	3.1885	0.065	0.013			
Mean egg Vol.	C_1	20.3822	1.127	0.217	-1.22	26	0.233
	C_2	20.5530	1.014	0.195			

For 27 second clutches, laid by the same female within one season, there was no significant difference between mean egg breadths and volume. Generally the second clutch contained slightly larger eggs, but this was not significant.

A series of paired t-tests were carried out to compare the mean egg lengths, breadths and volumes of clutches laid in consecutive years by the same females.

Table 1.11 A comparison of mean egg size of eggs laid in two consecutive years by the same females.

		Mean	s.d.	s.e.	t	Deg. of freedom	P
Mean egg L.	C_1	4.5188	0.148	0.020	-1.70	55	0.095
	C_2	4.5358	0.153	0.021			
Mean egg B.	C_1	3.1895	0.062	0.008	0.07	55	0.946
	C_2	3.1890	0.068	0.009			
Mean egg Vol.	C_1	20.6311	1.031	0.138	-0.64	55	0.525
	C_2	20.6841	1.036	0.139			

For 56 clutches laid in two consecutive years by the same females, the mean egg length, breadth and volume did not significantly change. Generally, clutches were of slightly larger estimated volume in the second year of measuring.

Incubation

Over the period of study, a total of 193 incubation periods were recorded. In order to determine an incubation period, a nest had to be found at the time of laying and then visited at hatching.

In this study, no attempt has been made to study incubation periods of individual eggs. Periods shown in Table 1.12 therefore represent the time period between incubation initiation and hatching of the first egg.

Table 1.12 A frequency distribution of the incubation periods of Redshank on Banks Marsh.

Incubation period (days)	1983	1984	1985
22	0	0	3
23	2	8	11
24	5	28	32
25	5	22	17
26	9	17	4
27	4	6	2
28	4	4	3
29	1	2	2
30	0	0	0
31	1	0	1
(n)	31	87	75

In 1983 the mean incubation period was 26.27 days (s.d. = 1.7). Mean incubation periods in 1984 of 25.52 days (s.d. = 1.32) and 24.97 days in 1985 (s.d. = 1.63) were recorded for 87 and 75 clutches respectively.

The incubation periods over the three field seasons ranged from 22-31 days. The mean was least in 1985, possibly arising as a result of decreased levels of disturbance caused by field workers.

Some of the longer incubation periods of 28 days, and more, were almost certainly due to single parent incubation. On several occasions a bird continued to incubate after its mate had deserted. This was confirmed by the capture of a bird at a second nest whilst its first nest was still in use. A visit to a single parent nest often revealed the eggs,which had not been incubated for some time, to be cold and wet, suggesting that single parents devoted less time solely to incubation. This would have to be tested by studying brooding rhythms in pairs and in single adult incubated nests.

In 1985, a nest found with one egg on 23 April contained 3 eggs by 26 April. When checked on 27, 29 and 30 April the eggs were cold and wet. A large tide on 30 April covered the eggs by as much as 1 metre of water. Following this tide, which did not move the eggs, incubation began. Therefore, in this case there was a protracted incubation period due to a delayed onset of incubation.

In 1983 a nest with four eggs was flooded on consecutive days 8-9 days after incubation had begun. On both occasions the eggs were washed out of the nest. After each flood the eggs were found and re-placed in the nest. Incubation continued and three out of four eggs hatched after 27.5 days. At another nest, a clutch of three eggs was deserted just prior to hatching. The eggs remained unincubated for two nights and a day, after which they were added to another nest. All the eggs hatched out despite the lack of incubation at such a critical time. These accounts give an indication of the tolerance exhibited by Redshank eggs. Such tolerance may be essential in a system where nests and eggs are periodically at risk from flooding and chilling.

Four periods of extra long incubation were recorded. In 1983 two birds sat for a minimum of 35 and 37.5 days. In both cases the eggs were damaged as a result of flooding. In 1984 two birds sat on infertile eggs for 62 and 64 days. In the first case, only one bird (a female with an infected cloaca) was ever caught at the nest. At the second nest one egg hatched after 25 days. The other three eggs were infertile and were incubated for a further 39 days. In this case we do not know what happened to the ringed chick after it left the nest.

Incubation periods appeared to be longer in the early half of the season. To test this, the relationship between date of clutch completion and incubation period was examined by a correlation analysis.

Table 1.13 The relationship between date of clutch completion and incubation period (Pearson's correlation coefficients (r)).

Year	Pearson's (r)	Probability	(n)
1983	-0.4527	0.005	31
1984	-0.1408	0.097	87
1985	-0.4652	0.001	75

With the exception of 1984, there is a negative correlation which is significant. Therefore, as seasons progress, incubation periods generally decline. The 1984 result is not significant. In both 1983 and 1985 the early season was punctuated with very bad tidal flooding. Long spells of high water may hamper incubation, particularly when nests are flooded. Consequently the incubation periods were longer in the early season. In contrast, there was no bad flooding in 1984, and therefore no delaying effects on incubation. Generally, atmospheric temperature is higher later in the season and therefore eggs chill less when the birds are disturbed. In 1984 the weather was generally warmer than average, with April and early May particularly warm. This may also explain why a significant negative correlation was not found in 1984 (see Discussion). In addition to climatic and tidal effects, other factors may influence the length of the incubation period.

Nest replacement

Many pairs lost their nests for a number of reasons (Appendix 3). These birds generally re-laid relatively quickly.

Where both birds were caught at both nests then the identity of the pair was known absolutely. Where only one bird was caught at one of the nests there was no certainty that the pair had remained faithful.

Birds could therefore be classified as (a) remaining faithful or (b) taking a new mate. Where this classification could be made it was possible to examine the effect of changing mate on the time taken to replace a lost or deserted clutch.

Table 1.14 The time taken to replace a clutch (from nest/brood loss or desertion).

Faithful pairs

Days between first and replacement nest.	Observed frequency	
	Nest lost.	Nest hatched (chicks presumably perished).
8	-	-
9	-	-
10	-	-
11	2	-
12	4	1
13	1	5
14	-	1
15	-	2
16	1	-
17	-	-
18	-	-
19	-	1

The mean time to replace a nest ranged from 12.4 days (s.e.0.565) in those cases where nests were lost, to 14 days (s.e. 0.632) where broods have perished after leaving the nest.

A Mann-Whitney test was carried out to determine if the observed difference was significant (Mann-Whitney W = 50.5, P = 0.026). Therefore the time taken to replace a clutch is significantly less than the time taken to produce a repeat clutch after brood loss. This difference is almost certainly due to the time the brood survives.

Table 1.15 The time taken to replace a clutch from nest/brood loss or desertion. Bird taking a new mate

Days between first and replacement nest	Observed frequency	
	Nest lost	Nest hatched (chicks presumably perished)
9	1	
10	1	
11	1	
12	-	
13	2	
14	1	
15	-	
16	1	
17	-	
18	-	
19	-	1
20	1	

Where a pair has split up and one bird re-mated, the time taken to replace a nest averaged 13.25 days (s.e. 1.25). There was no significant difference in nest replacement time between faithful pairs and birds with new mates (Mann Whitney W = 63.5 p = 0.67).

The only real difference that exists concerns the date of brood loss. In this case, replacement is calculated from the day the chicks left the nest to the date of completion of the replacement clutch. Therefore, the time for replacement is overestimated if the brood survived for several days before perishing.

Thus, Redshanks may replace clutches and broods if they are lost. Presumably broods are only replaced if they are lost at an early stage of development.

Birds nesting with a new mate are able to replace a lost clutch just as quickly as a pair remaining together. On one occasion a female was involved with two males at separate nests and on another occasion a male is thought to have been involved with two separate females at two nests simultaneously.

Finally in 1985, one female is thought to have re-laid twice after losing nests.

Birds caught

The basis of much of this study depended on the accurate sexing of Redshank that were caught. As mentioned in the Methods, several techniques were used. Hale (1971) showed from a study of skins that there were slight differences in size between a male and female Redshank.

Table 1.16 The number of birds caught (1983-1985) and the annual trapping success.

Year.	No. of birds caught.	Total birds caught including re-traps.	No. of traps set.	% trap success.
1983	250♦	338	510	66%
1984	277	380	634	60%
1985	219+	269	528	51%

Note: ♦ 2 adults caught in mist nest

+ 3 juveniles caught in mist nest

The column on trapping success if of particular interest. The success dropped dramatically in 1985 and caused many problems to the general running of the project. Full discussion of the yearly variations in trap success are given at the end of this chapter.

Ageing

In 1983, all unringed birds (unrings) were not examined closely. These birds were not therefore subject to the standard ageing procedure used in 1984 and 1985. Some birds were of known age if they had been ringed as chicks, but these birds were a very small percentage of the overall catch.

Table 1.17 a The number of controls and unrings caught and the proportion of unrings considered to be first-year birds.

Year	Controls caught	Total unrings caught	Unrings 1-year old	Unrings >1 year old
1983	156	94	20*	74
1984	160	117	32	85
1985	156	60	24	36

* underestimate (all birds not fully examined).

Table 1.17 b Total birds caught and proportion that were 1st year birds.

Year	Total adults caught	Total no. of 1st years *	The no. of first years as a % of total birds caught
1983	250	23	9.2
1984	277	37	13.3
1985	216	28	12.9

* ringed and unringed at capture.

Where birds were of unknown age, it was important to determine if these were first year birds or older. All birds were aged as outlined in the Methods. Birds were therefore classified as first year birds if they had retained some juvenile inner median coverts. In addition to examination of the inner median coverts, the leg colour, bill colour and degree of feather abrasion was scored.

All birds caught in 1984 and 1985 were divided into one-year olds, two-year olds and birds of three years of age or more. Bird age was then correlated with the leg and bill colour and the degree of feather abrasion observed. As the parameters involved were of an arbitrary nature, a non-parametric analysis was considered most appropriate. The main aim of the analysis was to determine if the above recorded variables changed with age.

Table 1.18 A non parametric correlation analysis to examine the relationship between leg colour, bill colour and feather abrasion with age (Kendall correlation coefficients), 1984 data.

	Leg colour (1-6)	Bill colour (1-3)	Feather abrasion (1-5)
Male age	0.441*** (135)	0.348*** (135)	-0.432*** (135)
Female age	0.336*** (135)	0.446*** (135)	-0.386*** (135)

n.s. not significant:
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ (used throughout thesis)

Note: Leg colour ranged from dull yellow (3) to bright red (6).
Bill colour ranged from dull grey-pink (1) to bright red (3).
Feather abrasion ranged from none (1) to very heavy (5).*

These results indicate that leg and bill colour get brighter as the birds get older and that older birds have less feather, and in particular primary abrasion, than do younger birds.

So far, all first year birds ringed as chicks have been found to have retained some juvenile type inner median coverts. This appears to be a very reliable method of ageing Redshank.

*

Table 1.19 A non parametric correlation analysis to examine the relationship between leg colour, bill colour and feather abrasion with age (Kendall correlation coefficient), 1985 data.

	Leg colour (1-6)	Bill colour (1-3)	Feather abrasion (1-5)
Male age	0.219** (105)	0.339*** (105)	-0.315*** (105)
Female age	0.479*** (104)	0.750*** (104)	-0.437*** (104)

All correlations are significant. Therefore young birds of both sexes tend to have dull coloured legs and bill and exhibit more feather abrasion.

The above Tables were all constructed using birds of known age groups. Birds which retained their juvenile inner median coverts and were of unknown age were classified as first summer breeders. Birds which were unringed and did not possess juvenile inner median coverts were classified as being a minimum of two years old. These may, however, have been first time breeders.

Bird measurements

Not all birds caught were measured (see Methods). Of those adults measured it was possible to construct a Table to demonstrate the size differences between sexes (Table 1.20). For the benefit of this analysis, birds were sexed according to methods outlined at the beginning of this chapter.

Table 1.20 The annual variation of mean measurements of female Redshank caught at the nest (1983-1985).

Female	1983			1984			1985		
	$\bar{x}$	s.d.	(n)	$\bar{x}$	s.d.	(n)	$\bar{x}$	s.d.	(n)
Weight	132.5	8.34	125	134.0	8.19	138	133.3	6.79	106
Right-wing measurement	169.8	3.82	125	169.5	4.08	138	168.2	4.04	107
Tarsus measurement	48.0	2.24	125	47.5	2.10	138	47.1	1.91	107
Bill to feathers	42.0	1.94	124	41.76	1.76	137	41.9	1.91	99

Table 1.21 The annual variation of mean measurements of male Redshank caught at the nest (1983-1985).

Male	1983			1984			1985		
	$\bar{x}$	s.d.	(n)	$\bar{x}$	s.d.	(n)	$\bar{x}$	s.d.	(n)
Weight	125.1	7.28	97	126.3	6.54	118	126.5	6.83	62
Right-wing measurement	166.0	4.21	97	166.5	3.07	118	166.1	3.59	62
Tarsus measurement	47.4	2.17	97	46.9	2.00	118	46.7	1.92	62
Bill to feathers	40.7	1.83	97	40.6	1.90	118	41.2	1.44	62

Tables 1.20 and 1.21 indicate that females are on average larger than males in every recorded measurement. There is, however a degree of circularity involved as some birds were actually sexed on the basis of size. Birds were also sexed according to cloaca shape and size and there was generally good agreement between the two techniques. There is obviously a degree of overlap between male and female measurements, but these results seem to indicate size is an important predictor of sex.

Mate choice

It was felt that mate choice may be made on the basis of size or perhaps even on the basis of summer plumage attained. As will be seen in Chapter 2 there is a very strong positive correlation between male and female age caught at any one nest. Such a relationship may still be based on some cue, e.g. size, plumage or other characters.

To test the above, the size and plumage of all males and females caught together as pairs were correlated and a multiple regression analyses carried out to determine if any relationship existed. In these analysis, male and female size parameters were correlated together as were male and female summer plumage scores for the different body regions.

In 1983 there were no significant correlations between male and female size, suggesting that selection was not made on the basis of size. In 1984 there was a significant positive correlation ($r = 0.207$, $p < 0.05$). between male and female weight. All other relationships showed no significant correlation. Fewer birds were caught in 1985 and as a consequence correlations were slightly higher. There was again a significant correlation ($r = 0.256$, $p < 0.05$) between male weight and female weight. Additionally there were significant correlations between male age and female weight ($r = 0.257$, $p < 0.05$) and male age and female wing measurement ($r = 0.327$, $p < 0.01$). Finally, there was a positive but non significant correlation between male wing measurement and female wing measurement ($r = 0.226$, n.s.).

In 1984 the data set was subject to a correlation analysis to determine if mate selection was taking place on the basis of summer plumage attained. In the analysis, the number of summer feathers on male mantle, breast, scapulars and secondaries was correlated with the number of summer feathers on the female mantle, breast, scapulars and secondaries.

Firstly, it appears that there is absolutely no selection on the basis of summer plumage attained. The number of summer plumage feathers on the male mantle does not correlate significantly with number of summer plumage feathers on the female mantle (r =0.129, n.s.) and male breast summer plumage does not correlate significantly with female breast counts of summer feathers (r = 0.159, n.s.).

It therefore appears that mate selection is not taking place on the basis of plumage. There may, however, be some selection on the basis of size.

In those birds where summer plumage was quantified by detailed counts, it was possible to relate the amount of summer plumage attained on each body region to each other.

The hypothesis being tested was: birds with a lot of summer plumage on one body region also had a lot on other body regions.

The results are shown in Tables 1.22 and 1.23.

Table 1.22 A correlation analysis to examine the relationship between the number of summer plumage feathers on each body region (Pearson's correlation coefficients (r)).

Summer plumage feathers on	Mantle	Breast	L. scaps.	R scaps.	L. secs.	R. secs.
Mantle						
Breast	0.703***					
L. scapulars	0.740***	0.679***				
R. scapulars	0.736***	0.657***	0.880***			
L. secondaries	0.375***	0.355***	0.363***	0.399***		
R. secondaries	0.354***	0.331***	0.383***	0.434***	0.650***	

(For all females, n = 116) 1984.

Table 1.23 A correlation analysis to examine the relationship between the number of summer plumage feathers on each body region (Pearson's correlation coefficients (r)).

Summer plumage feathers on	Mantle	Breast	L. scaps.	R. scaps.	L. secs.	R. secs
Mantle						
Breast	0.774***					
L. scapulars	0.779***	0.648***				
R. scapulars	0.674***	0.613***	0.837***			
L. secondaries	0.071	0.077	0.195*	0.226*		
R. secondaries	0.293**	0.271**	0.341***	0.436***	0.458***	

(For all males, n = 116) 1984.

The number of summer plumage feathers on each body region are highly and significantly correlated with each other. Thus, birds tend to have a relatively even distribution of summer feathers on each body region.

Future studies would therefore benefit by reducing the amount of feather counts taken. It would probably suffice to assess summer plumage on the basis of a mantle or breast count alone. This would give a good indication of overall plumage attained and would reduce bird handling time.

The amount of summer plumage attained did not appear to be an important basis for mate selection. Furthermore, there was no sex difference in the amount of plumage attained. (See appendix 11)

The next idea tested was that the amount of summer feathers attained may vary with age. To test this, the number of summer feathers on each body region was correlated with male and female age.

Table 1.24 The relationship between age and number of summer plumage feathers present on each body region (Pearson's correlation coefficients (r)), 1984 data.

No. of summer plumage feathers on:	Female Age	Male Age	n=116
Mantle	-0.083	-0.111	
Breast	0.133	0.063	
Left scapulars	-0.085	-0.003	
Right scapulars	0.064	0.028	
Left secondaries	0.062	0.109	
Right secondaries	0.026	0.195	

All correlation coefficients were non significant.

Finally, it was suggested to me that plumage may be a good predictor of breeding success and that well coloured birds may be more successful.

This idea was tested by examining the date of clutch completion and the number of eggs laid and hatched in relation to an individual's summer plumage scores. The results of the correlation analysis are given in Table 1.25.

Table 1.25 The relationship between date of clutch completion, eggs laid and eggs hatched, with number of summer plumage feathers present on each body region (Pearson's correlation coefficients (r)).

(a) **Females** (n = 116).

No. of summer plumage feathers on:	Date of clutch completion	Eggs laid	Eggs hatched
Mantle	0.063	-0.123	0.008
Breast	-0.022	-0.085	0.101
Left scapulars	0.082	-0.185	0.045
Right scapulars	0.047	-0.022	0.105
Left secondaries	-0.021	0.033	0.152
Right secondaries	-0.081	-0.019	0.053

(b) **Males** (n = 116).

Mantle	0.026	-0.043	0.153
Breast	-0.085	0.065	0.181
Left scapulars	0.006	0.020	0.156
Right scapulars	— 0.029	0.039	0.126
Left secondaries	-0.132	0.028	0.028
Right secondaries	-0.186	0.128	0.053

All correlation coefficients were non significant.

Results tabulated in Tables 1.24 and 1.25 indicate that there was no relationship between male and female age with amount of summer plumage attained and between date of clutch completion and number of summer feathers present. Therefore a bird's plumage is not a predictor of its timing of laying or of its age.

Finally, it was shown that the number of eggs laid and hatching was in no way related to an individual's summer plumage. In conclusion it was demonstrated that plumage does not relate to an individual's sex, breeding time or breeding success (at least at the egg hatching level).

Mate fidelity

The following analyses concentrate on two types of mate fidelity:

(a) Those birds that nest together on two or more consecutive years.

(b) Those birds that nest together on two or more occasions.

Table 1.26 Mate fidelity. The number of pairs recorded nesting together on 2-5 consecutive years.

No. of consecutive years together	Frequency of pairs observed
2	56
3	11
4	3
5	1

Table 1.27 The number of pairs recorded nesting together on two or more occasions.

No. of years caught together	Frequency of pairs observed
2	31
3	22
4	4
5	3

The above Tables represent a crude analysis of Redshank mate fidelity. In Table 1.27 fidelity is recorded as any pair that has nested together on more than one occasion. Of these pairs caught together on 4 and 5 years, five of the seven pairs may have been together for at least six years. Finally, one pair was caught together in 1974, 1978, 1979, 1980 and 1982. These were therefore associated over a span of 9 years. The last records hint at a very high degree of mate fidelity. In contrast, at least two adult Redshank have been found with 6 and 7 different mates.

Several things have an effect on mate fidelity, notably survival, previous years nest success, and arrival times on the breeding ground. For fuller discussion see Chapter 3 on breeding site fidelity.

To undertake an analysis of mate fidelity the number of birds caught on consecutive years must be known. The following analysis allows for a more quantitative assessment of the level of mate fidelity exhibited.

Table 1.28 Mate fidelity: a quantitative assessment.

Years	No. of birds caught on consecutive years	No. remaining faithful to previous mate	% faithful	No. taking new mates
1983/84	100	60	60	20
1984/85	101	34	33.7	30
1982/83/84	35	16	45.7	-
1983/84/85/	45	6	13.3	-
1982/83/84/85	17	0	-	-

Thus, 45.7% of those birds that returned in years 1982, 1983 and 1984 retained the same mate. Likewise, 13.3% of those birds that returned in years 1983, 1984 and 1985 retained the same mate. The percentage returning over two consecutive years is greater in 1983, 1984, presumably due to the increased number of birds caught in 1984. In contrast, the lower mate fidelity index calculated for 1984, 1985 is in part due to decreased catching efficiency and subsequently number of birds caught. A fuller explanation is dealt with in Discussion.

Several reasons have been advanced as to why a pair should remain faithful or separate. One aspect that was examined concerned the effect of one years nesting success on the following years mate fidelity. The data set used for the analysis was gathered in 1983-84. In 1984 almost all pairs were successful due to the lack of tidal flooding (see Appendix 3).

Table 1.29 <u>A chi-square analysis to determine the effect of nesting success in one year on the following years mate fidelity (1983-1984 data)</u>

		Pair state (1983-1984)	
		Remained faithful	Took new mate
Previous years nesting success	No eggs hatched	20	14
	At least one egg hatched	40	6

$x^2_{(1)} = 6.82,\ p < 0.01$

Therefore, nest success in one year does have an effect on the following years mate fidelity.

Pairs which were unsuccessful were more likely to split up and take a new mate the following year.

This result uses 80% of the birds caught in both 1983 and 1984. A further 20% of birds caught consecutively in 1983 and 1984 were of unknown pair state in one of the years.

A follow up analysis was carried out on the 1984-1985 data to determine if the very good breeding success in 1984 was carried through to increased mate fidelity in 1985.

Table 1.30 A chi-square analysis to determine the effect of nesting success in one year on the following years mate fidelity (1984-1985 data).

		Pair state (1984-1985).	
		Remained faithful	Took new mate
Previous years nesting success	No eggs hatched	0	3
	At least one egg hatched	34	27

$x^2(1) = 3.6$, n.s.

Therefore, breeding success in 1984 showed no effect on mate fidelity in 1985. From Tables 1.29 and 1.30 I conclude that breeding success in one year can have an effect on mate fidelity but that other factors may also be important.

Egg chipping and hatching

Prior to the hatching of the eggs, the eggs begin to 'chip' or 'pip'. When this occurs, small dents and fractures begin to appear, normally in the upper half of the eggshell. At such time the adults behaviour begins to modify in readiness for the change in roles. The adults begin to communicate with the hatching embryo, the level of communication increasing up to the hatch. Chipping periods are incredibly variable and may yet prove to be good predictors of a chick's survival potential. Weaker chicks may take longer to hatch and may therefore have less chance of survival (unfortunately this could not be studied because of the low recapture rate of chicks).

Table 1.31 The time taken for an egg to hatch from first signs of hatching.

Chipping interval (hours)	Observed frequency 1983	1984	1985
30-40	-	2	-
41-50	-	-	1
51-60	-	-	-
61-70	7	5	19
71-80	14	17	17
81-90	6	18	15
91-100	10	27	8
101-110	5	9	1
111-120	1	1	4
121-130	-	2	-
131-140	-	1	-
141-150	1	-	-
Mean chipping period (Hrs)	85.7	88.5	81.0
s.d.	16.3	16.2	14.3
n	44	82	65

The overall chipping period (1983-1985) is calculated as (85.3 hours, s.d. = 15.95, n = 191).

Thus the mean chipping period from first egg chip to hatching is 3.5 days. Chipping period was not examined to determine if laying order had an effect on hatching time.

Nests were checked regularly to determine that incubation was still in progress, to record chipping periods, and to note the date of hatch. It was essential to monitor nests closely in order that hatch date could be predicted. This was an important part of the study as it was intended to ring as many young as was possible. Nests were therefore monitored closely, allowing several calculations of nest success to be made.

Hatch success

This may be defined in 3 ways.

A) The number of nests hatching at least one egg as a percentage of all nests found.

B) The number of eggs hatching from the total laid as a percentage (requires clutches of known size).

C) The percentage of eggs hatching from nests which hatched at least one egg (requires clutches of known size).

Table 1.32 Nest hatching success (Category A).

Year	No. of nests hatched	No. of nests found	% nests hatched
1983	78	198	39.39
1984	166	197	84.26
1985	106	165	64.24

Hatching success of nests varied from 39-84% The best year, 1984, was 53% better than the poorest year, 1983. The reasons for differential nest hatching success are discussed at the end of this Chapter.

Table 1.33 Egg hatching success (Category B).

Year	No. of nests found*	No. of eggs hatched*	No. of eggs laid*	% eggs hatched
1983	190	218	722	30.19
1984	186	532	716	74.30
1985	157	376	597	62.98

* all clutches of known size.

In those clutches of known size, the percentage of eggs hatching ranged from 30-74% over the three study years. The best year was 59% better than the poorest year of egg hatching, which again was 1983.

Table 1.34 Hatching success in successful nests (Category C).

Year	No. of nests hatching*	Eggs laid in these nests	No. of eggs hatched	% eggs hatched
1983	78	310	218	70.32
1984	155	618	532	86.08
1985	102	402	376	93.53

* known clutch size

In those nests hatching at least one egg there was a difference in success of 25% between the poorest year (1983) and the best year, 1985. In 1983 an average of 2.8 eggs per successful nest hatched from a clutch of 4 eggs. In 1985 an average of 3.74 eggs hatched for every 4 laid in a successful nest. At individual nest level, hatch success ranged from 0/4 to 5/5.

Analysis indicate that hatching success should be clearly defined (see Discussion).

The egg/nest hatching figures may be converted to chicks per pair and chicks per adult. These give an estimate of maximum potential productivity. Subsequent loss of chicks must therefore reduce productivity per pair/individual.

Table 1.35 An estimate of chick productivity at egg hatching level.

Year	No. of nests of known clutch	No. of chicks hatched	Mean no. of chicks/pair	Mean no. of chicks/adult
1983	190	218	1.15	0.575
1984	186	532	2.86	1.43
1985	157	376	2.39	1.20

These results are discussed later in this Chapter. Sources of nest loss are given in Appendix 3.

A further 30 nests were found in the three field seasons in the Old Hollow meadows and in the enclosure on the seaward side of the sea wall. In these, nest hatching success (Category A) ranged from 28.5-45.5%. The majority of nests lost were crushed by cattle. Category C hatch success (% hatched from successful nests) ranged from 80.-87.5%. These figures are in line with those obtained for marsh nests.

Further nests were found off the plot, but were not subject to detailed data recording and checking. In these nests, the main priority was to capture the parent as part of the breeding site fidelity, natal philopatry study (discussed in Chapter 3).

Observations suggested that an eggs hatch order may be related to its order of laying. A simple chi-square analysis was carried out to test this idea.

Egg hatch order in relation to laying order

Table 1.36 The relationship between egg laying and hatch order (Raw data, all years).

		Order of egg hatch			
		1	2	3	4
Egg laying order	1	8	2	2	7
	2	3	4	1	5
	3	2	4	10	5
	4	3	0	3	34

n = 93

Table 1.37 A chi-square analysis to examine the relationship between egg laying order and order of hatch (All years).

a)

Egg 1

	Observed frequency	Expected frequency
Hatch order 1	8	4.75
2	2	4.75
3	2	4.75
4	7	4.75

$x^2{}_{(3)}$ 6.46, n.s.

b)

Egg 2

	Observed frequency	Expected frequency
Hatch order 1	3	3.25
2	4	3.25
3	1	3.25
4	5	3.25

$x^2{}_{(3)}$ 2.69, n.s.

c)

Egg 3

	Observed frequency	Expected frequency
Hatch order 1	2	6.25
2	4	6.25
3	10	6.25
4	5	6.25

$x^2{}_{(3)}$ 6.20, n.s.

d)

Egg 4

	Observed frequency	Expected frequency
Hatch order 1	3	10
2	0	10
3	3	10
4	34	10

$x^2(3)$ 77.4, $p < 0.001$

Analysis of the first, second and third egg hatch orders indicated that no relationship existed between laying order and order of hatch. Thus only the fourth egg hatches non randomly. This was the expected result (full details are given in Discussion).

Where an individual chick was known to have hatched from an egg of known laying order it was possible to relate chick size (weight, bill size and tarsus length) to egg size (length, breadth and estimated volume). This was done during the three seasons field work and the data pooled.

Egg chick correlates.

Table 1.38 The relationship between egg length, breadth and volume with chick weight, tarsus and bill length. All chicks known to have hatched from specific eggs (Pearson's correlation coefficients (r)).

Chick variables	Egg variables: Egg length	Breadth	Volume	(n)
Weight	0.593***	0.611***	0.729***	142
Tarsus	0.311***	0.363***	0.407***	138
Bill to feathers	0.330***	0.313***	0.385***	138
Bill to rear nares	0.252**	0.270**	0.316***	129
Bill to front nares	0.335**	$0.171^{n.s.}$	0.289**	79

Egg length, breadth and volume correlates significantly with chick weight, tarsus and bill length. Therefore large chicks hatch from large eggs and smaller eggs produce smaller chicks. In the case of egg volume and chick size, the correlation coefficients are particularly high. It would therefore appear that egg volume is the best predictor of a chick's potential size at hatching.

The correlation analysis examining chick size in relation to egg size gave a good indication of the strength and direction of any relationship which existed. This analysis was followed up by carrying out a series of step-wise multiple regression analysis (Nie et al 1975).

The dependent variables were chick weight, tarsus, bill tip to feathers, rear and front nares measurements. Independent variables were egg length, breadth and calculated volume. The aim of an analysis of this kind is to determine which of the independent variables or combination of independent variables best predict for the dependant variables.

In Table 1.39 an analysis was carried out to determine which measured egg variables best predicted chick weight. In other words, if an egg is of known length, breadth and volume, which of these is the best predictor for the weight of the chick hatching from the egg. In all the multiple regression analysis, results were firstly checked to determine for normality of distribution. When satisfied the analysis was run.

The results are displayed as a series of Beta and F - values. For the benefit of the reader, F - values are printed with associated significance values. F-values printed as non-significant (n.s.) indicate that Beta values for the appropriate independent variable were non significant. These Beta values are not included in the Table of results. Significant levels for F - ratios associated with Beta values are : * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. The degrees of freedom indicate the number of independent and dependent variable comparisons which have been made.

Finally, the cumulative variance figure is an estimate of the amount of variation which is explained by one or more independent variables. For further details see Nie et al 1975.

Table 1.39 Beta values and F - ratios for the relationship between chick weight and egg biometrics (all years).

Dependent variable		Independent variables		
		Egg length	Breadth	Volume
Chick weight	Beta	0.228	-	0.596
	F	4.84*	n.s.	33.1***

Significance values associated with F - ratios (d.f. = 2,74).
A total of 77% of the cumulative variance was explained.
Chick weight may be predicted from the following formula.
Chick weight = 0.667.Egg volume + 1.961 Egg length - 6.983.

Table 1.40 Beta values and F - ratios for the relationship between chick tarsus and egg biometrics (all years).

Dependent variable		Independent variables		
		Egg length	Breadth	Volume
Chick tarsus	Beta	-	-	0.398
	F	n.s.	n.s.	14.1***

Significance values association with F - ratios (d.f. = 1,75).

A total of 45% of the cumulative variance was explained.

Table 1.41 Beta values and F - ratios for the relationship between chick bill to feathers and egg biometrics (all years).

Dependent variable		Independent variables		
		Egg length	Breadth	Volume
Chick bill to feathers	Beta	0.408	-	-
	F	14.9***	n.s.	n.s.

Significance values associated with F - ratios (d.f. = 1,75).

A total of 45% of the cumulative variance was explained.

Table 1.42 Beta values and F - ratios for the relationship between chick bill to rear nares and egg biometrics (all years).

Dependent variable		Independent variables		
		Egg length	Breadth	Volume
Chick bill to rear nares	Beta	-	-	0.306
	F	n.s.	n.s.	7.73**

Significance values associated with F - ratios (d.f. = 1,75).

A total of 34% of the cumulative variance was explained.

Table 1.43 Beta values and F - ratios for the relationship between chick bill to front nares and egg biometrics (all years).

Dependent variable		Independent variables		
		Egg length	Breadth	Volume
Chick bill to front nares	Beta	0.335	-	-
	F	9.5**	n.s.	n.s.

Significance values associated with F - ratios (d.f. = 1,75).
A total of 36% of the cumulative variance was explained.

The results exhibited in Tables 1.39 - 1.43 indicate the strength and inter-relationship between independent variables and a dependent variable.

Egg volume and egg length are the best predictor of chick weight. Thus by measuring an egg's length, breadth and volume, the weight of a chick (hatched from measured egg) can be predicted. In this case, 77% of the cumulative variance in chick weight is explained by egg length and volume. Other sources of variation could be the time of chick weighing and the accuracy of the egg volume estimate. Thus, the longest and largest eggs (volume) produce the heaviest chicks.

The best predictor of tarsus length and bill tip to rear nares length is egg volume. In this case, 45% and 34% of the cumulative variance is explained.

Finally, a measurement of egg length is the best predictor of bill tip to feathers and bill tip to front nares measurement.

If, for example, chick weight was related to potential survival, then clearly this would be a very useful analysis in that the inference would be that large eggs produce large chicks which have an increased chance of survival. Unfortunately, chick weight has so far not been found to be related to chick survival.

Chick measurements

A total of 1001 chicks were ringed in the nest. Many of these were measured fully. However, as analysis of all chick measurements would be very time consuming, I have concentrated analysis on those chicks which hatched and were of known hatch order.

Table 1.44 The mean weight, tarsus and bill measurements of chicks of known hatch order.

Chick variable	mean	s.d.	(n)
Weight (g)	15.61	1.32	169
Tarsus (mm)	28.08	1.38	169
Bill to feathers (mm)	12.58	0.61	171
Bill to rear nares (mm)	11.09	0.58	145
Bill to front nares (mm)	9.80	0.73	114

Chicks of known order of hatching were weighed and measured. The relationship between chick weight, tarsus and bill length was examined to determine if a heavy chick also had a long tarsus and bill. This is particularly important where a biologist decides that only one measurement shall be taken.

Table 1.45 gives the results of the Pearson's correlation analysis examining the relationship between the different chick variables measured.

Table 1.45 A correlation analysis to examine the relationship between chick weight, tarsus and bill measurements with each other. (Pearson's correlation coefficients (r)).

Chick variable	Weight	T	B/f	B/rn	B/fn
Weight		164	166	143	112
Tarsus (T)	0.419***		169	145	114
Bill to feathers(B/f)	0.337***	0.341***		145	114
Bill to rear nares(B/rn)	0.297***	0.260**	0.774***		114
Bill to front nares (B/fn)	0.315***	0.248**	0.659***	0.868***	

The results in Table 1.45 are almost all highly significant. Over the years there has been some debate as to which bill measurement should be taken. These results, and later results on chick growth, clearly demonstrate that the three bill measurements are all highly correlated. Thus, for scientific purposes, it may suffice simply to use the bill tip to front nares measurement as recommended by the B.T.O. for measuring adults (see Chapter 4 for further discussion).

The relationship between egg laying order and egg size and egg laying order and egg hatch order suggested that a relationship may exist between chick size and order of hatch. This idea was tested by relating chick measurements to order of hatch in a correlation analysis. The effect of hatch date on chick size was also examined.

Chick size in relation to hatch order

Table 1.46 An examination of the relationship between chick measurements, hatch order and date of hatch. (Pearson's correlation coefficients (r)), 1984 data.

Chick variable	Chick Hatch order	Chick Date of hatch	(n)
Weight	n.s.	-0.203**	169
Tarsus	-0.321***	n.s.	169
Bill to feathers	-0.220**	-0.194**	171
Bill to rear nares	-0.267**	-0.305***	145
Bill to front nares	-0.181*	-0.359***	114

These results highlight some important points.

(a) As the order of hatch increases, the size of chick produced decreases. Thus, the last chick to hatch is generally the smallest (but see chick weight versus order of hatch);

(b) Nests hatching later in the season produce smaller chicks (note tarsus correlation). These data have to be tied in with: egg size in relation to laying date (Chapter 2); egg size in relation to laying order and egg hatch order in relation to laying order.

In 1983 -1985, the loss of nests due to flooding prevented this analysis from being undertaken. In these years birds which nested early were forced to re-lay later in the season as a result of nest loss due to flooding. This greatly affected other analysis concerning age versus laying date and egg size versus laying date (For full discussion see end of this Chapter and Chapter 2).

In order to ring as many chicks as possible, nest sometimes had to be visited more than once as the hatch was often asynchronous. This allowed some data to be gathered on the length of time chicks remained in the nest.

Table 1.47 The length of time chick (s) remained in nest after hatching.

Time a single chick spent in nest (hrs)	Frequency observed 1983	1984	1985	1983-1985
0-04.00	-	6	3	9
04.01-08.00	13	23	15	51
08.01-12.00	2	6	-	8
12.01-16.00	-	3	2	5
16.01-20.00	2	12	7	21
20.01-24.00	5	3	-	8
24.01-28.00	-	-	2	2
Mean stay in nest.	10.95	10.20	10.25	10.21
s.d.	7.03	5.90	6.76	6.35
(n)	22	53	29	104

The results in Table 1.47 demonstrate a bimodal frequency. Peak 1 indicates that 57.7%of chicks have remained in the nest for no more than 8 hours. In contrast, 29.8% of chicks stayed in the nest for a period greater than 16 hours. For exceptions and possible interpretation see discussion at the end of this Chapter.

Brood attendance

A large amount of the data gathered in this section are subjective and may be open to misinterpretation. Without individually marked birds or known birds (some could be identified by voice, behaviour and plumage), it was not always possible to determine if a brood was attended on successive days by the same parent.

At 84% of nests visited at the time of hatch, two adults were present; in the remaining 16% only one adult appeared to be present. This may be due to the fact that one partner was away feeding. However, under normal circumstances, a second bird would normally appear within a short time in response to the alarm calls of its mate.

Once the chicks have left the nest they are more difficult to locate. Additionally, unless one adult is marked in some way, it is impossible to know its sex as it stands guard over the brood.

Broods out of the nest were subject to many hours observation. If the chicks were caught they could be aged, by counting to the original date of ringing in nest or, when unringed, by calculation using a regression formula constructed from chicks of known age for various measurements.

If the number of adults could be accurately determined, then this was related to the brood age. During the 3-years of study we have never found a brood splitting up. In 1983 a brood was found which appeared to consist of chicks of three separate ages. These were being guarded by two adults. For further details see Discussion.

Table 1.48 Brood care in Redshank. The number of broods of known age being guarded by two adults.

Brood age (days)	Frequency observed
1-5	11
6-10	7
11-15	4
16-20	7
21-25	6
26-30	1

Table 1.49 The number of broods of known age being guarded by a single adult.

Brood age (days)	Frequency observed
1-5	7
6-10	8
11-15	3
16-20	9
21-25	21
26-30	4

Tables 1.48 and 1.49 demonstrate several points.

(a) Young chicks are normally tended by two adults but on occassion young chicks may be found to have only a single adult in attendance.

(b) Once the brood has reached 20 days then the tendency is that only one bird will be responsible for guarding duties.

In the broods aged more than 26 days there is a slightly lower figure than expected. This can best be explained by the fact that fledging takes place at c 27 days.

Once the broodhas fledged, it is very difficult to ascertain if it is still being guarded by parent (s). On two occasions fledged chicks were being guarded by one and two adults.

By this stage in the breeding cycle, the bond between parent and offspring is very much weakened. In the most extreme situation parents actually desert their chicks for lengthy periods of time. Even when the chicks are relatively small (10-15 days), adults will disappear into neighbouring ditches for short periods of time, presumably to feed.

Fledging period

This is designated here as the length of time between hatching and first rudimentary flight. Few exact periods have been determined.

Known fledging periods (in days).

*	F	+	F	F/c	*
c 25,	26.5	28,	28,	28,	c28

* = could flutter/fly
F = Fully fledged
\+ = flew when released
F/c = Fledged chick captured

Both chicks known to have flown on 28th day could do so well; one was seen to fly 70 metres before running to hide.

These are positive results. On the negative side, we have been able to prove that birds could not fly at a given age.

Age at which young Redshank did not fly (in days).

24, 24, 24, 24.75, 25, 25.25, 25.25, 25.25, c 26, 27, c 28

From the above results it can be concluded that fledging period varies between individuals. Interestingly, two of the fledging periods of 28 days were siblings.

In contrast to the known periods, the second set of results clearly indicate that chicks of 24-25 days of age are not capable of flight. The chick estimated at 28 days of age had the longest wing and greatest degree of feather development of all chicks caught. It could be that this chick had not been forced to try to fly. Presumably first flight is stimulated in some manner (see Discussion).

Fledging success

This is most difficult to calculate as there are several problems involved:

(a) When searching for chicks it is difficult to know if all chicks in a brood have been found. An obvious aid is knowing how many chicks have left a given nest. Once the brood has been identified then the original number of chicks present is known.

(b) To calculate an overall fledging success one must know how many broods survive to fledging and what percentage of chicks within these broods actually fledge. The main problem is that broods can move, fledge, or all die off. It is sometimes impossible to know what has happened unless a brood has been followed closely.

Table 1.50 An estimation of fledging success from broods which were followed closely.

																Total
No. fledged	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	17
No. in brood (left nest)	4	4	3	3	3	4	4	3	4	3	4	4	2	4	4	53

Thus, a total of 17 chicks fledged from 53 chicks ringed in the nest.

In the above Table fledging success (minimum) is estimated at 32.1%. In the above broods the fledging success would have been greater if some chicks fledged but were not seen/caught. The overall fledging success is, I think, much lower as many broods simply died and disappeared within the first few days of their life.

A second calculation may be made using all those Redshank which have fledged and returned to breed in their first year. In this case 13 chicks have returned to breed from a total of 43 chicks ringed in the nest (30.2%). This figure compares favourably with the field estimate of 32%. But this is the end result of a pre-fledging and post-fledging period of mortality. If 13 chicks have returned, at least 13 chicks must have fledged. If overwinter mortality (1st winter) is 55% (Cramp & Simmons 1983), then clearly a large number of fledgings must have existed to result in the final figure of 13 returned to breed (all years).

$$\frac{45}{100} \times \text{total fledged} = \text{total survived to breed in 1st year (13)}$$

$$\text{Total fledged} = \frac{13}{0.45} = 28.8 \text{ fledglings.}$$

Thus, 28.8 Redshank must have fledged from a total of 43 chicks ringed in nests of known clutch size (70% or 2.814 fledged chicks per pair).

If one considers that more than 13 may have survived, but were either not on the study area or were not caught, then clearly the estimated number fledging would be even greater.

An analysis based on exactly the same principle has been carried out in the data gathered over the period of this study (1983-1986).

Table 1.51 Estimated fledging success of Redshank assuming that only 45% of those birds fledged actually survive to 1 year old.

Ringed:	1983	1984	1985
Returned:	1984	1985	1986
No. returned as 1st years	4	3	1
No. in brood fledged from. (nest of known clutch size).	13	11	4
Estimated total fledged*	**8.8**	**6.6**	**2.2**
Estimated fledging success	**67.7**	**60**	**55**

Note: * assuming a 45% 1st winter survival (Cramp & Simmons 1983)

Here, estimated fledging success ranges from 55-68%. In at least two cases extra birds from the above broods are known to have returned to breed in their second year. It seems highly likely that others have gone uncaught whilst others have returned to breed off the study area.

This is a theoretical estimate of fledging success based on the number of chicks which are known to have fledged and an estimated overwintering 1st year mortality of 55% (Cramp & Simmons 1983). If this mortality figure is an overestimate then so will be the estimate of fledging success.

In three years of study no more than two broods were ever thought to have fledged more than 1 chick. On one occasion, in 1985, a brood was located off the plot from which three weakly flying chicks flew. However, there was no way of knowing if these were all part of one brood.

Generally, in broods of known origin, no pair ever fledged more than two chicks and the majority fledged only one. Many broods of unknown origin and therefore unknown initial brood size, were followed in some detail. In 29 cases only one chick was found, even though brood ditches were searched extensively, even after first capture. In many of these cases the same chick was subsequently re-captured more than once, which suggests that it was the only one present. In one such brood a single chick was captured eleven times. Initially broods of 2 and 3 chicks are frequently encountered, but in older broods one chick is most common.

These figures suggest (quite strongly) that fledging success is probably very low. However, these figures are all for broods fledging at least one chick. When unsuccessful broods are accounted for the overall fledging success clearly may be markedly lower. For further details on fledging success and pre-fledging survival see Chapter 5.

No quantitative data were gathered on feeding and brood movements. The quality of different feeding areas could only be determined by large scale invertebrate sampling. The few data gathered on brood movements are integrated into the Discussion as these are too few and rather anecdotal to warrant inclusion here.

DISCUSSION

In Chapter 1, arrival, courtship and nesting preliminaries are discussed in a very short space. No single 3-year study could possibly concentrate on all topics of breeding biology because the demands would be too great. The main body of this research involved studying the breeding biology of Redshank from egg laying to chick fledging.

For good reviews of Redshank wintering, distribution and taxonomy see Hale (1971, 1973). For a full account of Redshank courtship see Ashcroft (1978) and Hale & Ashcroft (1982, 1983). Feeding behaviour (mainly on wintering grounds) has been studied by Goss-Custard (1969, 1976, 1977, 1978/1979). A detailed description of food items taken by Redshank may be found in Glutz (1977) and in Cramp & Simmons (1983).

This discussion concentrates on those aspects of Chapter 1 demanding elaboration and clarification.

Laying season

The laying season of Redshank on Banks Marsh is protracted well beyond the length of season found in inland breeders. In meadowland neighbouring the study area eggs could only be found between late April and early June. On the study area eggs were found well into July.

In individual areas within the study area laying is apparently synchronous, with small groups all laying at the same time. Presumably social stimulation, and local variation in vegetation cover and soil saturation is involved here. These two factors vary locally. The length of the grass varies in accordance with the regularity of tidal inundation. The higher areas (channel edges) are flooded less regularly and, as a consequence, grasses begin to grow here first. In addition there are different levels of winter grazing by wildfowl in different areas of the green marsh. Thus, at the start of the season, vegetation (nest cover) is more advanced in some areas than others. In a similar context environmental temperature may also be important. For the effect of rainfall on laying date see Yates (unpubl. 1982).

Within any one season there is a relationship between timing of spring tides and timing of laying. It also appears that a relationship may exist between winter/spring body condition and timing of laying. In this case temperature would be the most important factor. At low air temperatures Redshank food is less available (Goss-Custard 1969) and subsequently they feed less efficiently. Under such circumstances (notably extreme winters such as 1984-85) mortality may be increased and many birds may arrive back on the breeding grounds late. Low environmental temperatures would also slow up the rate of vegetation growth. Thus, after a cold spring birds may arrive back late and find the breeding grounds in poor condition. This may be an explanation for the slow start to the 1985 breeding season.

The results also indicate that older more experienced birds tend to nest earlier than the less experienced 'unrings'. Although there are obvious exceptions and confusion effects (see p29), age does partly determine timing of laying. For the effects of climate on laying dates see Yates (unpubl. thesis 1982). A similar age effect on laying has been found in this and other species by Gratto et al (1983), Grosskopf (1959, 1963), Oring and Lank (1982), Soikkeli (1967), Thompson et al (1986), Tuck(1972); but also see Parr (1980). In studies of Kittiwake and Arctic Tern, Coulson (1966) and Coulson & Horobin (1976) found similar trends. The confusion effect mentioned earlier arises when the saltmarsh is extensively flooded and many clutches lost. Resulting re-lays are laid at a time when many birds are laying their first clutches (see Laying seasons, 1983 and 1985). Initially it was felt that the second peak in laying activity was entirely due to replacements, with birds moving in from other areas. Data for 1984 indicate that a second wave of laying occurs, as usual, despite the lack of tidal flooding all over.

Many other factors determine timing of laying. For special reviews see Green, Greenwood & Lloyd (1977), Miller (1983a),Perrins (1970), Pienkowski (1984b),and Vaisanen (1977). Some Redshank are physiologically capable of breeding at under 1 year. Redshank fledging in late July probably are not capable of breeding until later in the following season. Therefore, in any one season, some first years breed early, whilst others (majority) breed later. Some Redshank do not begin to breed until their second or third year, although they may be present on the breeding grounds. In these cases genetic factors may be involved; but see Parr (1979, 1980) for the limiting of nesting by lack of suitable breeding areas.

Egg laying

The laying times, though apparently exhibiting a normal distribution curve, are in fact an artefact of the normal field day. Had intense observation been carried out throughout the night and early morning, then almost certainly frequency of laying times would have been more even.

Laying intervals appear to be similar to those found by Grosskopf (1958a). However, the longer intervals which were not recorded by Grosskopf (1958a,1963) are of particular interest. The longer intervals were produced by very old (10-12 years) and young (1 year) birds suggesting that these birds were in some way stressed. Unfortunately, no effort was made to relate an individual's egg quality and body contition to feeding quality/efficiency and arrival times. The shorter laying intervals indicate that in some birds, at least, egg laying does not present much of a problem.

Clutch

The mean clutch sizes recorded between 1983-85 are smaller than those recorded by Grosskopf (1958a) and Cramp & Simmons (1983). This difference is almost certainly because I have included unincubated clutches of 1 and 2 eggs. The small (unincubated) clutches may represent efforts of young birds nesting for the first time. Such clutches were apparently not found by Grosskopf (1958a, 1963). The nest finding effort in this study was exhaustive and consequently many nests were found at the laying stage. In these cases, clutch size was recorded before eggs began to disappear as a result of breakage and and predation. In Grosskopf's study, searching may have been less intensive, resulting in fewer single egg clutches being found.

Several clutches received extra eggs after incubation had begun (up to 11 days after). These were apparently laid by 'foreign' females and as a result of laying time these eggs did not hatch. In other nests different looking eggs (both pattern and shape) appeared at the laying stage. However, as these clutches were never of more than four eggs it is difficult to say whether these were 'freaks' or indeed were laid by another female.

Tables 1.5 and 1.6 describe the egg data gathered over the three years. The data from Table 1.5 suggested that real differences may exist in egg size in relation to laying order. This prompted the follow-up analysis of variance and t-tests. The maximum minimum date (Table 1.6) outline the range of measurements that were encountered. In terms of length, longer and shorter eggs than previously recorded were encountered (see Cramp & Simmons 1983; Glutz 1977).

A similar trait was experienced with egg breadth.

The data portraying egg size versus laying order deserve special attention. Firstly, the data sets from 1983 and 1985 were excluded because of the pattern of laying and re-laying. It was felt that the nest laying distribution in 1984 was undisturbed by tidal rhythm and inclement spring weather, thus this data set was selected.

Primarily, an analysis of variance test indicated that variation was greater between eggs of different laying orders than within all eggs of any one order. Further comparative statistics were thus justified.

The results obtained clearly indicate that the breadth and subsequent volume of the first, second and third eggs are significantly larger than the fourth egg. Thus, fourth eggs tend to be narrower and consequently of less volume. For a review of egg size within a clutch see Miller (1979a).

The 'within year' and 'between year' analysis of clutch biometrics are of particular interest. In second clutches, laid by known females, there was no difference between mean egg lengths, breadths and volumes with the first clutch (as Vaisanen et al 1972). A similar result was also found when clutches of known females were compared between years. Thus Redshank lay eggs of a similar shape and size both between and within years. The egg colouration and patterning also remain consistent from one clutch to the next. On several occasions females were identified before trapping by egg recognition. Trapping these individuals then confirmed female identity. For more data on female egg patterning and shape between years see Nethersole-Thompson (1951), Ratcliffe (1980), and Baerends et al (1970).

Concerning egg sizes laid by a female in consecutive years, the result is perhaps rather surprising since an age effect on egg size has been discovered: see (Chapter 2) and Anderson (1951); Coulson (1963), Coulson & Horobin (1976), Gratto et al (1983), Kendeigh (1975), Preston (1958), Thomas (1983) and Vaisanen et al (1972) on other species. A review of the data set revealed that the vast majority of females involved had previously bred. Any change in egg size probably occurs over the first 1-2 years and thereafter egg size remains constant. As a consequence, changes in egg measurements would be overshadowed by the general constancy of the majority of clutches. As a consequence, no change in clutch measurements were detected between and within years for known females.

Incubation certainly began on some occasions prior to clutch completion. However this is difficult to quantify as eggs may be covered without being properly brooded (Nethersole-Thompson & Nethersole-Thompson 1979). In those cases where incubation does begin, it is beneficial that the last (fourth) egg is the smallest. This may be true for several reasons:

(a) the smallest egg should hatch quickest;

(b) a small egg represents a smaller investment loss should it be deserted due to delayed hatching.

The latter has been observed on several occasions (but see Miller 1979a for a brief review).

The range of variation in incubation period was primarily due to the degree of disturbance a particular nest experienced. This disturbance varied with position of nest and catchability of birds, but also with environmental conditions, number of birds incubating, and possibly adult experience. Several areas were heavily disturbed. As the Redshank is a 'light sitter' it follows that incubation would be less efficient in a disturbed area. Under such conditions the air temperature would then become more important as unincubated eggs are then exposed to environmental conditions.

At the species level, birds which incubate alone, as opposed to those sharing incubation, experience a longer incubation period than expected (see Norton 1972). It therefore follows that a broken partnership (only one incubator) would be expected to hatch eggs after a longer period than average. In fact this was recorded with single adults incubating and hatching eggs after incubation periods of up to 31 days.

Most Redshank are prolific egg layers, laying repeat clutches readily. On at least one occasion a female was suspected of laying 3 clutches in one season. Birds which arrive late and begin nesting late may be less likely to re-lay. However, this needs testing experimentally. In 1983-85, 36 re-lays were found which had mainly arisen as the result of nest loss due to flooding. In 1984, a year of no flooding, more re-lays were found. The majority of re-lays (81%) were produced by birds which had hatched eggs but presumably lost chicks soon after leaving the nest. For similar findings see Zhmud (1983).

The speed at which the re-lay is produced and that fact that the second clutch is not smaller in size or total volume, supports the ideas of Oring et al (1983) and Lank et al (1985) that laying in some waders is not over stressful.

One particularly interesting point is that a bird deserting its mate can form a new partnership and produce a second clutch almost as quickly as an established and faithful pair. In the case of Redshank taking a new mate it is possible that there is a pool of available birds waiting to pair up. If a female is in breeding condition she is presumably more receptive to the advances of another male. Secondly, resources may be more available later in the season, allowing a female to reach breeding condition much quicker than earlier in the season.

Trapping and ageing

The trapping success (percentage caught from traps set) fell from 66% in 1983 to 51% in 1985. Generally the difference between 1985 and the other two seasons was that the Redshank showed a strong reluctance to enter the traps. As a consequence, traps were set for even longer, yet still the trapping success remained very low. One possible explanation is that the birds were stressed in some way as a result of conditions experienced over the winter period and as a result of this stress many birds were in poor condition, resulting in a weakened brooding drive. As shall be seen, the number of 'unrings' captured in 1985 was well down on the 1983 and 1984 totals. This may be interpreted in terms of an increase in overwinter mortality of younger inexperienced birds. For further details see Cramp & Simmons (1983) for differential survival over the winter period of older and first year birds; and Davidson&Clark (1985) for the effect of the 1984-1985 winter on wintering Redshank.

Another explanation for lowered trap success could be that young birds are easier to catch than old birds. Fewer young birds were caught in 1985, presumably because fewer survived the overwinter period. As a consequence, there were fewer birds in the study area which could be considered as easy to catch. Thus it appeared that the birds were more difficult to catch than normal. The catchability of young and old birds requires further research.

The ageing technique first discovered by Hale and published in the B.T.O. Wader Guide (Prater, Marchant and Vuorinen 1977) is supported and endorsed. I would add that first year birds normally have a dull coloured base to the bill and dull coloured legs. At this stage it could be said that consistency demands that when assessing colours some kind of standard procedure should be adopted. The amount of feather abrasion is also a useful ageing technique but, in the latter half of of the season, many birds of all ages have fairly heavily abraded primaries. Until a known young Redshank is caught, that has not retained at least one juvenile inner median covert, then this should remain as the major ageing criterion.

In 1983-85 many Redshank chicks were ringed. A small percentage of those returned each year, along with a larger number of unringed first year birds. The data are best from 1984-1985 as only a small number of chicks were ringed in 1983. Approximately 14% of young birds nesting on the study area had been ringed as chicks. The remaining 86% were unringed birds. Unringed first years may have hatched on the study area and not been ringed. I would suggest, however, that at least some of these unringed first years must have come from other areas of the Ribble Marsh (see Chapter 3 for further discussion).

On average, a male Redshank is smaller than a female and a young Redshank smaller than an older bird (see Chapter 2). For further details on Redshank measurements see Yates (Unpub. thesis 1982).

Mate choice in birds has, over the last few years, become a topic of some considerable interest; see Bateson (1983) and Coulson & Thomas (1983). Why do individual Redshank select particular mates? Do Redshank make an assessment of a possible partner's attributes such as size, voice, breeding plumage, or do they randomly select a mate from a pool of available birds? In a large population the problems of management and handling the data set can be quite overwhelming and I would therefore suggest that a study of a small population would be more likely to indicate possible answers to problems of mate choice. This study has shown (a) no mate selection taking place on the basis of summer plumage; and (b) a hint of selection taking place on the basis of size (weight). The relationship which was discovered, albeit a tenuous one, could arise as a result of mating times. In other words, birds mate in early season, mid-season and late season. If there was a relationship between female/male weight and timing of laying (see Chapter 2), then this relationship could arise without active selection having anything to do with it. I would therefore state that so far active mate selection does not seem to be size or plumage related. Active mate selection may be more likely to take place on the basis of behavioural attributes. These are not so readily quantified. There is, however, a relationship between male and female age, more of which is said in Chapter 2. Previous studies in Redshank (Grosskopf (1970), Yates (unpub. thesis 1982), and on other waders, Soikkeli (1967), have also established such a relationship. In Kittiwake, Coulson (1966) discovered a strong relationship between male and female age.

In Chapter 3 site tenacity is looked at in considerable detail; one of the major findings is that birds tend to return to their previous nesting ground. With this in mind, and the fact that many birds mate with birds of equal status in their first year (first time breeders), then the only requisite to maintain a strong relationship between male and female ages is that Redshank are highly mate faithful, probably until one member fails to return or arrives back late. Although the data are not extensive, they support the idea of a partnership joining and remaining stable until something causes a break-up. The effect of the previous year's nest success does have an effect on mate fidelity in some years. This is perhaps not as important as the late and non-arrival back of former partners.

The quantitative assessment of mate fidelity is based on those birds which were captured in consecutive years. Therefore, of 100 birds caught in 1984, and also caught in 1983, a minimum of 60%

remained faithful and 20% took new mates. Twenty birds in 1984 and 37 birds in 1985 were of unknown pair status. The main problem in 1985 was the large drop in catching efficiency which resulted in a lower number of birds being caught. This apart, there is a possibility that the lowered mate fidelity in 1985 is due to the late or non arrival back of some of the birds after the very hard winter of 1984-5.

As will be seen in Chapter 3, previous years nesting success has an effect on breeding site fidelity (see also Oring & Lank 1982; Oring, Lank &Maxson 1983), but perhaps more surprising is the result that nest success in one year has an effect on the following year's mate fidelity. Factors such as mate fidelity, breeding site fidelity, and breeding site tenacity are clearly inter-related. In those cases where divorce occurs, the main causes are probably death, late or early arrival back of one member of the pair, or movement away from previous nesting ground due to previous failure.

Most waders studied have been shown to exhibit a degree of mate fidelity; (Holland et al 1982; Holmes 1971b; Nethersole-Thompson & Nethersole-Thompson 1979; Parr 1980; Pienkowski 1984a; Soikkeli 1970). In many of these studies other factors, such as time of arrival and previous years' nest success, were not studied.

Nest hatching

Prior to hatching the chicks are very noisy within the eggs; to the human ear they may be heard 'clicking' (Driver 1967) and also 'peeping'. The chick calls apparently act to synchronise the hatch, thereby increasing the hatch potential of all chicks, thus assisting chick survival (Nethersole-Thompson 1973; Norton 1972; Vince 1966). A fuller account of the range and role of chick and adult calls is given in Appendix 4 and 5.

The chipping periods (time from first signs of hatch to actual hatch) were generally long, probably reflecting the degree of disturbance and environmental conditions. A similar range of chipping periods have been found in Greenshank (92.2 hours n = 19) by Nethersole-Thompson & Nethersole-Thompson 1979). In as far as is possible there is no evidence to suggest that chicks emerging after a long chipping period were weakened. However, some eggs which were very slow in hatching were deserted by brooding adults. This occurs less regularly in Greenshank (Nethersole-Thompson, pers comm).

The figures for nest and hatch success demonstrate the confusion that can arise when source of data and form of calculation are not clearly defined.

The nest hatching success (Category A) fluctuates in accordance with the amount of tidal flooding which occurred. In 1983 and 1985 there was much tidal flooding resulting in the loss of 36% and 16% of nests found respectively. The lack of flooding in 1984 (only 3% of nests flooded) allowed for a much greater nest hatching success. The Category B, total egg hatch success, reflects exactly the same trend as Category A. A brief look at Category C hatch success is interesting. In 1985 a successful nest hatched on average more eggs than in either 1983 or 1984. Once again the egg hatch success figures for 1983 were poorest. In conclusion, nests in 1983 were less likely to hatch and produced fewer chicks per nest when they did hatch than other years. A successful nest in 1985 produced on average more chicks than a successful nest in 1984. These results clearly demonstrate the effect of an environmental parameter (tidal invasion) on hatching success. One interesting point is the Category C comparison of egg hatch success in successful nests in 1984 and 1985. I would have expected hatch success to be as high in 1984 as in 1985. However, a simple explanation may be advanced here. In 1985 fewer first year and 'unrings' were captured (117 vs 60), whereas the balance of controls (160 vs 156) was much more even. If young and inexperienced birds are less efficient at incubation and hatching eggs, then clearly in 1984 you would expect this to be reflected by a lower hatch success. This idea and interpretation is supported further by data in Table 3.7 which suggest inexperienced birds are indeed less efficient as incubators.

When all nests of known clutch, and total number of chicks hatched from these nests are counted, then productivity per pair can be assessed (at egg hatch level). Once again 1983 was the least successful year with a mean of 1.15 chicks hatching from 190 nests of known clutch and outcome. In 1984, 2.86 chicks hatched from 186 nests of known clutch and outcome. The difference is enormous and highlights quite clearly productivity differences at the egg hatching stage.

Most wader research has made some attempt to quantify nest and egg hatching success. Not surprisingly, figures range widely from one year to another and from one locality to another. In Wangerooge, Grosskopf (1960) found that in 72 nests containing 286 eggs 86% hatched. In studies of Greenshank, Nethersole-Thompson & Nethersole-Thompson (1979) found an overall hatch success (category B) of 76.7% This figure varied annually from 47.8%-100%. In this study predation and environmental conditions were the most important causes of egg/nest mortality. The Nethersole-Thompson's study also had comparative Category C results, with 92.2 and 91% of eggs in successful nests hatching in two separate localities. Thus, when a nest hatches it usually hatches with high success. Other hatch success figures for sandpipers are sparse.

Egg hatch order

The data show that there is a relationship between order of laying and hatch order, particularly for the last egg. This would suggest that incubation frequently begins prior to clutch completion, as supported by field observations. Under such conditions the fact that the fourth egg is generally of small volume (see p35) is an advantage as it should hatch quicker. Additionally, as stated earlier, where this egg is abandoned, the loss is less than would be the case for a larger egg. On several occasions Redshanks have abandoned eggs with embryos still active and calling within; sometimes an individual parent will remain behind to continue incubation. On one occasion a single chick hatched from an egg 24 hours after the other three chicks had hatched. Eggs of other laying order have also been abandoned when they have fallen behind. For more information on egg hatch order see Miller (1979a).

The data on the relationship between egg size and chick size support the findings of many other studies. The multiple regression analysis indicate that egg volume is the best predictor of a chick's weight and tarsus measurement. In the case of chick weight, 77% of cumulative variance is explained in a regression equation of egg volume and length with chicks weight. Egg volume is therefore the best indicator of a chick's potential size and possibly survival (this study; Davis 1975; Kålås & Byrkjedal 1984; Ricklefs 1984; Thompson et al 1986; Vaisanen et al 1972). However, it is very difficult to relate chick size at hatching to fledging potential as broods are very difficult to follow.

Several researchers, notably Galbraith (1986unpub. thesis) and Kålås & Byrkjedal (1982) have preferred to use mean chick weight in relation to mean egg volume, because it is often difficult to know which egg a specific chick has hatched from. I have found that an equally interesting relationship can be examined by relating chick size to hatch order (see Methods). The results indicate that chick tarsus and bill measurements are negatively correlated with hatch order. Thus the last to hatch (often from the fourth egg) is often the smallest and perhaps potentially the weakest. This relationship is very real when one considers the variation in size and hatch order of eggs 1-4 (see also Miller 1979a) Chick weight does not correlate with hatch order due to its variable nature around the first 3 hours after hatch (for full details see Yates, unpubl. thesis 1982). In addition, chicks do not feed until they have left the nest, so they are constantly using up yolk reserve (Pienkowski 1983, 1984a; Yates unpubl. thesis 1982).

The results showing the relationship between chick size and date of hatch are of similar interest. In this case negative correlations exist for all the measured parameters, except chick tarsus. Therefore, as the season progresses, chicks hatching are decreasing in size, except for tarsus measurement. Of all the chick appendages, the tarsus is the most fully developed at the time of hatch (55-60% of adult tarsus). Tarsus size does not appear to decrease in chicks hatching later in the season. If chicks hatched later in the season had a smaller tarus they may be at a considerable disadvantage. Compared with the early season when vegetation is short and feeding places abundant, the demands of the latter half of the season are greater. It is essential later in the season to have a long tarsus to combat long grass, scarcity of wet areas for feeding, and increased level of predation from hungry Lesser Black-backed Gulls, Herring Gulls and Kestrels feeding broods. Clearly, genetic control of tarsus length could mean that later in the season smaller eggs do not necessarily produce chicks with shorter legs. The reasons why egg size and thus chick size decrease with date of hatch (or timing of laying) are explained fully in Chapter 2.

Considering the differences in weather conditions between all three seasons, it is surprising that the mean length of nest stay by chicks is so consistent. One very interesting point concerns the range of periods spent in the nest and the number of occasions chicks were recorded for each time period. In particular, a single factor explains the presence of a bimodal frequency (see Table 1.47). Those chicks that have only spent a short period of time in the nest are those that have hatched 3rd or 4th. If the hatch is relatively synchronous, then the chicks hatch over a shorter period of time. Once dry, and conditions are suitable, the brood leaves.

Those chicks which spend a long period in the nest are most likely the result of an asynchronous hatch; one or sometimes two eggs are often well behind the others. The hatched chicks are held in the nest whereas the late-coming chicks leave the nest almost immediately they are dry.

On a very few occasions, chicks were recorded leaving the nest in the morning but were re-called to the nest in the evening. At this stage there is no way of knowing if a prolonged stay or a short stay improves or decreases a chick's chance of survival. Certainly when weather conditions are unfavourable (very hot, cold, or wet), chicks are held in the nest. Presumably the warmth and protection gained outweigh the risks of chilling/overheating. Similar observations have been made on other species, particularly Greenshank and Dunlin (Nethersole-Thompson & Nethersole-Thompson 1979; Soikkeli 1967).

Once the chicks have left the nest they enter a phase of life demanding much care and protection by their parents. This is also a difficult time for the observer as broods are difficult to follow, demanding much patience and effort.

In the majority of cases, both adults are still attending the nest at the time of hatching. When only one adult was in attendance we sometimes later found the second bird at a second nest. Such behaviour may have arisen as a result of a bird deserting its first mate. However, on at least one occasion one bird was associated with two separate mates at two nests at the same time.

We have never discovered that a brood split up, with some chicks going with the male and some with the female. If this happens it does so rarely (see Tuck on behaviour of Common Snipe Gallinago gallinago 1972). On one occasion three chicks of unknown age (estimated as 4, 6.5 and 8.75 days old) were captured in a ditch in close proximity to each other, with only two adults present. It is possible that there were 3 separate broods, but on previous occasions pairs tended not to mix. Indeed fights have been seen when pairs have moved too close to each other. The possibility remains that one pair had accidentally picked up a couple of chicks. Cases of chick adoption are fairly rarely recorded; nevertheless there are some reliable records of this occurring in Redshank and Dunlin (Hakansson 1978; Hilden 1977; Thin 1942).

Brood care is variable with some pairs staying with their young right up to fledging; in other cases a single adult carries out all chick rearing duties. The normal would appear to lie somewhere in between. In a very few cases where it was known, brood attendance was by the male, the female deserting some time after tht tenth day. This is similar to that recorded in Greenshanks (Nethersole-Thompson 1951; Nethersole-Thompson & Nethersole-Thompson 1979).

Some fledglings are attracted to an attendant adult, presumably by the calls. Young birds would frequently fly in and follow an alarm-calling adult before flying away again. This could easily confuse an inexperienced observer into estimating erroneous fledging periods.

Accurate estimates of fledging success require many hours of fieldwork and a fair amount of luck. At 25 days of age the wings are developed and a weak flutter/run is possible. Flying takes place, or is at least possible, from 26.5 days. There may be some considerable variation, but at no stage would this variation match that found in Lapwings (see Jackson & Jackson 1980).

Quite what stimulates a first flight is unknown. Chicks which were caught hiding sometimes flew/fluttered on release when chased. The largest chick caught, at 28.25 dqys, flew fully 70 metres before running and then hiding. This chick made no attempt to fly when approached but preferred to hide. It would appear that there is a transition period from hiding and running to flying. Presumably flying may be induced under certain conditions of danger. Grosskopf (1958a,1960) estimates fledging at 25-35 days. Other estimates of 25 days and 23 days were made by Rayfield (1943) and Robson (1953). In captivity, Heinroth (1927) and von Frisch (1959) estimated fledging at 25 and 28 days respectively.

Fledging success

Unlike hatch success, the calculation of fledging success is fraught with many problems. The most obvious is that following a brood and determining how many chicks survive is very difficult. The figures for fledging success of followed broods will always be an underestimate because some fledglings may be missed. Moreover, in a large population of mobile birds it is very difficult to assess broods moving, dying, fledging; and other broods appearing as a result of movement or birth. To assess overall fledging success, the number of successful broods must be calculated. This is very difficult to achieve in a large population.

The fledging success estimated from field observations suggest that about one-third of chicks which hatch actually fledge in successful broods. The overall number of broods which are successful is unknown.

Theoretical calculations of fledging success suggest that in some successful broods fledging success may be as high as 70% This figure differs widely from the more accurate field based estimate. In the case of the theoretical calculation the overwinter mortality estimate of first year birds would appear to be too high.

Good field observations suggest that normal fledging success lies somewhere between 25-50% per successful pair.(No brood was ever observed at the time of fledging with more than two surviving chicks).

Finally, winter mortality would surely range widely between years. In the hard winter of 1984-85, three dead Redshank, ringed on the Ribble, were picked up within a 14-day period. In each case the cause of death was described as starvation due to freezing of feeding grounds. During this spell Redshank were found dead all along the south coast of England and also along the French coast (Davidson & Clark 1985).

At the present time I can see no way of assessing fledging success in a densely populated area. In those broods that are followed, a basic calculation is possible and may be useful when certain problems are highlighted. The main problem is that only surviving broods are followed; the broods that perish simply disappear. The answer lies in assessing how many broods perish each day as opposed to moving, fledging or simply being missed.

Grosskopf (1960) estimated that 56% of eggs hatched gave rise to fledging. I would make a cautious final estimate of 20-30%

fledging success as an overall figure. For a theoretical estimate and further discussion see Chapter 5.

For a full comparison of the Redshank with the closely related Greenshank see Appendix 4.

Chapter 2

Female age and size-related reproductive differences. Possible breeding quality indicators

Introduction

Pioneering work by Grosskopf (1959a, 1970) on the Redshank strongly suggested that breeding birds of different ages were nesting at particular times of the reproductive season. Furthermore, this study suggested that mate selection was taking place on the basis of size. Little other quantitative work has been done on the breeding biology of Redshank, other than the exhaustive study of Ashcroft (unpubl. thesis 1978), and Yates (unpubl. thesis 1982) on the Ribble Marshes.

On the closely-related Greenshank, Nethersole-Thompson has carried out two exhaustive studies; in Speyside (N.E. Scotland) (1951) and Sutherland (N.W. Scotland) (1979). These studies have greatly added to our basic knowledge of sandpipers and have also given an insight into the more specific details of breeding biology. In particular the effect of age on laying data, both within and between seasons, have been highlighted. Recent analysis (Thompson, Thompson, and Nethersole-Thompson 1986) give a further insight into how members of the population contribute to breeding effort. In particular the analysis show that older birds nested earlier in the season, that egg weight is related to laying time, and that climatic factors cause between-year fluctuations in laying date. In the Redshank study, analyses have concentrated on highlighting within-year differences. There has been no recent study carried out on the Greater Yellowlegs T. melanoleuca and the Lesser Yellowlegs T. flavipes. The Spotted

Redshank T. erythropus has been the subject of many years research by Raner (see Nethersole-Thompson & Nethersole-Thompson 1986).

Studies of other sandpipers have tended to concentrate on accumulating general information which is also important to our understanding of sandpiper breeding systems. Exceptions have been the very detailed study of Spotted Sandpipers (Oring & Knudson 1972; Oring & Lank 1982; Oring, Lank & Maxson 1983; Oring & Lank 1985), the study of Dunlin (Soikkeli 1967, 1970a, 1970b), and more recently a study of Semipalmated Sandpipers (Gratto, Cooke & Morrison 1983; Gratto, Cooke & Morrison 1985). This last study examined the hatch success and potential reproductive success of first-year and older birds.

Many other studies of sandpipers have examined various aspects of breeding history, but have neglected to examine age related effects and possible size effects in relation to potential breeding quality.

Studies of non-shorebirds have examined such factors in more detail, presumably because

(a) these birds often nest colonially, making study easier and

(b) some birds, such as gull species, may be aged accurately on the basis of plumage differences up to several years (4 in some cases). In Redshank, accurate ageing is only possible for first-year birds (see Methods).

Studies of other Charadriiformes, in particular the gulls and terns, have isolated age-related reproductive differences and have in many ways led the field by their far-sighted approach. Many of the questions posed are now being tackled by wader workers. However, as suggested above, there are many very real practical problems to overcome.

The major non-wader works, for example studies on Kittiwake (Coulson & White 1958; 1960; Coulson 1963, 1966, 1968; Coulson & Wooler 1976; Thomas 1983) have examined age structure of population, age-related to breeding time, age related egg-size differences and age versus reproductive quality. Other gull studies (Davis 1975, Mills 1979) have also examined factors affecting egg size. These studies have attempted to take our understanding of populations and the role of individuals a step further. Finally, studies of Arctic Terns (Coulson & Horobin 1976), Common Terns and Roseate Terns Sterna dougalli (Nisbet 1978) have studied age-related factors and their effect on overall reproductive success. Other Charadriiformes studies, notably of skuas (Furness , unpubl. 1977) have examined reproductive success and related this to age of individuals.

At the end of this Chapter I have compared the findings of other researchers along with my own.

This Chapter presents the results of the major part of the study carried out over 3 breeding seasons.

The main aims were:

(a) to study the effect of age on laying time, egg size (length, breadth and volume) and reproductive quality;

(b) to relate age to individual quality (weight, size, plumage);

(c) to study the rôle birds of different age groups play in the population.

Timing of laying

Results

Data on timing of layihg are presented in Figures 5, 6 and 7. The data are shown in two classes:

(a) The number of birds (caught per 5-day period) which had bred in previous years (controls);

(b) The number of birds (caught per 5-day period) which had not been previously caught. These included birds ringed as chicks which were known to be breeding for the first time, and 'unrings'.

FIG.5. The date of clutch completion of Redshank of different ringed status captured on the nest. 1983

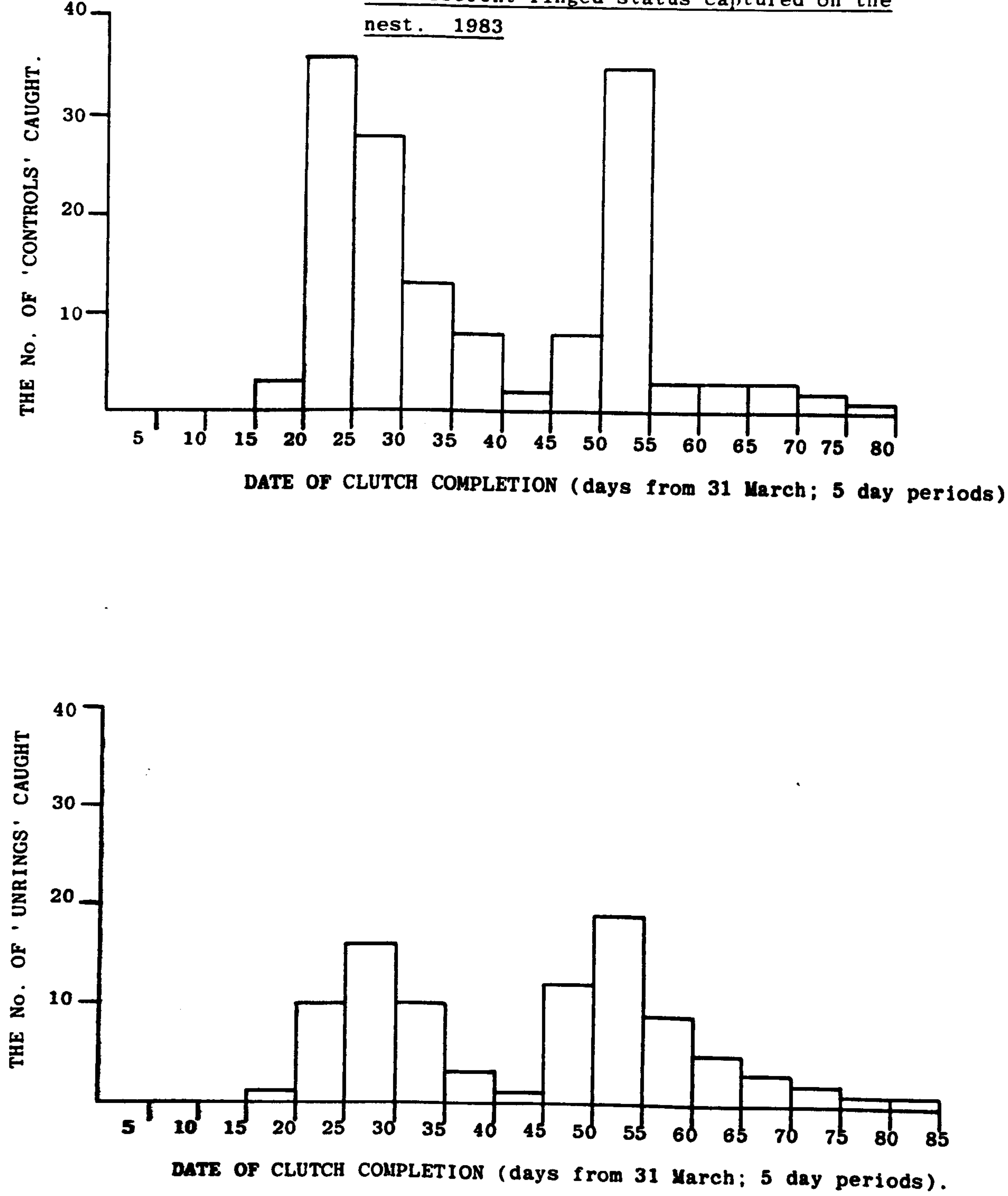


FIG.6. The date of clutch completion of Redshank of different ringed status captured on the nest. 1984.

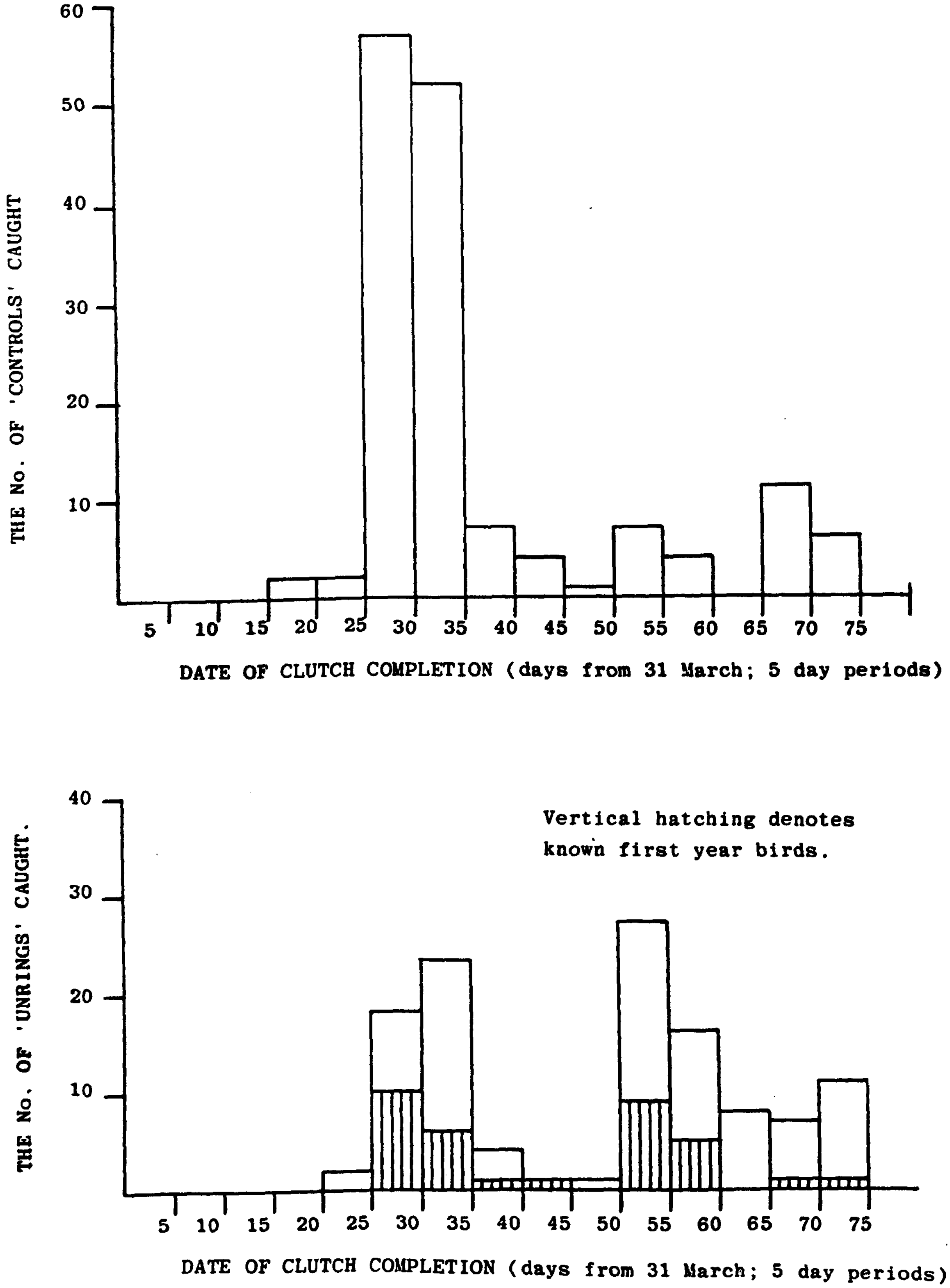
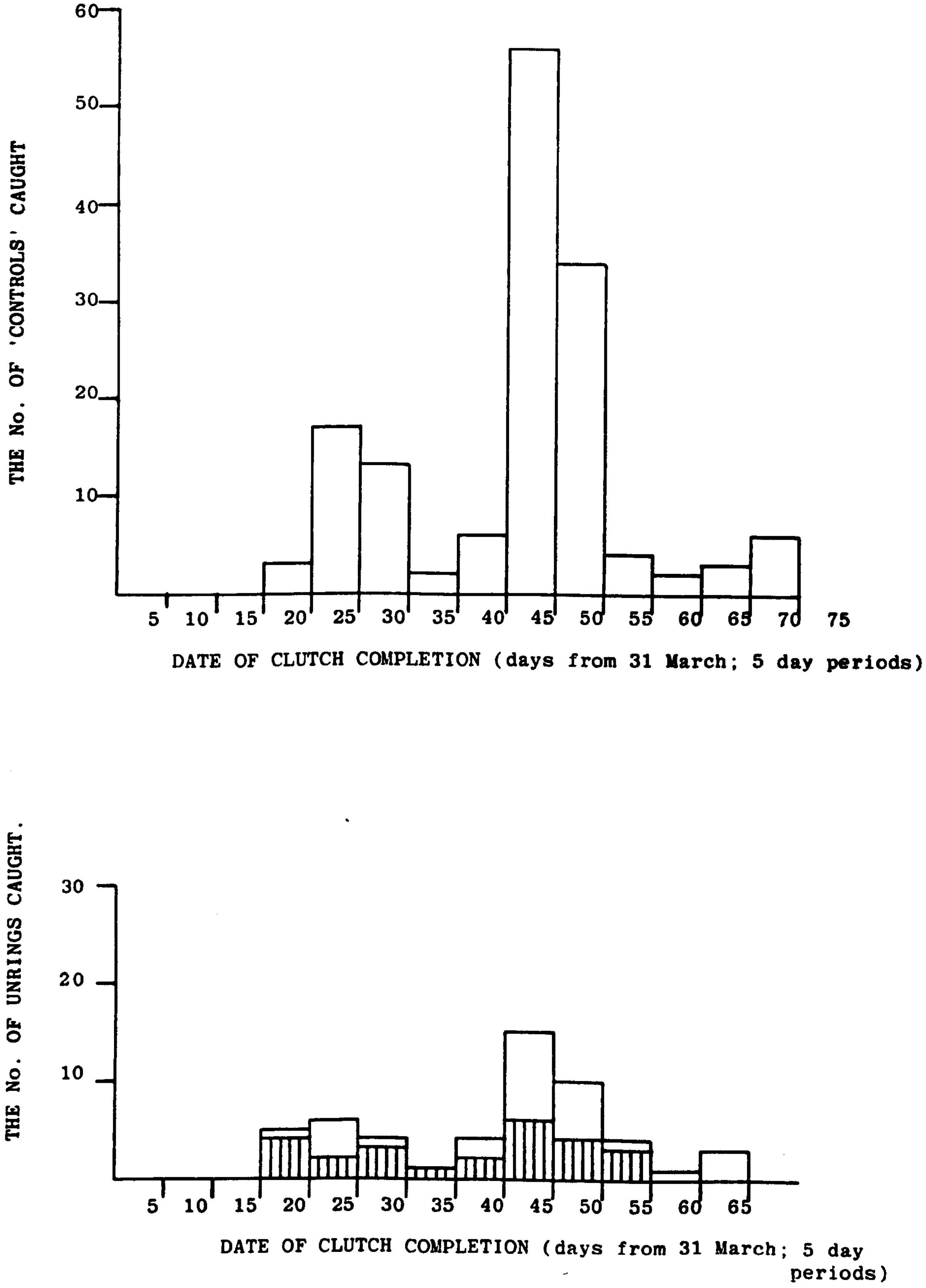


FIG.7. The date of clutch completion of Redshank of different ringed status captured on the nest. 1985.



In 1983 and 1985 there was extensive flooding of the study area during the breeding season. This culminated in 36% and 16% of all nests being lost due to tidal flood water. Reference to Figures 2b, 3b and 4b indicates the predicted tidal cycle for all years. In 1983 the marsh was extensively flooded on three occasions; 27 April, 13 May, 14 June. In 1984 the study area was heavily flooded on 15, 16 and 17 April; on 15 May some minor flooding occurred but only a few nests were lost. In 1984 laying began after the main spring tides of mid-April and consequently only 3% of nests were lost due to flood tides. In 1985 the marsh was badly flooded on 5, 6, 7 and 8 April prior to nesting; further extensive flooding occurred on 4, 5 and 6 May. These floods were devastating, destroying wholly or at least partially three-quarters of the nests present at the time. No subsequent flooding occurred in 1985.

Figures 5, 6 and 7 demonstrate the temporal distribution of clutch completion dates shown in Chapter 1 (Figures 2a, 3a and 4a).

In 1983 controls and 'unrings' show a bimodal frequency. The majority of controls (62%) have nested early in the season and are mainly responsible for the first nesting wave. After the May flood many nests were lost and much re-laying subsequently occurred. The large number of controls in the second wave may have nested first time round but were not caught. The majority of 'unrings' (56%) were trapped from nests completed later in the season.

The data for 1984 appear to indicate a much clearer picture. Once again clutches were completed mainly in the early season. However, a number were also completed (a sizeable percentage of these being re-lays) later in the season. The majority of birds trapped from the first wave of nests (72%) were controls. Some 'unrings' and first years were also caught from the first wave but the majority (59%) were responsible for nests found in the later waves. Only a small percentage (19.5%) of controls was trapped from nests of the second and third waves.

The 1985 season exhibited an interesting pattern of dates of clutch completion (see Figure 4a Chapter 1). Birds trapped from these nests showed an expected pattern. Redshank trapped from the first wave of nests proved mainly to be controls. However, the first wave was much smaller than previous years (see Discussion, Chapter 1, on timing of laying). The majority of 'unrings' (70%) were caught from the second wave of nests. The large number of controls caught from the second wave (76%) represents the large number of nests which were found at this stage. At the start of the season, laying began very slowly, with many birds apparently delaying laying until later in the season. The overall number of nests found and the overall number of 'unrings' caught was well down on the two previous seasons. For possible reasons see Discussion.

The 1984 season was least affected by tides and bad weather. It is likely that the pattern obtained for this year represents the 'true' picture for an undisturbed nesting season.

Table 2.1 A Chi-square analysis to examine the relationship between adult experience and laying dates. Birds already ringed are considered to be experienced, whereas unringed birds are considered inexperienced (1983 data).

Adult status	Timing of laying Nested in first wave	 Nested in subsequent waves
Experienced	90	55
Inexperienced	41	52

$X^2_{(1)} = 6.69$ $p < 0.01$

Table 2.2 A Chi-square analysis to examine the relationship between adult experience and laying date. 1984 data. Adult status as above

Adult status	Timing of laying Nested in first wave	 Nested in subsequent waves
Experienced	124	30
Inexperienced	48	70

$X^2_{(1)} = 43.9$ $p < 0.001$

Table 2.3 A Chi-square analysis to examine the relationship between adult experience and laying data. 1985 data. Adult status as above

Adult status	Timing of laying Nested in first wave	 Nested in subsequent wave
Experienced	35	111
Inexperienced	16	37

$X^2_{(1)} = 0.49$ n.s.

In 1983 and 1984 experienced breeders (controls) bred earliest. Inexperienced (unrings) birds tended to nest slightly later in the season. In 1985, a bird's experience did not relate to its timing of laying. This arose because of the delayed start to the breeding season, resulting in many older birds nesting later in the season.

The inexperienced birds caught may be divided into first year birds and birds of greater than one year old. In 1984, 37.5% of unringed birds caught from the first nesting wave were first year birds. Twenty three percent of unringed birds caught in the second nesting wave were first year birds.

In 1985, the number of unringed birds caught was very much lower than in 1983 and 1984. Of those unringed birds nesting in the first wave, 62.5% were known to be first years. In the second nesting wave, 40.5% of the unringed birds were first years.

First year birds were therefore found in both the early and late nesting waves. There is no way of knowing what percentage of unringed birds which were not first years were nesting for the first time.

Correlates of Redshank Breeding Biology

At each nest found, an attempt was made to catch, measure and age the incubating adults. An effort was also made to measure (length and breadth) as many eggs as possible and to determine the date of clutch completion for all nests. At any nest, where all the above was achieved, the relationship between a bird, its eggs, and its date of clutch completion could be examined. By dealing with the data set as a whole, it was hoped to build up a general picture of breeding variables within the population. The following analysis therefore concentrates on groups of birds rather than individuals.

The statistical analysis of the breeding data was carried out on the statistical Package for Social Sciences (Nie _et al_ 1975). Analysis were mainly by Pearson's correlation and multiple regression analysis to examine the relationship between dependent and independent variables.

These analysis therefore determined both the strength and direction of relationships where they existed.

Table 2.4 A correlation analysis of female size parameters.
Pearson's correlation coefficients (r).

(a) Year 1983

Variables	Age	weight	wing	tarsus	bill
Female age					
Female weight	(125) n.s.				
wing	(125) 0.212*	(124) 0.172 n.s.			
tarsus	(125) n.s.	(124) 0.414***	(125) 0.147 n.s.		
Bill to feathers	(124) n.s.	(124) 0.202*	(124) 0.227*	(124) 0.384***	

(b) Year 1984

Variables	Age	weight	wing	tarsus	bill
Female age					
weight	(138) n.s.				
wing	(138) 0.230**	(138) 0.268**			
tarsus	(138) n.s.	(138) 0.174*	(138) n.s.		
Bill to feathers	(137) n.s.	(137) 0.290**	(137) 0.119 n.s.	(137) 0.303***	

(c) Year 1985

Variables	Age	weight	wing	tarsus	bill
Female age					
weight	(106) 0.190 n.s.				
wing	(107) 0.194*	(106) 0.245*			
tarsus	(107) n.s.	(106) 0.482***	(107) n.s.		
Bill to feathers	(99) n.s.	(98) 0.283**	(99) 0.224*	(99) 0.286**	

The tabulated results indicate that wing length is the best predictor of female age. Not surprisingly, female age does not correlate with her weight, possibly because weight tends to fluctuate so much over a short period of time. One female has been recorded losing 22 gms within 2 days.

Once the relationship between female age and size had been examined, the relationship between female parameters and date of clutch completion, egg size and reproductive success was examined. The results are displayed in a series of Tables indicating both the strength and direction of relationships where they existed.

Table 2.5 Relationship between female age and measurements with date of clutch completion, egg biometrics and male age. Pearson's correlation coefficients (r). 1983 data

	Date clutch completion	Total clutch volume	Mean egg length	Mean egg breadth	Mean egg volume	Male age	Eggs hatched	Eggs laid
Female age	(123) -0.120^{ns}	(97) 0.199*	(102) 0.201*	(102) 0.157^{ns}	(102) 0.203*	(105) 0.541***	(128) 0.128^{ns}	(128) ns
Female weight	(120) ns	(96) 0.237*	(101) 0.246*	(101) 0.178^{ns}	(101) 0.246*	(103) ns	(125) ns	(125) ns
Female right wing	(120) ns	(95) 0.316**	(100) 0.335***	(100) 0.186^{ns}	(100) 0.279^{**}	(102) ns	(125) ns	(125) ns
Female tarsus	(120) ns	(95) 0.163^{ns}	(100) 0.157^{ns}	(100) ns	(100) ns	(102) ns	(125) ns	(125) ns
Bill to feathers	(119) ns	(95) 0.131^{ns}	(100) 0.116^{ns}	(100) 0.102^{ns}	(100) 0.127^{ns}	(102) ns	(124) 0.226*	(124) 0.178^{ns}

Table 2.6 Relationship between female age and measurements with date of clutch completion, egg biometrics and male age. Pearson's correlation coefficients (r). 1984 data

	Date clutch completion	Total clutch volume	Mean egg length	Mean egg breadth	Mean egg volume	Male age	Eggs hatched	Eggs laid
Female age	(143) -0.186*	(115) 0.222*	(115) 0.185*	(115) 0.218*	(117) 0.234*	(129) 0.511***	(143) 0.115^{ns}	(143) ns
Female weight	(138) -0.292**	(110) 0.190*	(110) 0.317***	(110) 0.116^{ns}	(112) 0.249**	(124) ns	(138) ns	(138) ns
Female right wing	(138) ns	(110) 0.241**	(110) 0.244**	(110) 0.164^{ns}	(112) 0.237*	(124) 0.185*	(138) ns	(138) ns
Female tarsus	(138) ns	(110) 0.132^{ns}	(110) 0.160^{ns}	(110) ns	(112) ns	(124) ns	(138) 0.107^{ns}	(138) 0.134^{ns}
Bill to feathers	(137) ns	(110) ns	(110) 0.249**	(110) ns	(112) ns	(123) ns	(137) ns	(137) ns

Table 2.7 Relationship between female age and measurements with date of clutch completion, egg biometrics and male age. Pearson's correlation coefficients (r). 1985 data

	Date clutch completion	Total clutch volume	Mean egg length	Mean egg breadth	Mean egg volume	Male age	Eggs hatched	Eggs laid
Female age	(101) ns	(50) 0.224^{ns}	(50) ns	(50) 0.440**	(50) 0.342*	(80) 0.599***	(111) 0.126^{ns}	ns
Female weight	(98) -0.111^{ns}	(48) ns	(48) 0.481^{***}	(48) ns	(48) 0.251^{ns}	(75) -0.324**	(106) ns	ns
Female right wing	(99) ns	(49) ns	(49) 0.187^{ns}	(49) 0.187^{ns}	(49) 0.215^{ns}	(76) 0.249*	(107) ns	ns
Female tarsus	(99) -0.289**	(49) ns	(49) 0.408**	(49) ns	(49) 0.177^{ns}	(76) -0.179^{ns}	(107) -0.121^{ns}	ns
Female bill to feather	(91) ns	(45) ns	(45) 0.373**	(45) ns	(45) 0.234^{ns}	(71) ns	(99) ns	ns

In all three years of this study, male age was found to be significantly and positively correlated with female age. Thus male and female Redshank tended to be mated with birds of similar age to their own. This relationship may be explained by the fact that surviving Redshank generally remain mate faithful and that the life expectancy of male and female Redshank is the same (Yates, unpub. thesis 1982). Most surviving Redshank that return therefore mate for life.

There was also a significant and positive relationship between female age and mean egg volume in all years. In 1983 and 1984, female wing length and weight also correlated positively with mean egg volume as well as with mean egg length. Thus, older, larger females tended to produce longer and larger (volume) eggs in 1983 and 1984. In all years, older females were found to produce eggs of greater volume.

Older birds are more experienced and are therefore probably better able to obtain the necessary food required at the pre-egg laying stage.

In 1983 and 1985, no relationship was found between date of clutch completion and female age. In 1984 there was a negative and significant correlation between female age and date of clutch completion. Thus, in 1984, older females tended to nest earlier than did younger birds. The data obtained in 1983 and 1985 have been affected by the tidal patterns which brought about the destruction of many nests in the early half of the season. Much relaying occurred as a result of these tides; many birds which had nested, but were uncaught prior to flooding, therefore appeared to be nesting for the first time. This was a confusing factor which clouded the true relationship which may have existed between female age and date of clutch completion. Additionally, in 1984, there was a significant negative correlation found between date of clutch completion and female weight. Thus, the early nesting females were heavier than the late nesting females.

Finally, these analysis tentatively suggest that a relationship may exist between female age and the number of eggs hatched. Such a relationship could exist if young birds were less attentive or less efficient incubators than older birds.

Table 2.8 Relationship between date of clutch completion, male age and egg measurements with each other. 1983 data. Pearson's correlation coefficients (r).

	Date c.c.	T.c.v.	M.e.l.	M.e.b.	M.e.v.	Male age	Eggs hatched	Eggs laid
Date of clutch completion								
Total clutch volume	(96) 0.264**							
Mean egg length (per clutch)	(101) 0.242*	(97) 0.589***						
Mean egg breadth	(101) 0.285**	(97) 0.685***	(102) 0.463***					
Mean egg volume	(101) 0.310**	(97) 0.748***	(102) 0.797***	(102) 0.903***				
Male age	(103) -0.154 ns	(84) ns	(88) ns	(88) ns	(88) ns			
Eggs hatched per nest	(123) -0.133 ns	(97) ns	(102) ns	(102) ns	(102) ns	(105) ns		
Eggs laid per nest	(123) ns	(97 0.767***	(102) ns	(102) 0.286**	(102) 0.235*	(105) ns	(128) 0.491***	

In 1983 male age shows a negative non significant correlation with date of clutch completion. Thus, although both older male and female Redshank tended to nest earlier in the season, the relationship was not a significant one.

The clutch volume and mean egg measurements correlated positively and significantly with the date of clutch completion. Therefore, as the season progressed the eggs being laid tended to increase in length, breadth and volume. This relationship is difficult to interpret. Possibly early breeders are able to do so because they have invested less in their clutches. In those birds which were flooded and then relaid, the birds may have benefitted by investing slightly more in their clutch second time round. The most probable explanation, however, is that the relationship has arisen as a result of large eggs being laid by the older birds which relaid following nest loss in the early part of the season.

Table 2.9 Relationship between date of clutch completion, male age and egg measurements with each other. 1984 data
Pearson's correlation coefficients (r)

	Date c.c.	T.c.v.	M.e.l.	M.e.b.	M.e.v.	Male age	Eggs hatched	Eggs laid
Date of clutch completion								
Total clutch volume	(115) ns							
Mean egg length (per clutch)	(115) ns	(115) 0.509***						
Mean egg breadth	(115)ns -0.156	(115) 0.728***	(115) 0.327***					
Mean egg volume	(117)ns -0.118	(115) 0.773***	(115) 0.742***	(115) 0.875***				
Male age	(129 -0.285**	(106) ns	(106) ns -0.115	(106) ns	(108) ns			
Eggs hatched per nest	(143)ns -0.141	(115) 0.262**	(115) ns	(115) 0.231*	(117) 0.194*	(129) ns		
Eggs laid per nest	(143) ns	(115) 0.710***	(115) ns	(115)ns 0.170	(117)ns 0.104	(129)ns 0.125	(143) 0.263**	

The 1984 results differ from the 1983 results in several important respects.

Firstly, male age shows a significant and negative correlation with date of clutch completion. Thus, in 1984, older males and females tended to nest earlier in the season.

Secondly, there is a weak negative relationship between clutch volume and mean egg measurements with the date of clutch completion. Thus, as the season progressed the eggs being laid tended to get smaller. This is almost certainly due to the fact that the majority of older birds laying larger eggs were caught early in the season and the majority of younger birds (laying smaller eggs) were caught later in the season. The relationship is further examined in Table 2.11.

Table 2.10 Relationship between date of clutch completion, male age and egg measurements with each other. 1985 data
Pearson's correlation coefficients (r).

	Date c.c.	T.c.v.	M.e.l.	M.e.b.	M.e.v.	Male age	Eggs hatched	Eggs laid
Date of clutch completion								
Total clutch volume	(59) ns							
Mean egg length per clutch	(59) ns	(63) 0.201 ns						
Mean egg breadth	(59) ns	(63) 0.415***	(63) 0.325**					
Mean egg volume	(59) ns	(63) 0.408***	(63) 0.721***	(63) 0.886***				
Male age	(95) ns	(36) ns	(36) ns	(36) 0.234 ns	(36) ns			
Eggs hatched per nest	(133) 0.510***	(63) 0.189 ns	(63) 0.181 ns	(63) ns	(63) 0.199 ns	(104) ns		
Eggs laid per nest	(133) ns	(63) 0.951***	(63) ns	(63) ns	(63) ns	(104) ns	(144) 0.190*	

In 1985 no relationship was found between male age and date of clutch completion (as was the case for female age and date of clutch completion). Therefore, older birds do not appear to have nested significantly earlier than younger birds.

Additionally, no relationship was found between date of clutch completion and egg and clutch size. This is almost certainly because male and in particular female age was not found to be related to clutch completion date. The very unusual laying pattern observed in the 1985 season is discussed at the end of this Chapter.

The relationship between egg measurements and date of clutch completion was further investigated, using the data set from 1984. In 1984 the laying pattern was not affected by inclement weather or the tidal cycle. The resultant egg laying pattern was considered to be the normal laying pattern under optimal conditions.

The analysis displayed in Table 2.11 was carried out on clutches where the specific egg laying order was known.

The effect of female age and date of clutch completion on egg size.

Table 2.11 The relationship between female age and date of clutch completion with egg biometrics. 1984 data
Pearson's correlation coefficients (r)

		Female age (1-3)	Date of clutch completion (days from 31 March)	(n)
Egg 1	Length	0.305**	-0.035^{ns}	78
	Breadth	0.361***	-0.154^{ns}	
	Volume	0.408***	-0.069^{ns}	
Egg 2	Length	0.321**	-0.067^{ns}	78
	Breadth	0.252*	-0.157^{ns}	
	Volume	0.338**	-0.149^{ns}	
Egg 3	Length	0.257*	-0.141^{ns}	78
	Breadth	0.339**	-0.209^{ns}	
	Volume	0.371***	-0.214^{ns}	
Egg 4	Length	0.157^{ns}	-0.072^{ns}	77
	Breadth	0.377***	-0.295**	
	Volume	0.331**	-0.223*	
	Date of clutch completion	-0.361**		78

Note: Females aged 3 years or more were designated as being 3 years old. It was hoped that this would highlight any age-related differences occuring in the first 3 years of life.

The results of the analysis highlight three points. Firstly, the correlation coefficient between female age and date of clutch completion has been increased by grouping birds of 3 years breeding experience or more together. Thus, older females breed earlier in the season than do younger birds.

Secondly, female age correlates positively and significantly with egg measurements. Therefore, older females lay larger eggs than do young birds.

Finally, the relationship between egg size and date of clutch completion is examined in more detail. As the date of clutch completion increases, eggs tend to decrease in size (length, breadth and volume). The correlation coefficients are not significant, except for the fourth egg. Therefore, as the season progresses, fourth eggs significantly decrease in size.

A series of stepwise multiple regression analyses was carried out using the S.P.S.S. package to determine the strength and direction of relationship between one dependent variable and a series of independent variables (Nie et al 1975).

Tables 2.12 and 2.13 examine the relationship between female weight and wing length with a series of female variables.

Table 2.14 examines non-climatic factors which have an effect on timing of laying. In this instance the independent variables were male and female age and female size. The analysis was carried out to determine which of these (if any) could be used as a predictor of an individuals timing of laying. I have excluded the effects of climate because I am particularly interested in timing of laying within a year (thus all birds present on the breeding area experienced the same weather conditions). If I were examining the timing of laying between years then climatic factors would have to be included.

Finally, a series of multiple regressions were conducted to determine what aspects of females age, size or timing of laying best predicted her egg and clutch size (total volume). These results are shown in Tables 2.15-2.18.

All results are discussed fully in the Discussion at the end of this chapter. As in Chapter 1 (Tables 1.39-1.43) F-values are printed with significance values attached. Beta values not included in the results had associated F-values which were not significant. All data are shown separately for each year of study.

Table 2.12 Beta values and F-ratios for the relationship between female weight with age and other female parameters measured.

(a) 1983

Dependent variable		Independent variables			
		Female age	wing	Tarsus	bill[1]
Female weight	Beta	-	-	0.356	-
	F	ns	ns	11.5**	ns

Significance values associated with F-ratios (d.f.1,79)
A total of 39% of the cumulative variance was explained

(b) 1984

Dependent variable		Independent variables			
		Female age	wing	Tarsus	bill[1]
Female weight	Beta	-	0.251	-	0.277
	F	ns	7.2**	ns	8.8***

Significance values associated with F-ratios (d.f. 2,98)
A total of 40% of the cumulative variance was explained

(c) 1985

Dependent variable		Independent variables			
		Female age	wing	Tarsus	bill[1]
Female weight	Beta	-	0.399	0.543	-
	F	ns	7.5**	13.9***	ns

Significance values associated with F-ratios (d.f. 2,23)
A total of 75% of the cumulative variance was explained
Note: bill[1] = bill tip to feathers length

The results shown in Tables 2.12 (a-c) are not consistent between years. In 1983 a females tarsus measurement was the best predictor of her weight. In 1984 wing length and bill tip to feathers length was the best predictor of her weight. In 1984 wing length and bill tip to feathers length was the best predictor of female weight. Finally, in the last year of study, the best predictor of female weight was found to be female wing and tarsus length.

Weight fluctuates in females both within and between days. The fluctuating nature of the dependent variable probably best explains why no clear predictive measurement was found to exist.

Table 2.13 Beta values and F-ratios for the relationship between female wing measurements and female age, and other female parameters measured.

(a) 1983

Dependent variable		Female age	weight	Tarsus	bill[1]
			Independent variables		
Female wing	Beta	0.284	-	-	0.250
	F	7.4**	ns	ns	5.7**

Significance values associated with F-ratios (d.f. 2,78)
A total of 42% of the cumulative variance was explained

(b) 1984

Dependent variable		Female age	weight	Tarsus	bill[1]
			Independent variables		
Female wing	Beta	0.270	0.290	-	-
	F	8.5***	9.8***	ns	ns

Significance values associated with F-ratios (d.f. 2,98)
A total of 40% of the cumulative variance was explained

(c) 1985

Dependent variable		Female age	weight	Tarsus	bill[1]
			Independent variables		
Female wing	Beta	0.544	-	-	-
	F	10.1**	ns	ns	ns

Significance values association with F-ratios (d.f. 1,24)
A total of 60% of the cumulative variance was explained

In all years (1983-85) female age was a good predictor of wing length. Thus wing length is in part dependent on female age. Therefore, as a female gets older her wing length increases. In

1984 Table (2.13b) female weight was also a good predictor of female wing length. Almost certainly this relationship has arisen because young birds have shorter wings due to the degree of feather abrasion experienced (see Discussion).

One could infer that age could perhaps be predicted from wing length. For obvious reasons this was not tested.

Multiple analysis to determine the dependency of date of clutch completion on male and female parameters.

Table 2.14 Beta values and F-ratios for the relationship between date of clutch completion with female age and size and male age

(a) 1983

Dependent variable		Female age	weight	wing	tarsus	bill	Male age
Date of clutch completion	Beta	-	-	-	-	-	-
	F	ns	ns	ns	ns	ns	ns

(b) 1984

Dependent variable		Female age	weight	wing	tarsus	bill	male age
Date of clutch completion	Beta	-	-0.191	-	0.193	-	-0.229
	F	ns	4.0*	ns	4.1*	ns	5.8*

Significance values associated with F-ratios (d.f. 3,97)
A total of 35% of the cumulative variance was explained

(c) 1985

Dependent variable		Female age	weight	wing	tarsus	bill	male age
Date of clutch completion	Beta	-	-	-	-	-	-
	F	ns	ns	ns	ns	ns	ns

The results of the regression analysis shown in Tables 2.14 (a-c) are very interesting.

In 1983 and 1985 no independent variables were significantly related to date of clutch completion. These results are as discovered in the Pearson's correlation analysis. I would suggest that the main reason for a lack of relationship between independent and dependent variables was the flooding of the study area which resulted in substantial nest losses. Nests lost were replaced, thus giving the impression that many birds completed their clutches much later in the season than actually was so (see Discussion).

In 1984, male age was the best predictor of a pairs date of clutch completion. The older the male the earlier the laying began. Interestingly, female age did not significantly relate to a pairs timing of breeding. Had female age been grouped (as in Table 2.11) then it is possible that this too would have related negatively to a pairs date of clutch completion. The 1984 data also indicated that heavier females laid earlier than lighter females.

Egg and clutch variables

Table 2.15 β values and F-ratios for the relationship between total clutch volume and female age, measurements and date of clutch completion.

(a) 1983

Dependent variable		Independent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion.
Total clutch volume	Beta	-	-	0.391	-	-	0.301
	F	ns	ns	15.6***	ns	ns	9.2***

Significance values associated with F-ratios (d.f. 2,78)
A total of 54% of the cumulative variance was explained

(b) 1984

Dependent variable		Indpendent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion
Total clutch volume	Beta	-	-	0.228	-	-	-
	F	ns	ns	5.4*	ns	ns	ns

Significance values associated with F-ratios (d.f. 1,99)
A total of 33% of the cumulative variance was explained

(c) 1985

Dependent variable		Independent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion
Total clutch volume	Beta	0.480	-	-	--	-	-
	F	7.2*	ns	ns	ns	ns	ns

Significance values associated with F-ratios (d.f. 1.24)
A total of 57% of the cumulative variance was explained

Note: In 1985 the number of eggs measured was very much smaller than in the first two years. Of those eggs that were measured, the majority were from the first half of the season.

The results shown in Table 2.15 (a-c) are inconsistent between years. In 1983 female wing length and date of clutch completion were the best predictors of a females final total clutch volume. In 1984 female wing length was the best predictor of clutch volume. In 1985 fewer clutches were measured. In this year female age was found to be the best predictor of total clutch volume. Thus, older females produced clutches of largest total volume.

Table 2.16 β values and F-ratios for the relationship between mean egg length and female age, measurements and date of clutch completion.

(a) 1983

Dependent variable		Indpendent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg length	Beta	0.167	0.248	0.307	-	-	0.267
	F	2.7*	6.3***	8.9***	ns	ns	7.6***

Significance values associated with F-ratios (d.f. 4,76)
A total of 56% of the cumulative variance was explained

(b) 1984

Dependent variable		Independent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg length	Beta	-	0.320	-	-	-	-
	F	ns	11.3**	ns	ns	ns	ns

Significance values associated with F-ratios (d.f. 1,99)
A total of 41% of the cumulative variance was explained

(c) 1985

Dependent variable		Independent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg length	Beta	0.419	-	-	-	0.462	-
	F	7.4**	ns	ns	ns	9.1**	ns

Significance values associated with F-ratios (d.f. 2.23)
A total of 77% of the cumulative variance was explained.

Table 2.16 (a-c) examines the dependance of mean egg length on female age, size and date of clutch completion. In 1983 mean egg length was dependent on female wing length, date of clutch completion, female weight and female age. Thus older heavier long winged females laying later in the season produced eggs of largest mean egg length.

In 1984 heavier females produced eggs of larger mean egg length.

In 1985 mean egg length was dependent on bill length and female age.

Table 2.17 β values and F-ratios for the relationship between mean egg breadth and female age, measurements and date of clutch completion.

(a) 1983

Dependent variable		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg breadth	Beta	-	0.177	0.236	-	-	0.340
	F	ns	2.9*	5.2**	ns	ns	11.0***

Significance values associated with F-ratios (d.f. 3,77)
A total of 47% of the cumulative variance was explained

(b) 1984

Dependent variable		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg breadth	Beta	0.236	-	-	-	-	-
	F	5.8*	ns	ns	ns	ns	ns

Significance values associated with F-ratios (d.f. 1,99)
A total of 33% of the cumulative variance was explained

(c) 1985

Dependent variable		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg breadth	Beta	0.459	-	-	-	-	-
	F	6.4*	ns	ns	ns	ns	ns

Significance values associated with F-ratios (d.f. 1,24)
A total of 50% of the cumulative variance was explained.

In 1983 (Table 2.17a) mean egg breadth was found to be dependent on date of clutch completion, female wing length and female weight. Thus the eggs of greatest mean breadth were produced by long winged heavy females which completed their clutches later in the year.

In 1984 and 1985 the oldest females produced eggs of largest mean egg breadth. In both these years no other independent variables were found to be related to mean egg breadth.

Table 2.18 β. values and F-ratios for the relationship between mean egg volume and female age, measurements and date of clutch completion.

(a) 1983

Dependent variable		Independent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg volume	Beta	0.173	0.254	0.269	-	-	0.360
	F	3.1*	7.0***	7.1***	ns	ns	14.4***

Significance values associated with F-ratios (d.f. 4,76)
A total of 57% of the cumulative variance was explained.

(b) 1984

Dependent variable		Independent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg volume	Beta	0.249	0.211	-	-	-	-
	F	6.8**	4.9**	ns	ns	ns	ns

Significance values associated with F-ratios (d.f. 2,98)
A total of33% of the cumulative variance was explained.

(c) 1985

Dependent variable		Independent variables					
		Female age	weight	wing	tarsus	bill	date of clutch completion
Mean egg volume	Beta	0.441	-	-	-	0.337	-
	F	6.7**	ns	ns	ns	3.9*	ns

Signifiance values associated with F-ratios (d.f. 2,23)
A total of 64% of the cumulative variance was explained.

Results tabulated in 2.18 (a-c) examine the relationship between mean egg volume and female age, size and date of clutch completion.

In 1983 the oldest, heaviest, long winged females, which laid later in the season, produced eggs of the largest mean egg volume.

In 1984 the oldest, heaviest females produced the eggs of greatest volume.

Finally, in 1985, the oldest females with the longest bill produced the eggs of largest mean volume. Thus in all years the eggs of greatest mean volume were produced by the older birds. These results are as outlined in the bivariate regression analysis.

DISCUSSION

The data exhibited in Figures 5, 6 and 7 outline the temporal distribution of nesting times of experienced and inexperienced birds (controls and unrings). Firstly, there is a bimodal frequency of the number of birds caught over the whole season. Secondly, in each year the number of control birds outnumber 'unrings' and ringed first year birds. Finally, the effects of the tides, described in Chapter 1 and in the results section of this Chapter, show how laying time is related to tidal cycle.

In 1984 tidal flooding was minimal (peak tide 9.6 m on 15 May) and the timing of laying for all birds was unaffected by flooding. As a result of this and because flooding greatly altered the timing of breeding (many nests were wholly or at least partially destroyed), the data from 1983 and 1985 are considered to be less useful. Clearly in 1983 and 1985 the temporal breeding distribution, and consequently timing of breeding of birds of different age groups, has been affected by the loss of nests.

Before discussing the results in detail, I should like to make one important point. Over the three years the number of controls caught from nests of known date of clutch completion ranged from 145-154 birds. The number of 'unrings' caught from nests of known date of clutch completion was 90, 113 and 50 birds in years 1983, 1984 and 1985 respectively. Clearly, whilst the number of controls caught remained constant, the number of 'unrings' caught dropped dramatically in 1985. Table 1.17 (Chapter 1) indicates that the total number of birds caught, and nests found, were also well down in 1985. Thus in 1985 recruitment was down, reflected in the lower number of birds caught and fewer nests later in the year. The reasons for this drop in recruitment and lack of nests in the latter part of the season can only be guessed at. Winter weather conditions were the worst for many years. In particular, at its worst, many south of England coastal sites were frozen, as were beaches in S.W. England and even parts of the coast of France. As a result of this, many feeding grounds were frozen and no longer suitable for Redshank.

Mortality for this period was very high (Davidson & Clark 1985). It is well documented that young Redshank move further south to overwinter than do older birds (Hale 1973; Cramp & Simmons 1983). In those areas which are normally favoured, feeding grounds were almost completely unsuitable. I would therefore suggest that it is likely that young Redshank and less experienced birds would have suffered greater mortality during this period than more experienced birds. In addition to this, it is probable that raptors such as the Peregrine _Falco peregrinus_ would have a greatly increased energy requirement due to the very cold conditions. Under such conditions raptors could cause very high mortality to wintering waders (Whitfield 1985).

The drop in the number of unringed birds found nesting on the marsh can therefore at least partially be explained in terms of an increase in winter mortality brought about by a very cold spell of weather. The more experienced birds would be less affected as they ought to be more able to compete for limited feeding sites. It is known that some Redshank do defend feeding territories overwinter, but whether these are very experienced birds is not actually known (Goss-Custard 1977; Goss-Custard _et al_ 1984).

Another possibility is that some birds have chosen not to breed in 1985. There is absolutely no evidence to support this, but it is known that some waders, such as Dunlin, Knot _Calidris canutus_ and Black-tailed Godwits _Limosa limosa_ do not breed in every year (Prater 1981). These may be young, old or sick birds.

In 1983 and 1984 older experienced Redshank were more likely to begin nesting earlier than inexperienced birds. Experienced birds generally arrive back on the breeding grounds first and mate first. Young birds tend to arrive on the breeding ground later in the season and have to seek out a mate. In the case of older birds which remain faithful, presumably breeding can begin slightly earlier as both birds have experience of each other and of their breeding ground. For similar findings in other species see Ashkenazie & Safriel 1979b; Gratto et al 1985; Hilden & Vuolanto 1972; Maxson & Oring 1980; Miller 1979b,1983a; Oring & Lank 1982; Oring et al 1983; Reynolds 1984; Soikkeli 1967 and Thompson et al 1986.

In 1985 there was no apparent association between bird age and timing of laying. Many birds appeared to delay breeding until the latter half of the season. This may have been as a result of the slow growth rate of vegetation which is necessary to conceal nests.

Before discussing Tabulated results in detail, I should like to make clear the situation concerning 'unrings'. In 1983, 1984 and 1985 the percentage of 'unrings' caught that were first years were 21% (a slight underestimate), 27% and 40%. The remainder of these birds were greater than 1-year old. The majority of 'unrings' not aged as first-years may be birds breeding for the first time as second years. Obviously some 'unrings' could simply have been missed from previous years, but calculations based on the chick returning data suggest a proportion of birds bred for the first time as two-year olds. Indeed, Grosskopf (1970) suggested that most start breeding at two years of age.

The results in Tables 2.4 (a, b, c) highlight several points. Female wing length correlates with female age; thus as a female gets older the wing length gets longer. This probably only applies to the first two or three years of life. Young birds have heavily abraded primaries and secondaries as well as abraded coverts and scapulars. The abrasion is so extensive that wings are measurably shorter just prior to a moult. Juvenile Redshank do not moult their primaries until the following autumn when they are just over 1 year old. Adult Redshank moult primaries in the autumn. Thus, in the spring, a first year Redshank's primaries are older than an adult Redshank's primaries and thus are more heavily abraded, making the wings shorter.

The variable nature of weight as a measured parameter is well known. In particular, weight has been found to fluctuate widely throughout the incubation period (see Mercer 1966; Kålås & Byrkjedal 1984). The exact cause of this variability is unknown. One possibility is that weight is directly related to amount eaten and, more importantly, to the time when food was last taken. If a bird was caught 1 hour or 4 hours after feeding then the weight would vary accordingly. Equally, the time taken to return to the nest could be important, especially if birds feed prior to return. Finally, climatic conditions which affect availability of food could presumably affect the actual daily weight of an individual. Weight does fluctuate and as a consequence the use of weight as an indicator of size and age is only of limited use. Bill, tarsus, and to some extent wing length, remain relatively constant throughout the season. Wings do show some degree of shortening as the season progresses, due to feather wear.

Tables 2.5, 2.6 and 2.7 present the results from a series of correlation analysis. The first and a most important point is there was a highly significant relationship between male and female age. Thus male and female tend to mate with birds of similar age. Similar results of age association have been found in Dunlin (Soikkeli 1967); Redshank (Grosskopf 1970; Yates, unpubl. thesis 1982) and Kittiwake (Coulson 1966).

The relationship between date of clutch completion and male and female age are at first somewhat confusing. A much closer look reveals that the trend observed in Figures 5,6 & 7 are in fact endorsed. In 1983 both male and female age show a negative but non-significant relationship with date of clutch completion. Thus, older birds tended to nest earlier but this was not significant. Many older birds did not nest until later in the season. These may have been birds that waited until suitable habitat was available. In other cases, older birds may have nested but lost their nests. The problem is that many of the birds that re-laid were not found nesting first time round and, as a result, the date of first clutch completion was recorded later than should have been. Therefore, older birds, possibly nesting early in the season, were recorded as laying later in the season for the first time.

In 1985 the main problem was the fact that a large number of birds were recorded as laying for the first time later in the season. The first wave of laying was very small, the general impression being that many birds delayed breeding until later in the season. Some flooding did occur and a large majority of the first nests were lost, but the main point here is that many of the older birds apparently delayed breeding. In the early part of the season the vegetation was short and nests were very easy to find; it was felt that very few nests were missed and that the overall drop in the number of nests found was very real. The reasons for the possible drop in breeding numbers and delay in breeding have already been mentioned (namely adverse winter conditions resulting in increased winter mortality of birds and slow rate of vegetation growth). Certainly there is no doubt that Redshank mortality was greatly increased over the winter of 1984-85 (Davidson & Clark 1985). The effect of winter conditions in a bird's breeding condition is more difficult to determine without detailed physiological examination.

The 1984 results were least affected by tidal rhythm and as such represent a realistic pattern of laying times of birds of different age groups. In 1984 the significant negative correlations between male and female age with date of clutch completion are truly representative, and because of this the data set was further used to examine the relationship between egg size and female age and egg size anddate of clutch completion (see later).

The major points of interest are that there is a significant negative correlation between female weight and date of clutch completion in 1984. Thus heavier females nested earlier in the season. Interestingly, in 1984 female age did not correlate with female weight; this result therefore suggests that early nesting birds were in better condition.

In all years older more experienced birds produced significantly larger eggs. Thus, in 1984, older birds tended to nest earlier, producing larger eggs than young birds which nested later in the season. Presumably experienced birds arrived back first, knew the best feeding areas, were more attractive to a mate, and as a result were able to find a mate and prepare for egg laying quicker than inexperienced birds.

The relationship between female age and female size with egg measurements is a very interesting one and has been discovered in several other studies: Byrkjedal & Kålås 1985; Coulson & White 1958; Coulson 1963; Coulson & Horobin 1976; Crawford 1980; Kendeigh 1956: Miller 1979a; Mills 1979; Moss & Watson 1982; Preston 1958: Rahn et al 1975; Ross 1979; Thomas 1983; and Vaisanen et al 1972. Only Yates (unpubl. thesis 1982) has recently examined for the possibility of such a relationship in a sandpiper. More recently Byrkjedal & Kålås (1985) have found such a relationship in the Dotterel *Charadrius morinellus* and

Golden Plover Pluvialis apricaria. In the Greenshank, a negative correlation was found between female age and egg weight. Older females were laying early but producing lighter eggs than yonger birds laying later (Thompson et al 1986). I have found no statistical evidence of age or adult size having an effect on hatch success. For relationship between female size and egg size at species level see Appendix 6. It is possible that such a relationship may exist, especially if unringed birds were compared against birds of all ages. So far the only wader study to show that younger birds are less successful is that carried out on Semipalmated Sandpipers (Gratto, Cooke & Morrison 1983) (but see this study, Chapter 3).

The final correlation analysis to be carried out (Tables 2.8, 2.9 and 2.10) highlights some very interesting points. The apparent differences which at first appear confusing are readily understandable and do fit an expected trend. In 1983 there were significant positive correlations between date of clutch completion and egg size. Thus, as the season progressed, the eggs got larger. This may be explained by the fact that some older birds delayed breeding until later in the season whilst other birds had to relay as a result of flooding. Most of those re-laying had not been caught in the first wave; as a consequence the impression gained was one of old birds laying larger eggs later in the season. Thus the relationship between date of clutch completion and egg size arose.

The data set from 1984 was much better due to the lack of tidal flooding. Older birds nested early and young birds later. Older birds produced larger eggs and younger birds laid smaller eggs. A negative relationship was therefore expected between date of clutch completion and egg size. The relationship was found to be negative but not significant. Further analysis of the data set confirmed both the direction and significance of this relationship (see Table 2.11). The analysis showed a greatly increased significant positive correlation between female age and egg size and female age and date of clutch completion. The relationship was now broken down for first, second, third and fourth eggs. In all cases egg volume showed a negative correlation with date of clutch completion. Thus as the season progressed, smaller eggs were being laid. The relationship was significant only for the fourth egg which in particular is significantly smaller later in the season.

My overall assessment is as follows: old birds nest early, laying large eggs; young birds nest later, laying small eggs; the young birds invest less in the fourth egg as the season progresses. Reasons for investing more or less in the fourth egg are reviewed by Miller (1979a) for shorebirds; and for investing less in the last egg of Herring Gull by Davis (1975) and Parsons (1970, 1975).

Multiple Regression Discussion

The Multiple Regression analyses were carried out in order to determine the strength, direction and degree of relationship between a series of independent variables and a dependent variable. Due to the very nature of weight as a parameter (p112 this Chapter), it is not surprising that the results of the Multiple correlation analysis (Table 2.12) are not consistent.

When female wing is the dependent variable we see that in all three years the best predictor of wing length is age; and in 1984 age and weight. In 1984, 40% of wing length variation can be accounted for by female age and weight. Other variations may be genetic, but the possibility does exist that had age been grouped then more of the variation may have been accounted for.

In the next series of multiple regressions, date of clutch completion (dependent variable) was best predicted by male age (Negative relationship) and female tarsus and weight (Negative relationship). In this case only 35% of the cumulative variance was explained. Other factors, such as female age were obviously not as important, but had female age been grouped from one year to three years then this may not have been so. Once again acertain degree of variation in laying time may be due to genetic make up.

Over the years many wader studies have attempted to find out what determines the timing of laying in different species. Those factors which determine start of laying at the beginning of each season may be different from those factors operating within seasons. I have been mainly concerned with Redshank laying times within seasons.

In those studies examining timing of laying, a number of different proximate and ultimate factors have been described which have an effect on the timing of laying. In many waders, timing of laying is determined by the age of the birds involved; this is the case in Semipalmated Sandpiper (Ashkenazie & Safriel 1979 a); the Least Sandpiper (Miller 1983a); the Dunlin (Soikkeli 1967); Stilt sandpiper _Micropalma himantopus_ (Jehl 1973); Greenshank Nethersole-Thompson & Nethersole-Thompson 1979, Thompson _et al_ 1986); and Red-necked Phalarope _Phalaropus lobatus_ (Hildén & Vuolanto 1972). Other studies have indicated that food supply may be linked to timing of laying: Galbraith 1985; Harris 1967; Heppleston 1972; Hilden 1978; Hilden & Vuolanto 1972; Hogstedt 1974; Holland _et al_ 1982 and Oring _et al_ 1983. However, in many of these cases environmental conditions are stressed as being the major determinant to dictating timing of laying. Several studies, notably Byrkjedal (1980), Green et al (1977), Holmes (1972), Nethersole-Thompson (1973), Nethersole-Thompson & Nethersole-Thompson (1979), Nettleship (1973), Parmelee (1970), Pienkowski (1984b) have indicated that timing of snowmelt and thus environmental temperature may be very important in determining timing of laying. Finally a number of studies have indicated that the timing of laying is such that eggs hatch when food is most available for their young (Hildén 1978; Holmes 1972; Nettleship 1973, 1974; Soikkeli 1967). For a full review of factors affecting timing of laying see Appendix 7.

Clearly a number of different variables from day length to individual quality are involved in determining timing of laying. Within a season the majority of birds present are exposed to the same conditions. Their resultant timing of breeding must therefore arise as a result of difference in quality, possibly relating to experience of feeding and nesting areas, attractiveness to a mate, or genetic factors.

The final series of multiple regression analyses (Tables 2.15, 2.16, 217 and 2.18) are concerned with discovering the best predictor of a female's egg size. In 1983, mean egg volume was dependant on date of clutch completion, female wing, female weight and female age. In total 57% of the cumulative variance was explained. The reasons for the above have been discussed already, namely older birds laying large eggs were forced to lay later in the season, suggesting large eggs were laid later in the season. The relationship between egg volume and female size and age has also been established.

In 1984 both female age and weight are the best predictors of mean egg volume. These are positive correlations, so large (heavy) older females produce larger eggs. In Greenshanks, older females lay earliest but invest less in their clutch (eggs are lighter than birds laying later). It would seem that the benefit of early laying outweigh the possible disadvantage of producing smaller eggs (Thompson et al 1986).

In 1985 female age again proved to be the best predictor of egg volume. The only female size parameter which was a good predictor of egg volume was female bill length. In every year female age did at least partly determine egg volume. Female weight was also important to some extent.

These results highlight the problems that can arise when comparing results gathered over several field seasons. Each year is very different and to attempt to combine data would be wrong and perhaps erroneous. I have outlined the main trends and attempted to interpret them in the light of other findings, but accept that there may be shortfalls.

My overall aim was to relate age (male and female) and female size to date of clutch completion and egg size. The only season this could be done properly was 1984 when there was no serious tidal flooding. In 1983 and 1985 flooding destroyed the majority of nests from the early part of the season; as a consequence the breeding pattern was affected. Although flooding could be considered to be a 'natural' part of the breeding cycle of Redshank, it played no part in the thinking of this study as it completely 'fogged' any relationships which may have existed.

Students of wader research, and indeed other groups of birds, must therefore try to ensure that the patterns observed are a true reflection of what is actually taking place and is not an artefact of some natural disaster which has occurred in the population.

Chapter 3

Breeding site tenacity and natal philopatry

Introduction

This Chapter outlines the degree of breeding site fidelity, breeding dispersal, natal philopatry and natal dispersal exhibited in Redshank. If we are to understand wader populations and possible effects of reclamation and afforestation on these populations we must have a full understanding of fidelity and dispersal, particularly in adults.

In a review, which discussed breeding site fidelity and natal philopatry, Oring & Lank (1984) addressed the problem in an organised manner. In particular the following definitions were advanced.

Breeding area fidelity This refers to breeding of adult birds in the same location in successive years. I have termed this breeding site tenacity.

Breeding dispersal The dispersal of breeding adults between breeding efforts. I have used this term to cover both inter and intra-year breeding site movements.

Natal philopatry This refers to the return and breeding of young birds in the same area of their birth

Natal dispersal The dispersal of young birds prior to first breeding. In this instance I concentrate on the actual distance moved between birth site and first nest site.

Many ornithologists have attempted to calculate breeding site tenacity and breeding dispersal. In particular, researchers have calculated that sex differences exist both in site tenacity and in dispersal distances. The overall long term aim has been to relate dispersal and fidelity to mating systems. Some waders may be considered to exhibit low breeding site fidelity, some moderate, and others high breeding site fidelity. Most workers have concentrated on actual fidelity rather than breeding site dispersal. An example of a species exhibiting low breeding site fidelity is the Dotterel (Nethersole-Thompson 1973; Kålås & Byrkjedal 1984).

The majority of waders so far studied exhibit a moderate degree of breeding site fidelity. Ringed Plover Charadrius hiaticula exhibit moderate site fidelity with no sex differences found (Pienkowski 1984a). Mountain Plover C. montanus, Lapwing, Stilt Sandpiper, Common Sandpiper and Red-necked Phalarope also exhibit moderate site fidelity (Graul 1975; Galbraith 1986; Jehl 1973; Holland et al 1982 and Hilden & Vuolanto 1972).

Some species with high breeding site fidelity show definite sex differences in breeding site fidelity. In Oystercatcher the male exhibits a greater degree of site fidelity, as do Temminck's Stint Calidris temminckii, Least Sandpiper and Dunlin (Harris 1967; Hildén 1979; Miller 1983a; Soikkeli 1967).

A number of birds exhibit a high level of breeding site fidelity but so far specific sex differences have not been elucidated; for example Golden Plover, Semipalmated Sandpiper, Western Sandpiper, Greenshank, Spotted Sandpiper and Turnstone Arenaria interpres. For a full review, including references, see Appendix 7.

Some waders, notably Greenshank, Golden Plover, Common Sandpiper and Dunlin, have a tendency to use the same nest scrape in consecutive years. Clearly in these cases the calculation of breeding dispersal is easy. No Redshank was found nesting in the same scrape in consecutive years on the Ribble. This is almost certainly due to the nature of the saltmarsh habitat rather than to a lesser degree of site fidelity.

The ringing of individual birds is essential to obtain an accurate estimate of breeding site tenacity and dispersal. It was also an essential element of this study that both birds at any given nest were captured. Where this was achieved it allowed for the examination of affects of mate faithfulness and mate change on breeding site dispersal to be determined.

Analysis of data gathered allowed for the effects of previous years nest success on the following years breeding dispersal to be examined. This aspect is particularly relevant to our understanding of how populations may react when stressed due to a bad run of nesting years. Many areas of saltmarsh, wet meadowland, rough pastureland, fringe moor/pastureland and blanket bog are now increasingly under threat from reclamation, drainage and improvement. In the case of the moorlands, so much re-afforestation is now taking place that it is difficult to predict what the effects of such schemes may be. Undoubtedly some species are now undergoing a general decline. In particular Redshank, Lapwing and Golden Plover appear to be badly affected by changes in land use (Sharrock 1976). Almost certainly Greenshank, Dunlin and perhaps Common Sandpiper will also decline as the effects of large scale blanket afforestation take their toll (N.C.C. publ. 1986; Tompkins 1986). Apart from merely declining, many populations of birds may be compressed into smaller areas of less suitable quality. Such compression could have very interesting effects on a given population and may well lead to density dependent factors having an effect which perhaps previously did not do so.

Ideally we require much more basic information on density, population fluctuations, nest and fledging success, and the contribution of different aged birds to the success of the population. Without such base level information it would be very difficult to assess if a population was remaining stable or was declining.

The last 10 years have seen an upsurge in the study of breeding biology of waders. In particular, some ornithologists are now examining breeding populations in habitats of varying quality (Fuller 1982; Galbraith 1986; Galbraith et al 1984; Stroud & Reed 1986). Undoubtedly these are exciting times for the student of wader biology. Much of the habitat change offers exciting possibilities for the closer examination of populations, the role of the individual, and density-dependent factors which may possibly radically affect breeding success and therefore the balance and distribution of any given population. It is however very sad to see the demise of so many marginal areas which add so much to the diversity and quality of our lives.

In a very general sense, Redshank and saltmarsh could be considered as under threat. Although still relatively abundant in coastal areas, Redshank have declined greatly inland, almost certainly due to land drainage and improvement (Sharrock 1976). It is therefore important that we have the information required to provide future researchers with quantified data which may be used as a baseline for further studies. These may then be compared with data gathered from other populations and may be useful as early warning predictions of possible population decline. A knowledge of breeding site tenacity and breeding dispersal is essential if we are to compare stable unthreatened populations with those that are declining or are being forced into less suitable habitats.

On a more local scale, an attempt has been made in this study to determine (a) the level of recruitment taking place and (b) to determine where the recruitment is coming from. On the Ribble Marshes the study sanctuary zone is only a fraction (c 25%) of the entire Reserve. The remainder of the Reserve is grazed intensively by cattle from April to September. Grazing is known to affect breeding success of Redshank quite drastically (Yates unpub. thesis 1982).

The study of natal philopatry and natal dispersal allowed at least some thoughts to be formed on the problem of population decline. In these times of increasing threat to marginal land such as saltmarshes, how big should a protected area be in order that populations within will remain unaffected by habitat loss outwith a given site? To answer such a broad question, hard facts are required on breeding site fidelity, dispersal and natal philopatry and natal dispersal.

Results

Breeding site tenacity

The return of male and female Redshank to their breeding grounds was calculated over the three year period of study.

Table 3.1 Breeding site fidelity of male and female Redshank.

Years	Males returned	%	Females returned	%	Overall return	%
1983-84	55/125	44%	46/125	37%	101/250	40.4%
1984-85	55/137	40%	46/140	33%	101/277	36.5%

The 1983-84 data may be further enhanced. In 1985, 27 Redshank were captured which had last been caught in 1983. These individuals were therefore alive and almost certainly present on the study site in 1984.

Year	Male returned	%	Female returned	%	Overall return	%
1983-84	71/125	57%	51/125	46%	128/250	51.2%

The above data are fully discussed later, but the general tendency appears to be for males to be either more site faithful or more long lived.

The data were further examined to test if the difference in return rates between males and females were significant.

Table 3.2 A Chi-square analysis to test for the significance of sex differences in recapture frequency.

Years 1983-84		Recaptured	Not recaptured
Redshank captured in 1983		84	84
	Male	55	70
	Female	46	79

$X^2_{(1)} = 1.063$ ns.

Years 1984-85		Recaptured	Not recaptured
Redshank captured in 1984		85	85
	Male	55	82
	Female	46	94*

* 1 bird recaptured on a neighbouring marsh

$X^2_{(1)} = 1.29$ n.s.

Therefore, there is no observable difference in frequency of return of males and females.

On determining that there were no sex related differences, a series of Chi-square analysis were carried out to test for age-related differences in frequency of return.

Table 3.3 A Chi-square analysis to determine the significance of recapture frequency of birds caught as 1 year olds and birds caught which were more than 1 year old.

		Recaptured 84	Not recaptured 84
Redshank captured in 1983	Age 1 yr	4	19
	Age >1 yr	97	130

$$X^2_{(1)} = 4.57 p < 0.05$$

Therefore in this case age at capture is related to the chance of recapture in the following year. Thus a first year Redshank is less likely to be recaptured the following year than an older bird (see Discussion and later for possible effect of age on breeding dispersal).

		Recaptured 85	Not recaptured 85
Redshank captured in 1984	Age 1 yr	9	28
	Age >1 yr	92	148*

* 1 bird recaptured on a neighbouring marsh

$$X^2_{(1)} = 2.14, \text{ n.s.}$$

This result is tending towards but is not quite significant. The non-significant result suggests that there may be annual fluctuations in differential return frequencies (see Discussion).

Table 3.4 A Chi-square analysis to test for differences in return frequency between first year Redshank caught for the first time and older unringed birds caught for the first time.

		Recaptured	Not recaptured
		84	84
Unringed Redshank captured in 1983	Age 1 yr	3	17
	Age >1 yr	18	56

$X^2_{(1)} = 1.42$, n.s.

		Recaptured	Not recaptured
		85	85
Unringed Redshank captured in 1984	Age 1 yr	8	24
	Age >1 yr	24	61*

* 1 bird recaptured on a neighbouring marsh

$X^2_{(1)} = 0.34$, n.s.

In both Tables there is no observable difference in return rates of unringed Redshank ringed as one or greater than one year old. This result suggests that a Redshank unringed on capture is just as likely to return if it was ringed as a one year old or was older.

Table 3.5 A Chi-square analysis to test for the differences in return frequency between controls (caught in previous years) and unrings (never caught before)

		Recaptured	Not recaptured
		84	84
Birds captured in 1983	Status Control	80	76
	Status Unrings	21	73

$X^2_{(1)} = 19.22$ $p < 0.001$

		Recaptured	Not recaptured
		85	85
Birds captured in 1984	Status Control	69	91
	Status Unrings	32	85*

* 1 bird recaptured on a neighbouring marsh

$X^2_{(1)} = 6.59$, $p < 0.05$

A bird which has been caught in previous years is more likely to be recaptured than a Redshank captured breeding for the first time. This has important implications in that it may suggest that older birds are more site faithful than younger birds which have only bred once before (see Discussion).

Table 3.6 Breeding site fidelity in Redshank and relationship with local breeding experience and breeding success in the previous year (1983-1985).

		% females returning to breed	
Years breeding experience	All birds	Successful breeders	Unsuccessful breeders
1	25 (30)	31 (22)	17 (8)
2	35 (9)	39 (7)	25 (2)
3	39 (11)	45 (9)	25 (2)
≥ 4	46 (42)	44 (32)	53 (10)

Note: Number in brackets denotes actual number returning

As Redshank get older they are more likely to return to their previous breeding grounds ($r_s = 1{\cdot}0$, $p < 0{\cdot}05$ $n = 4$). Therefore, an individuals age does at least partly determine whether it will return to breed in future years.

Breeding success also has a significant effect on breeding site tenacity. A chi-square analysis indicated that the percentage of successful birds returning differed significantly from the percentage of unsuccessful birds which returned. Birds which are successful appear more likely to return and breed in following years ($X^2_{(3)} = 8.41$, $p < 0.05$).

Table 3.7 The breeding success of female Redshank of different experience captured in 1983, 1984

	Age (Previous years breeding experience)			
	1	2	3	≥ 4
Total successful*	72	18	20	72
Total failed	48	8	8	19
% successful	60	69.2	71.4	79.1

* Hatched at least one egg

As a female Redshank gets older she is more likely to hatch at least one of her eggs than is a younger less experienced individual ($r_s = 1\cdot0, P < 0.05\ n = 4$). A bird's experience therefore appears to be a good indicator of its breeding potential.

Adult experience has not been related to chick rearing potential as too little data have been gathered. This relationship, though not studied, may be more meaningful than the relationship examined above.

Breeding site dispersal

Breeding Redshank have been monitored moving from one nest site to the next, both between and within seasons. On one occasion a female is thought have had three nests in one year (this bird was caught at two nests and suspected of having a third). This was strongly suspected due to (a) timing between nests; (b) position of nests; and (c) egg colouration. More usually, when a nest is lost the birds replace the nest or brood only once.

A total of 31 pairs which were monitored produced a second clutch. In the event of losing a nest four possibilities arise: (1) the birds leave the breeding grounds; (2) pair tries again; and (3) pair splits up and (a) male tries to nest again with a new mate or (b) female tries to nest again with a new mate.

Success of this fieldwork depended on catching both birds at first and repeat nests. For the above 31 nests two adults were caught at every nest and therefore one could realiably say that (a) pair remained faithful or (b) pair split up.

At a further 33 nests both birds were not caught and therefore the data could not be reliably used. Obviously, in some cases, the pair would have remained faithful but some would also almost certainly have split up.

Table 3.8 Intra seasonal breeding site dispersal of Redshank (1983-1985).

	Faithful pairs	Male with new mate	Female with new mate
(n)	18	8	5
Mean distance moved (m)	71.3	98.1	723
Median	54	98	578
S.E. Mean	19.9	26.3	225
Max. dist. moved (m)	400	246	1580
Min. dist. moved (m)	20	19	279

Because of the small sample size and non-normal data distribution, the above data have been analysed using non-parametric statistical tests.

Analyses were conducted using the Minitab statistical package (Ryan, Joiner & Ryan 1976). Results from Table 3.8 were compared using a Mann-Whitney test which compares the median of two samples. The test statistic (w) reflects the relative locations of the two samples. Where 'W' is larger than the sum of $n_1(n_1+n_2+1)/2$ we may suspect that the first sample has a significantly larger median. Were 'W' is smaller, we suspect that the first sample may have a significantly smaller median. In the analysis which follows W is printed along with a probability value. The probability value indicates the chance of predicting sample medians as being different when in fact they are the same. For further details see Ryan, Joiner & Ryan (1976).

Table 3.9 A Mann-Whitney two sample statistical analysis to determine the degree of difference in breeding dispersal distances between faithful pairs, males with new mate and females with new mate.

Variables compared	W	Mean W $(n_1(n_1+n_2+1)/2)$	Probability
Faithful pairs/male with new mate	223	243	0.28 n.s.
Faithful pairs/ female with new mate	172	216	$p < 0.001$
Male with new mate/ female with new mate	36	56	$p < 0.01$

Note: n_1 = number of samples in Variable 1
n_2 = number of samples in Variable 2

Thus from the above analysis the following conclusions may be made.

(a) If a pair remains faithful then in all probability they will not move very far from their previous nest site.

(b) If the pair divorce the female may be expected to move further from her previous nest site than does the male. Thus the female moves away in search of a new mate whilst the male remains in his old nesting site, presumably waiting for an unmated female to appear. Presumably males begin to sing intensively at this period in order to obtain a mate as quickly as possible.

Breeding dispersal of probable pairs

In these cases, a single bird only was caught at either the first or second nests. It was therefore impossible to establish if the pair remained the same at first and repeat nest.

Table 3.10 Intra seasonal breeding dispersal exhibited by birds of known sex, but unknown pair state (1983-1985).

	Male	Female
(n)	13	20
Mean distance moved (m)	62.4	110.9
Median	40	38
S.E. Mean	15.7	39
Max. dist. moved (m)	214	548
Min. dist. moved (m)	13	8

These results reflect trends outlined in Table 3.8. The males generally move a shorter distance from their previous nest site than do females. The size of the mean distances moved would suggest that most were in fact made by faithful pairs (c.f. mean movements, Table 3.8).

Breeding dispersal between seasons

As opposed to the within season movements, between season movements are of great importance if we are to understand the possible effects of site destruction and other sources of habitat loss during the breeding and non-breeding season on Redshank breeding biology. To determine a base scale of movement between seasons, trapping was carried out intensively on the study area. Additionally, some trapping was undertaken on the Old Hollow meadows and also on Banks Marsh itself, but off the study sanctuary zone. The aim was to attempt to determine how much movement was taking place to and from the study area.

Data from 1974-85 were analysed to determine breeding dispersal distances between consecutive seasons in faithful pairs, males with new mates and females with new mates (see Fig. 8).

Fig.8. The breeding dispersal (between years) of faithful pairs, males taking a new mate and females taking a new mate.

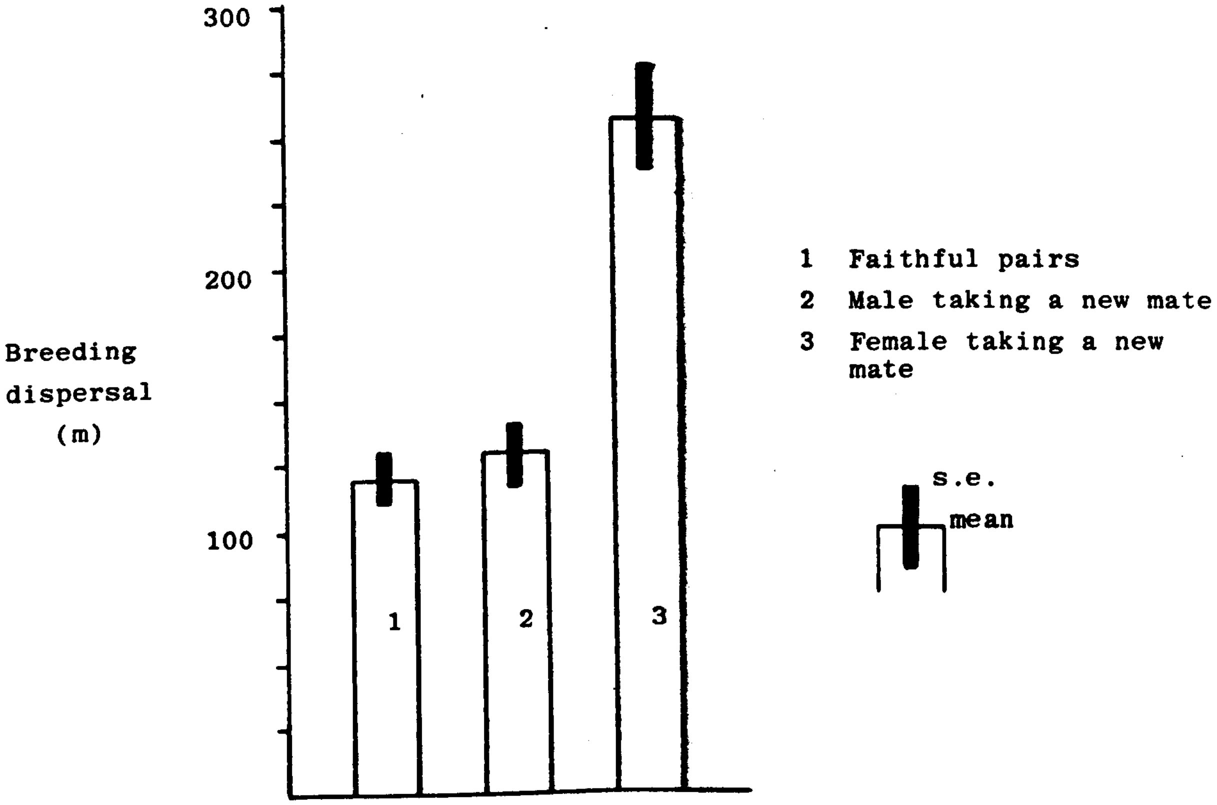


Table 3.11 The breeding dispersal of Redshank between consecutive years (data from 1974-1985).

	Faithful pairs	Male with new mate	Female with new mate
(n)	219	67	53
Mean distance moved (m)	119	129	257
Median	45	55	118
S.E.Mean	19	25	39
Max. distance moved (m)	1181	1271	1231
Min. distance moved (m)	8	5	15

These data were analysed using Mann-Whitney non parametric statistical tests.

Table 3.12 A statistical analysis to test for statistical differences in dispersal distance between faithful pairs, males taking new mate and female taking new mate (Mann-Whitney test).

Variables compared	W	Mean W	Probability
Faithful pair/male taking new mate	12171.5	12706	$p < 0.15$, ns
Faithful pair/female taking new mate	10001.5	11803	$p < 0.001$
Male with new mate/female with new mate	3286	4053	$p < 0.001$

These results are exactly as found for the within season movements. Therefore, there is no observable difference in breeding dispersal between pairs remaining faithful and males which have changed partner. Females nesting with a new mate move significantly further than faithful pairs and males nesting with a new partner (for full details see Discussion).

Previous analysis in Chapter 1 indicate how nest success in one year affected mate fidelity in the following year. It was therefore of particular interest to determine if nesting success or failure in one year influenced breeding dispersal the following year.

As in previous analysis, it was essential that two birds were caught at every nest in order that both partners were known. In the following year data were only used if birds in question were caught with a mate. Where a bird was caught on consecutive years, but its mate was unknown at one nest, then these data were not included (see Figure 9).

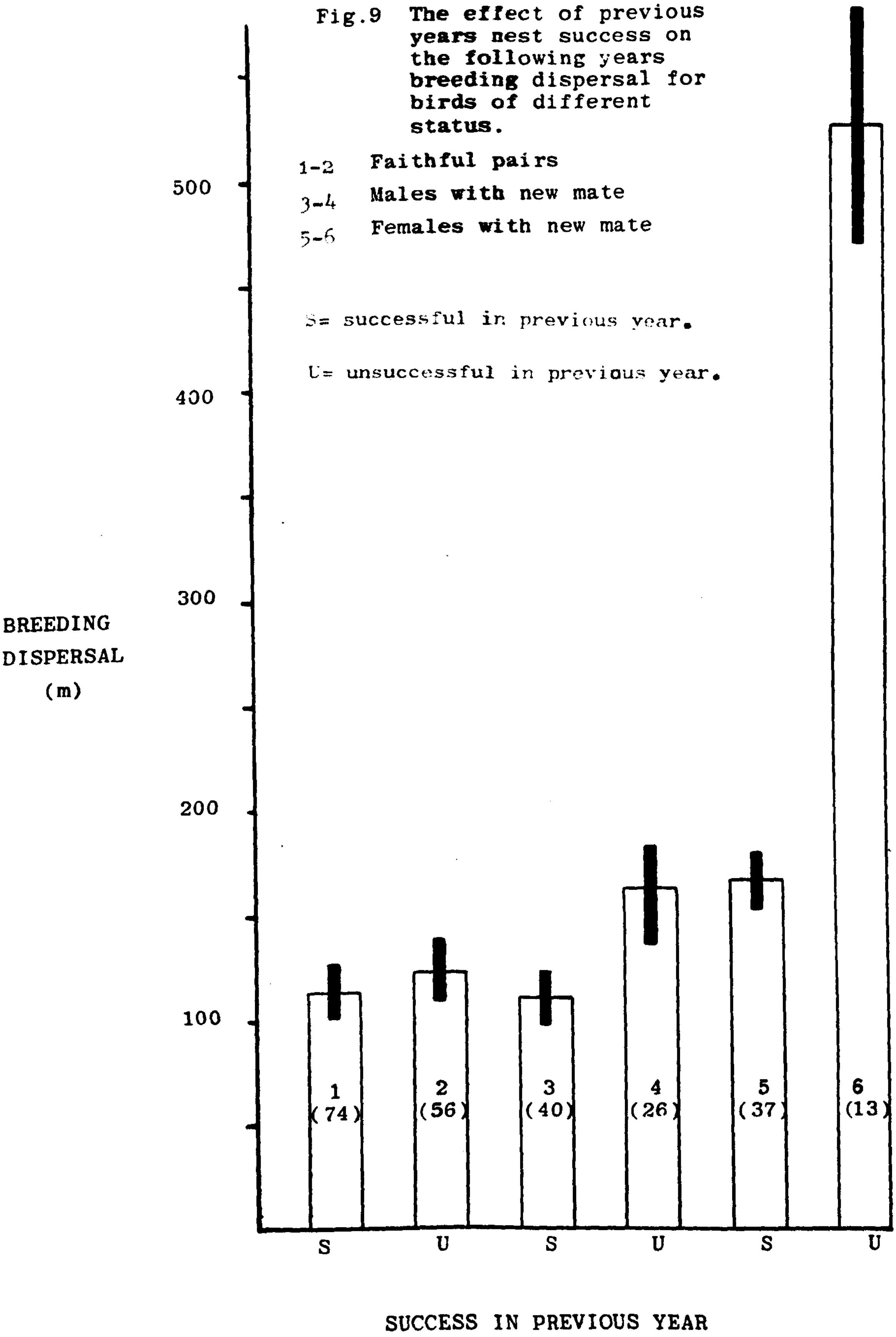


Fig.9 **The effect of previous years nest success on the following years breeding dispersal for birds of different status.**

1-2 **Faithful pairs**

3-4 **Males with new mate**

5-6 **Females with new mate**

S= successful in previous year.

U= unsuccessful in previous year.

Table 3.13 The effect of previous years nest success on following years breeding dispersal (1974-1985 data).

	Faithful pairs		Male with new mate		Female with new mate	
Success in previous year:	S	U	S	U	S	U
(n)	74	52	40	26	37	13
Mean distance moved (m)	114	123	110	161	165	524
Median	43	52	56	66	108	490
S.E. Mean	26	30	26	51	26	113
Max. dist. moved (m)	1181	1115	912	1271	661	1231
Min. dist. moved (m)	8	10	10	5	20	15

S = successful

U = unsuccessful

Table 3.14 Statistical analysis to test for the difference in dispersal distances between pairs, males with new mates and females with new mates which were either successful or unsuccessful in the previous year.

Variables compared	W	Mean W	Probability
Successful pairs/unsuccessful pairs	4431	4699	0.185 n.s.
Successful male with new mate/ unsuccessful male	1257	1340	0.28 n.s.
Successful female with new mate/ unsuccessful female	811	943	$p < 0.003$

Therefore, the previous years nesting success has a significant effect on the following years breeding dispersal in females taking a new mate. If the female is unsuccessful, she is more likely to move a greater distance. This is almost certainly related to the effect of success on mate fidelity which in turn may be related to the effect of success on overall return rates.

Natal philopatry

In order to calculate natal philopatry accurately it is essential to know:

(a) fledging success

(b) post-fledging mortality.

One requires to know what percentage of surviving birds ringed as chicks actually return to their birthplace. The main problem is (a) difficulty in calculating accurately the overall fledging success and (b) without knowing fledging success it is impossible to calculate the post-fledging survival.

The most basic calculation of fledging success can be achieved by simply calculating what percentage of chicks ringed actually return.

Table 3.15 A comparative analysis of the return frequences of chicks ringed in and out of the nest (1974-1985 data).

Ringed in nest

Year	1974	75	76	77	78	79	80	81	82	83	84	85
No. ringed	55	48	38	5	73	105	174	147	69	193	477	336
No. returned to breed*	1	0	0	0	1	3	2	3	3	8	4	1
% returned	1.8	0	0	0	1.4	2.8	1.1	2.0	4.3	4.1	0.8	0.3

* includes 3 birds caught breeding for the first time in 1986

Ringed out of nest

Year	1974	75	76	77	78	79	80	81	82	83	84	85
No. ringed	0	3	9	12	1	42	3	15	0	17	35	49
No. returned to breed*	0	0	0	0	0	5	0	1	0	2	1	3
% returned	0	0	0	0	0	11.9	0	6.7	0	11.8	2.8	6.1

* includes 3 birds caught breeding for the first time in 1986.

Without further analysis several points are very clear. The return rate of chicks ringed in the nest is much lower than those ringed out of the nest, almost certainly due to differential survival; older chicks are more likely to survive. Chicks ringed out of the nest are older and have a greater survival potential, and therefore are more likely to return. The data concerning chicks ringed out of the nest can be further broken down.

Of all the chicks ringed in the nest only a few were ever re-captured. These recaptures represent known age at last capture. Similarly, chicks captured out of the nest were also sometimes re-captured. As above, these could be used to represent estimated age at last capture. These data were used to examine the return frequencies of chicks of known or estimated age group.

Table 3.16 The return frequencies of chicks from known age groups

	Chicks ringed in nest Not re-captured prior to fledging	Chicks ringed in nest and captured again prior to fledging (Age in days at last capture)				
		1-5	6-10	11-15	16-20	21-25
1983	171	17	1	2	0	0
No. returned to breed*	7	1	0	0	0	0
% returning	4.1	5.9	-	-	-	-
1984	466	5	0	1	1	4
No. returned to breed*	2	0	0	0	0	2
% returning	0.4	-	-	-	-	50

* chicks returning from 1984 have one fewer year to return in than those from 1983.

Table 3.17 The return frequences of chicks of estimated age at last capture (chicks just captured) out of nest.

1983

Estimated age (in days) of chicks of unknown origin	1-5	6-10	11-15	16-20	21-25	26-30
No. of captures	9	5	1	1	1	0
No. returned to breed	1	0	1	0	0	0
% returning	11.1	-	100	-	-	-

1984

Estimated age (in days) of chicks of unknown origin	1-5	6-10	11-15	16-20	21-25	26-30
No. of captures	19	1	1	6	5	3
No. returned to breed*	0	0	0	0	0	1
% returning	-	-	-	-	-	33.3

* chicks from 1984 have had one fewer year to return in than those from 1983

Table 3.18 The overall return frequences of chicks of known and estimated age at last capture (age in days) 1983-1984.

Age (in days) at last capture known/estimated	in Nest	1-5	6-10	11-15	16-20	21-25	26-30
No. of captures	637	50	7	5	8	10	3
No. returned to breed	9	2	0	1	0	2	1
% returning	1.4	4.0	-	20.0	-	20.0	33.3

The breakdown of results indicate that chicks captured at an older age have a greater chance of returning the following year. Data gathered on return frequencies in 1986 have been added to this analysis. If one considers that post fledging mortality also would occur, and that some birds may only breed in their second year, then natal philopatry would appear to be very strong (see Discussion).

Chicks ringed in 1985 have only had one season within which they could have been re-captured; consequently the return rates are very low. It is noteworthy that the four chicks which were re-captured (1 found dead on the breeding grounds) had all been handled at a late stage of development. Of 22 chicks handled, which were known or estimated to be between 21-25 days old, 2 were subsequently found breeding in their first year (9.1%). In addition, two chicks were re-captured (albeit one found dead) on the breeding grounds from a total of 4 chicks known to be between 26-30 days at last capture. Thus, 50% had returned to their approximate site of birth. Younger chicks are less likely to survive than older chicks and thus are less likely to be re-captured as breeding birds.

Table 3.19 The sex of Redshank ringed as chicks which have returned to breed on the Marsh

	Frequency of returns	
Age of return	Male	Female
1	8	8
2	6	5
3	1	2
>3	2	1

In both males and females the majority of those returned (82%) have returned to breed as one and two year olds. Birds breeding for the first time at two years of age or more may presumably have bred previously, but not been captured. On the basis of chicks returned to breed, there is no difference in return frequency between male and females. However, if there is a difference in pre and post fledging mortality of the sexes, then a difference in return frequency of sexes could exist.

Table 3.20 The frequency of known first year male and female Redshank breeding in the three seasons of study.

Year	First year birds breeding Males	 Females
1983	9	14
1984	16	21
1985	8	20

Note: Birds were aged according to criteria laid down in Methods.

In 1983, 1984 and 1985 a further 74, 85 and 36 unringed birds respectively were captured from nests. It is felt that many of these birds may have been second year birds breeding for the first time.

The results from Tables 3.19 and 3.20 appear somewhat conflicting. From Table 3.19 it appears that one year old males and females are just as likely to breed as 2 year olds. From Table 3.20 data suggest that more females breed as 1 year olds. This latter finding is not significant (Mann-Whitney U Test Z = 1.53, p = 0.06). Therefore, there appears to be no difference in the number of male and female Redshank breeding as one year olds.

Age of breeding in relation to hatch date

Table 3.21 The timing of breeding in young Redshank (data for birds of 1 and 2 years old).

Chicks re-caught breeding: age at first attempt (years)	Redshank breeding which were ringed as chicks	Mean date of hatch*	Mean date of first breeding
1	16	69.4	43.5
2	11	82.4	46.1

* days from 31 March

Birds hatching later in the season appear to be more likely to begin breeding as two year olds.

Table 3.21 The relationship between date of hatch and date of first breeding in Redshank of known sex, breeding as 1 year olds (all ringed as chicks).

Birds found breeding as	1 year old	Mean date of hatch	Mean date of first breeding
No. of males	8	69.4	52.4
No. of females	8	69.4	34.6

Dates from Tables 3.20 and 3.21 are from 1974-1984.

The trend of first year males breeding later than first year females was further enhanced by examining the dates of clutch completion of first year Redshank caught in 1984/85.

Table 3.22 The mean date of clutch completion of first year male and female Redshank.

	No. of birds captured	Mean date of clutch completion (days from 31 March)
Males	24	43.6
Females	40	37.9

These data are supportive of data from Table 3.21. Possibly in some years the variation in dates of clutch completion is much more marked (for possible reasons see Discussion). In the above Table we have no idea of the origin of the birds or their date of hatch. Nonetheless it is of interest that females should apparently begin to breed earlier.

Natal dispersal

The analysis of measurements of natal dispersal are rather crude. The sample sizes are very small and the variations rather large. One could never be absolutely certain that birds breeding as 2 year olds had not bred the previous year.

Chicks which were ringed out of the nest were normally from an unknown nest site. When these chicks were caught in the sanctuary area it is likely that they had hatched from an unfound nest. Therefore, if these returned to breed (9 returned to breed) an estimate of natal dispersal could not be calculated. Estimating natal dispersal from nest site of chick to site of first breeding may not be valid as many broods may move over a large area. Perhaps it is just as valid to note if a first time breeder has returned to the site where it was reared (see Discussion).

Table 3.23 The natal dispersal of Redshank from the site of birth to the site of first breeding

Age at first breeding (years)	Dispersal distances from site of birth to site of first breeding (m)	
	Males	Females
1	271, 364, 686, 821, 1076	274, 314, 492, 551, 771, 874, 879
2	50, 357, 379, 620, 1692	89, 638, 1055
3		578, 877
>3		5800* (ringed marshside)
Dispersal range (m)	50-1692	89-1055
(n)	10	10
Mean	631.5	593.5
Median	499.5	594.5
s.d.	476.1	307.9
S.E. Mean	151	97

Note: Data taken from birds breeding at one or two years of age.

There was no significant detectable difference in the dispersal distances of male and female Redshank breeding as one or two year olds.

Several interesting natal dispersal movements were recorded. The movement of 5.8 km involved a female which was ringed as a nestling of a brood of two. This bird was ringed in 1973, found breeding in May 1977, and was subsequently re-caught in every breeding season except 1985.

Another bird, ringed as a very old (29-30 days) chick in July 1984 returned to breed in May of the following year. This bird was ringed well out of the study sanctuary zone and subsequently returned in the very heart of the study area (movement c 1.9 km). In this case the site of exact birth is completely unknown.

Two Redshank ringed as chicks moved from Old Hollow meadows to the sanctuary zone. These were recorded as natal dispersal distances of 1.076 km and 1.69 km. Movements have therefore been recorded of birds moving from breeding sites off the plot to sites on the plot. Clearly such movements could occur more commonly. However, as the majority of chicks off the plot are unringed the true figure of movement onto the plot cannot be calculated.

Only one chick ringed on the plot has been found nesting as a one-year old off the study sanctuary area (movement c 270m). This low number is due to the low trapping effort off the plot. In 1985 12 Redshank were caught to the east of the sanctuary zone; one of these birds had been ringed as a chick in 1984 on the plot. Finally, a further eleven birds were caught on Hesketh Outmarsh, a distance of 1.5 km from the most eastern edge of the sanctuary zone. In this case no birds ringed as chicks were caught; but one adult, ringed in 1984 on the plot, was caught.

Many birds nest on the sanctuary areas as first year birds. In all years (1983-85) only a small proportion of these birds had been ringed as chicks. (In 1984, 13.5% had been ringed as chicks whilst in 1985, 14.3% had been ringed as chicks).

A large number of first year birds are therefore nesting on the sanctuary area which are of unknown origin.

During the three years of study, a total of 1006 chicks were ringed in the nest. In 1983, 193 chicks were ringed from a possible total of 232 chicks from 190 nests of known clutch size. Thus 83.2% of chicks hatched from nests of known clutch size were ringed. In 1984 186 nests were found of known clutch size. In this case 477 of a maximum of 538 chicks were ringed (88.7%). In the last year of study, 336 chicks wese ringed out of 392 chicks which hatched from 157 nests of known clutch size. Thus 85.7% of all the chicks which hatched from nests of known clutch size were ringed.

In every year, the majority of chicks (at least 83%) which hatched from nests of known clutch size were ringed.

Chicks hatching from nests which were not found were obviously less likely to be ringed. However, in every year a number of chicks were ringed at varying ages away from their nest site.

Chicks which returned to breed in their first year as unringed birds were therefore less likely to have come from nests which had been found. As there is no real way of knowing what percentage of nests are unfound it is difficult to determine how many returning birds hatched from nests which were in the study area but were unfound.

The actual number of birds breeding as one year olds, which were not ringed as chicks, does at least suggest that many of these birds have come into the study sanctuary area from other areas.

DISCUSSION

The problems outlined, such as drainage, reclamation and afforestation, are now of such a nature that many areas of scientific interest have been lost or irreversibly damaged. The very fact that such areas have been lost, and that more areas will be lost, is a shameful reflection on our National Conservation bodys and Society as a whole. All too often attention has been rightly drawnto the reclamation of a mudflat, or to the damage of a wader wintering ground by some form of pollution. Unfortunately, attention to wader breeding grounds has not until recently been so dramatic, resulting in a loss of heathland, wetland, moorland and even upland plateaux. Although many of these areas are aesthetically important they are perhaps not deemed scientifically important. Consequently, little attention is gained when another acre is drained and cultivated. While this may be an acceptable face of compromise conservation, it has no real place in conservation which is rationally thought out and sensibly implemented.

How will our birds, and waders in particular, be able to cope with such habitat loss? Unfortunately we can only make reasoned guesses. While areas are being lost the plight of the waders becomes more desperate. It is possible that they will not survive under such a ferocious attack on their breeding grounds. Certainly at a local level populations of waders have shown marked declines.

The Redshank is a declining wader (Sharrock 1976). Many areas where they formerly nested no longer exist in the same form. As a consequence, Redshank have gradually been squeezed out of their former inland haunts; now they are more commonly associated with coastal plains Smith (1983). The coastal saltings are also under threat with large areas being drained every year. This discussion highlights the results and makes an indication of what may happen to Redshank populations in future years.

Both male and female Redshank can be considered to be highly site faithful; both show a tendency to return to their former breeding grounds (see also Grosskopf 1963). When one considers that some birds die over the winter months, and that some may be present on their former breeding grounds but not caught, then it does seem that they show a strong tendency to return. Although the trend is for males to show a greater tendency to return, there is no significant difference in return rates between males and females.

A first year Redshank is less likely to return to breed than an older Redshank, but a first year Redshank is just as likely to return as an unringed bird which is greater than one year old (but may be breeding for the first time). Redshanks which are known to be experienced (previous breeders) are more likely to return than inexperienced birds ('unrings').

Data displayed in Table 3.6 further support these findings, but also outline the effects of previous year's nest success on breeding site fidelity. Young (inexperienced) birds are less likely to return than older birds; and when successful in previous year older birds are more likely to return. When unsuccessful in previous year, young birds are less likely to return. Birds of 4-years breeding experience or more, actually return at an even higher percentage when unsucccesful in previous year than birds which were successful. Clearly, as a bird gets more experienced, the benefits of returning outweigh the disadvantages of returning after nest failure. It should also be remembered that success in one year has an effect on mate fidelity the following year. For further details see Thompson et al (1987).

The breeding dispersal results are very much as predicted for the monogamous Redshank (see Greenwood 1980 and Greenwood & Harvey 1982). Male Redshank disperse less between seasons than do female Redshank. Pairs remaining faithful disperse the shortest distance. Between year results were mirrored in the within year results. Thus mate fidelity has an effect on both breeding site fidelity and breeding dispersal.

Success in one year does have an effect on breeding dispersal. If a female is unsuccessful she is more likely to disperse a greater distance than a male which is unsuccessful. Very similar results were found in the Semipalmated Sandpiper (Gratto, Morrison & Cooke 1985) and the Spotted Sandpiper (Oring & Lank 1982, 1984).

To summarise, when a pair is successful the birds are more likely to remain together and return to the breeding ground. When a pair is unsuccessful the partnership is more likely to break up and the female to disperse a greater distance than the male. The fact that females disperse further probably explains why females are less likely to be caught in the same breeding grounds the following year.

Breeding site fidelity, breeding dispersal, and mate fidelity are all very closely related to the birds breeding success. As first year birds are less site faithful, it follows that they must be more prone to failure and thus divorce. However, I would stress that other, so far unidentified factors, may also be involved.

Reference to Table 3.7 makes quite clear that of all age groups of Redshank caught, in both 1983 and 1984, the first year birds were most unsuccessful. Therefore, first year females are more likely to fail, more likely to divorce, and subsequently more likely to disperse. If they do disperse, they are less likely to be re-captured as many would leave the study area (see Hildén 1979). This result has very serious implications for populations of Redshank which may for some reason experience several years of nesting failure. The older birds continue to return, even when unsuccessful, but the younger inexperienced birds are more likely to disperse and less likely to return. A possible end result is a gradual deterioration of breeding stock and subsequent abandonment of the area.

Redshanks are very social birds and seek out the company of their own kind. These birds can often be found nesting in a small group in an area of wet meadowland or rough pasture in a fraction of the area apparently available. It would seem probable that there is a point at which a group is no longer attractive to a young bird looking for an area in which to settle.

Recruitment to the Banks Marsh population would appear mainly to be from outside the study area. To test this idea, a study of natal philopatry and natal dispersal was set up. Before discussing the results in detail, it must be remembered that fledging success in the study area is thought to be low. Thus overall production of chicks at the point of fledging is low.

The natal philopatry results are exciting and clearly indicate that Redshank exhibit a very high degree of natal philopatry. When one considers that post-fledging mortality and uncaught returning birds are not accounted for, then I think that Table 3.18 clearly shows that Redshank are highly philopatric. This Table also indicates the very high degree of pre-fledging mortality that must exist up to 5 days of age. After this, mortality is probably greatly reduced as Redshank chicks can then begin to partially regulate their own body temperature (R. Robertson *pers. comm.*).

There appears to be no sex bias in return ratio of young Redshank, as would be predicted for a monogamous, non territorial species (but see Greenwood &Harvey 1982). In resource defence polyandrous species such as the Spotted Sandpiper, Oring & Lank (1982) discovered that males were more likely to disperse and that females exhibited a higher degree of site fidelity. Again this is as expected for the breeding system in question (Oring & Lank 1982).

A large number of Redshank are capable of, and do, breed in their first year (but see Grosskopf 1963); but an equally large number appear to wait until their second year. The results in Table 3.20 appear to indicate that females are more likely to breed in their first year than are males. In fact there is no significant difference in the age of first breeding in male and female Redshank.

One major point that determines whether a Redshank will breed in its first year appears to be the date on which it was hatched. A rudimentary analysis revealed two main points.

(a) Those which bred for the first time as one year olds hatched on average 13 days earlier than those which bred as 2 year olds.

(b) Females nesting as 1 year olds did so earlier in the season than did males nesting as 1 year olds. This worked both for chicks of known and unknown origin. It would therefore appear that females are either capable of breeding earlier or are more attractive to a male. Young males may be less able to compete with older birds and are therefore less attractive to unmated females.

In both Tables the mean dates of clutch completion are later for young birds than for older more experienced birds. The separation in laying date of old and young birds may be of genetic advantage. As older birds are mated and breed early, young birds returning to the site of their birth are less likely to mate up with their parents. The fact that Redshank breed at very high density means that young birds are less likely to encounter their parents. There is a dilution effect, with young birds being only a small percentage of the total number of birds present.

Finally, the urge to return would appear to be very strong, suggesting that there are indeed very great benefits to be gained. The benefits to older birds are relatively obvious; experience of feeding ground, predators, neighbours and an intimate 'knowledge' of breeding and chick rearing areas. The benefits to young birds are not so readily discernible. Perhaps young birds are able to gain some experience of the breeding grounds during the pre and post fledging periods. In addition, young birds may be better adapted to their site of birth for genetic reasons. I would suggest that many Sandpipers exhibit a high degree of natal philopatry. The problem is that most studies have calculated an index of philopatry based on the return of chicks ringed in the nest. I have already stressed that pre-fledging mortality is very high, thus ensuring that only a small percentage would live to return. Had calculations been based on the return of chicks which were alive at 1-year old, then I am sure that return rates would have been very much higher. Only a very few studies have tackled this problem in an organised manner, so our knowledge of natal philopatry is rather poor (see Soikkeli 1970a; Hildén 1979; Oring & Lank 1982). The degree of natal philopatry exhibited is at least partly determined by the breeding system of the species concerned. In highly territorial species, such as the Greenshank and Golden Plover, young birds may be prevented from entering the population (Nethersole-Thompson & Nethersole-Thompson 1979; Parr 1979, 1980). In less territorial species young birds may be able to squeeze into the population even at a later date or in a less suitable site. Young Redshank often nest in peculiar sites such as the bottom or down the sides of ditches; in this instant, the nest site is chosen badly as a result of the individuals lack of breeding experience. The overall abundance of apparently suitable sites suggests that birds need not nest in these areas at all.

What makes a particular site suitable is often very difficult to determine, but the fact is that birds such as Greenshank, Golden Plover and Dunlin will often return to the same scrape for two or more years despite an 'apparent' abundance of suitable sites. In these cases, these sites are presumably more suitable than other surrounding sites and therefore offer the occupants an increased chance of being successful.

The results of natal dispersal are also of particular interest when attempting to determine where recruitment comes from. The data set is very small and only includes those birds of known origin. There is no difference in the dispersal distance of young males and females; both move an average of 600 m from site of birth to site of first breeding. The longest distance recorded, 5.8 km, shows that some Redshank do move a substantial distance. Birds ringed within the study area could move out of the area (one case recorded) and birds ringed out of the study area could move into the study area (six cases recorded). The bias here is explained by the fact that some chick growth work and thus chick ringing was carried out away from the study area. However, only a small amount of adult work took place outside the study area and this revealed one known first-year from 12 birds. A final point is that chicks may move a great distance after they have hatched (see Yates, unpubl. thesis 1982; Thompson 1982); and may in fact be returning to the area in which they were reared, rather than where they were born. Although this could make a difference in terms of which birds return to the actual study area, the effect on a general philopatry statement are negligble. Thus birds returning to the site of birth or rearing could generally be considered to be highly philopatric as normally birth and rearing sites are close to each other.

Only a small percentage of first years breeding on the study area were actually ringed as chicks. It would therefore appear that recruitment is to a large extent coming from outside the study area, as in 1983-85 a very large effort was put into ringing as many chicks as possible. The surrounding area is very heavily grazed and consequently many nests are lost, but some pairs successfully rear chicks to fledging. The actual habitat is very poor, with only short grass in most areas. Many Redshank are forced to nest in small ditches and down the side of ditches to gain cover. At the same time, the vegetation cover in the ungrazed sanctuary is lush, offering many more available breeding sites. The chance of nest loss is also reduced due to the lack of grazing pressure. It may be that the sanctuary is a more favourable breeding area and as such attracts young birds in their first breeding year from other neighbouring areas. As the sanctuary is in the centre of the Ribble Marsh complex, it could actually attract a large number of birds into the area without them having to move a very long distance. In fact, chicks have come to the sanctuary from such areas (Old Hollow meadows and Hesketh Outmarsh).

In conclusion, old birds remain faithful to their breeding grounds. Young birds are less faithful if they were unsuccessful in the previous year. If a divorce occurs as a result of nest failure, the female is more likely to disperse a greater distance than the male. Young birds exhibit a high degree of natal philopatry, but birds born in poorer nesting areas may move to better grounds when they return in later years.

How then will birds cope with loss and drainage of their breeding grounds? Confronted with such a situation, old birds would hang on until they could physically no longer nest in their breeding ground. They would then be forced to move to an area where they were unadapted in every possible way. This could lead to density dependent competition and a possible effect on breeding success. At the worst, birds may not be able to enter a population and may be squeezed into less favourable fringe and poorer ground. (In the case of the Redshank this is probably less likely to happen). This would almost certainly lead to a drop in breeding success and a subsequent decline in offspring production. When young birds return and find their breeding grounds gone, movement may result in them nesting in unfavourable nesting sites. Failure in this case would be more likely to result in the birds leaving the area in search of new ground. These birds then lose the chance to become established and may find it difficult to enter a population elsewhere, due to the competition from older birds for males or nest sites. On a larger scale, there would be less chance of genetic exchange as fewer centres of population would exist. As the populations condense (this may not happen in some very territorial spedies) they become more susceptible to predation and more vulnerable to the possible effects of land use change. The main point would seem to be how much poorer are marginal breeding areas, and can birds adjust their breeding systems in order to adapt to these long term changes. Research on marginal land and its use by waders is currently being conducted (Galbraith & Furness 1983; Galbraith, unpublished 1986 and Galbraith et al 1984).

As far as the Ribble Redshanks are concerned, there is no sign of any population decline. The potential does exist, however, to determine:

(a) the level of nest failure in the grazed area

(b) chick production in grazed area

(c) movements of birds from grazed to ungrazed area (and vice versa).

This study has established that some of the recruitment to the study area is taking place from surrounding marshes. As the study area is only a part of the entire Ribble Marsh complex then this is perhaps not surprising. The majority of the Ribble Marsh green marsh is grazed; as a result of grazing many Redshank lose their nests and breed unsuccessfully. Even though pairs in the ungrazed marsh are probably more succesful, it appears that at least some of the young birds entering the study area to breed are fledging from surrounding marsh. If this is the case, the population within the sanctuary area may be at least partially dependent on birds from surrounding grazed marshes. Therefore, breeding success in ungrazed areas ought to be assessed in order to determine the number of young birds fledging and how faithful these birds are to their birth sites. It is possible that birds born on ungrazed areas actually seek out ungrazed areas as these are more favourable areas. If this were so, one would expect breeding density, breeding success and breeding times to differ between the two habitat types. This has not yet been tested.

If, as suspected, Redshank are moving into the ungrazed area the implications for reserve management may be serious. If breeding success in the surrounding areas declined, for some reason, the population in the sanctuary may go into decline.

On a more general level, there is the possibility that some of our Nature Reserves may in fact be too small (NCC Publication 1986; Tompkins 1986). If this is in fact so, then populations of Dunlin, Golden Plover, Greenshank and Redshank, within these Reserves, may go into a decline if surrounding areas are damaged. In short, if a population cannot be self sustaining within a given area, and surrounding areas are made unsuitable, then it is likely that populations of some waders may locally decline or become extinct. Such population declines have already been observed in Redshank (Sharrock 1976) and are expected in several of our upland breeding waders (NCC Publ. 1986; Tompkins 1986; Thompson _et al_ 1986).

Chapter 4

The growth and development of Redshank chicks

Introduction

The growth and development of sandpiper chicks has been little studied. Most researchers have avoided this aspect because it requires much time, and successful capture is by no means guaranteed. Many ornithologists have claimed that chick capture is near impossible, due to the nature of 'normal' wader terrain and also as a result of the hiding abilities of the chicks. In the case of Redshank, Grosskopf's description of chicks being 'past masters at sneaking away' is particularly appropriate (Grosskopf 1958a).

Grosskopf (1958a) attempted to follow many of the chicks he ringed in the nest, with only a moderate degree of success. This work on Redshank was followed up by Stiefel and Scheufleur (1984) and their results integrated with Grosskopf's study, undertaken on Wangerooge Reserve. On the Ribble marshes, both Ashcroft and Yates weighed and measured chicks of known age; but both studies were greatly affected by a small sample size of captured chicks.

Other wader species have been less intensively studied. The Lapwing was studied for several years in the New Forest. A series of very interesting results were obtained; in particular, growth rates and fledging periods were found to vary enormously between seasons. Differences were regarded as being mainly due to weather conditions and the effect on food supply (Jackson & Jackson 1975, 1980). Other studies on growth rate of Lapwing chicks were carried out by Fuller (1983) and Redfern (1983). More recently, Galbraith has studied growth rates of Lapwings and related the rate of growth to female quality and habitat quality (unpubl. 1986).

In a study of Common Snipe *Gallinago gallinago*, Green (1985) captured many chicks of known age which were ringed in the nest. The results obtained were compared with those of Williamson (1960), who studied Snipe growth after fledging. The combined data set gives a good account of Snipe growth from birth to after-fledging. Green concentrated on weight and 'bill to feathers' as his measurements. Tuck (1972) also published growth curves for Snipe.

Other studies, such as Lessells (1984) on the Kentish Plover *Charadrius alexandrinus* and Pienkowski (1983, 1984a) on Ringed Plover have also looked closely at chick survival and growth.

It is noteworthy that there is a close link between studies of growth and studies of chick survival. It is hoped that eventually measurements of growth rates may be used to predict survival potential and perhaps even the potential to return in future years.

The British Trust for Ornithology has now begun a scheme to study differential mortality in wader chicks. The overall aim is to determine the return rate of chicks ringed at different ages. The approach is simple; one would expect fewer chicks to survive which were ringed in the nest than older chicks ringed out of the nest. Such a project demanded that every chick ringed was measured and its age subsequently estimated. As part of the Ribble study, it was decided that Redshank chicks should be captured and measured and growth curves constructed. Using only chicks of known age it would then be possible to age chicks of unknown age, using Formulae decided upon. This technique was employed to determine the likelihood (frequency) of return of chicks of different age categories (see Chapter 3 Natal philopatry).

For the benefit of this study the overall aim was to determine if there was:

(a) inter seasonal growth rate variation

(b) intra seasonal growth rate variation

(c) inter sibling variation in growth

(d) differential growth rate of different parts of the chick.

These aims, if satisfied, would allow for a single age estimating Formula to be arrived at. If this could be achieved, subsequent calculations of differential survival and natal philopatry would be much more straight forward. Part (d) was undertaken to determine which measurement varied least within and between seasons and also between individuals of the same age. A technique requiring only one measurement would clearly greatly speed up handling time. The growth of feathers in the different body regions was also studied as this may also be used as an indicator of age and body condition.

In chicks of known origin (ringed in nest) the measurements of different variables could be related, where possible, to the size of the parent, the date of hatch, the size of egg, and also the order of hatch.

In the majority of cases too few data were gathered to accurately determine if such relationships existed.

Methods

The method of chick capture would obviously vary between species being studied and the study area. Prior to studying Redshank, I had a reasonable amount of experience with young waders; in particular Lapwing, Dotterel, Golden Plover, Greenshank and Common Sandpiper. Apart from the Lapwing and Dotterel, which are fairly easy to catch, the other species proved very difficult to work on. These three species, like Redshank, tended to keep their chicks in wet areas where there was an abundance of cover. Normally it was unusual to see chicks running around whilst observations were conducted from 150 m or less. Catching Redshank was therefore probably no more difficult. Without a basic knowledge of adult behaviour, the task of capturing young Redshank out of the nest would be much more difficult. Many hours observation were undertaken from different distances, and many searches for young birds were made before a pattern began to emerge.

The first and most important task was to ring as many chicks as possible in the nest. This greatly enhanced the chances of catching chicks of known age.

The selection of broods to be watched was very important. By sitting down c 150 m (sometimes closer) in the vicinity of broods, one could determine where they were. Normally broods were confined to some of the many ditches and creeks which dissect the saltmarsh. Once a brood locality was known, it was important to decide if an attempt should be made to find the chicks. Normally decisions were based on ditch size and position in relation to other ditches. If a ditch was very wide and deep then the brood was normally left alone. Experience was the most important attribute here. By deciding to move to another brood, much time was saved rather than attempting a search likely to be unsuccessful.

Where a brood was located on a suitable ditch (the smaller the better), the adult (s) were watched to determine the approximate position of the brood. When the chicks are small the adult remains fairly close to the young (based on evidence of chick position at capture to adult position). Once chicks are older the attending adults will move the young fairly quickly along the ditch. The majority of chicks caught were in saltmarsh ditches. Once the brood locality was estimated the ditch was rushed. The position of the adult was taken as the centre and searchers went below and above this point perhaps by as much as 30 m depending on the width of ditch and on the behaviour of the adult. The searchers then worked toward each other, searching the ditch slowly and methodically. This was a painstaking, messy task but doing it methodically greatly increased the chances of a find. Once in the ditch every possible hiding place was examined. The mud was carefully checked for fresh footprints and droppings and also for the presence of waxy flakes from the growing feathers. When these were found a search image could be formed for larger chicks. When conducted properly, and when assumptions about position were correct, chicks were normally found. The ditch was always searched to completion, even when one chick was found.

Experience suggested that chicks continued to move until the ditch had been reached. On a very few occasions chicks were spotted running as the searchers arrived at the ditch. On fewer occasions chicks moved along the ditch in front of the searchers. Normally chicks hid, presumably under instructions from attending adult (s).

If chicks were not found after a search, the searchers left the ditch and returned to the observation point. From adult behaviour and position, it was normally possible to tell if the brood had moved or if chicks had been missed. Frequently the adult would perhaps take up position on the same ditch, but lower or higher up than original position. When this occurred it normally meant that the ditch had been entered too close to the adult and the chicks were on the wrong side of the searcher. If the adult returned to the same position as before then this was a good indication that the chick (s) were small and had been missed.

The other most common occurrence was for the adult (s) to take a position on a new but nearby ditch. This normally meant that

(a) chicks had moved from one ditch to another, while or before the search was undertaken;

(b) the adult intended to move the chicks to this ditch; or

(c) the chicks were somewhere between the two ditches.

It was normally possible to determine what was happening or going to happen. If the adult began to move along the second ditch then one could assume that the chicks were already there; this ditch was then subjected to similar searching methods as outlined above. If the adult began to run around between ditches one could guess that the chick (s) were hiding on the top. Experience was again useful in that one could determine from the adults voice and level of excitement if the chicks were moving. If the chick was spotted (often running ahead of adult) it was important to get an exact location. If the second ditch was known to be large then it was imperative that the chick was caught before it reached the sanctuary of the ditch. Equally, if the ditch was known to be small and a good catching ditch, then the chick was allowed to reach it before the searchers rushed in.

When the decision was made to catch the chick on the top, a precise location was taken with a telescope of the last spot where the chick was seen. The observer directed the searcher to this spot, using a 2-way radio. Normally a brief search revealed the chick hiding in some vegetation. On occasions, however, the time taken to cover 100 m, and the nature of the ground, often allowed the chick to run to safety. As in the case of catching chicks in ditches, perseverance and judgment was highly important. It was also found to be possible to ease broods along a ditch to positions more suited for capture. By sitting on one side of the attending adult the brood could be shepherded into a narrow stretch of ditch, thus making capture more likely.

At the time of high tides the ditches filled to varying degrees, depending on tidal height. Adults could often be seen leading their chicks up the ditches away from the incoming water. Such behaviour was always indicative of brood position and often lead to a quick find. Equally, when the tide was well in, chicks were often forced to move into small side ditches or even forced onto the top of the green marsh. In such circumstances finding was very much easier as available hiding places were fewer in number. Knowledge of Redshank brood attending behaviour, a knowledge of study area, and patience, are all required if chicks are to be caught on a regular basis.

I have outlined the main methods employed for chick capture on the Ribble saltmarsh. In other areas different techniques would almost certainly be required.

Results

The relationship between egg size and female size and egg size and chick size (at hatch) has already been established (Chapter 2).

It was strongly suspected that a relationship may exist between

(a) egg size and chick fledging potential and

(b) between egg hatch order and chick fledging potential.

A brief review of the data set indicated that of those chicks of known origin, which were known to be alive after five days, the relationship between survival and egg size could not be examined. To do this, chicks surviving would have been required to have been ringed in the nest and have come from an egg of known size. This happened on too few occasions.

The relationship between hatch order and chick survival, however, may be examined

Table 4.1 The relationship between chick hatch order and probability of surviving to at least 5 days of age.

	Hatch order of chick	
	1 or 2	3 or 4
No. of chicks captured at 5-days of age or more	20	11

Note: At all nests, 4 eggs hatched

A Goodness of fit test indicates that the above is a non-random distribution. Chicks hatching first and second are more likely to survive to five days or more ($X^2_{(1)} = 2.61$ n.s.). However, this difference is not significant. The main problem is that the sample sizes are very small. I would tentatively suggest that earlier hatching chicks leave the nest in better condition and are therefore more likely to survive.

As outlined in the Introduction, chicks of known age were captured at various intervals to determine growth rates.

A total of 1107 chicks were ringed between 1983-1985. Of these, 104 were captured and ringed once they had left their nest; thus their nest and date of hatch was unknown.

Where possible, chick catching was attempted on broods of known origin (unmarked adults could often be identified by plumage, behaviour or location). Inevitably, many chicks were captured which were unringed.

Of the 1003 chicks ringed in the nest, 60 were subsequently re-captured a total of 91 times. Therefore, only 6.0% of all chicks ringed in the nest were subsequently caught again.

Of the 104 chicks captured and ringed out of the nest (origin unknown) 28 (27%) were re-caught a total of 68 times. Therefore, a total of 88 chicks were caught on a total of 159 occasions (other than original catch date).

The increased re-capture rate of chicks ringed out of the nest is an indication of differential mortality between nestlings and older chicks caught out of the nest (see Chapter 3).

Growth and development

At birth, young Redshank are weak and feeble. Within 1 hour of hatching the chicks are dry and are moving freely in the nest scrape. At the time of leaving the nest the chicks are strong and can run freely. At this stage chicks are still dependent on their parents for maintaining their body temperature and for protection from predators. As they get older, they are able to regulate their own body temperature but still depend on adults to warn them of approaching danger.

Table 4.2 The comparison of chick and adult measurements at chick birth

	Chick measurements in the nest	(n)	Adult female measurements	Chick measurement at birth as % of adult measurement (1984 data)
Weight (g)	15.58 ± 1.2	414	134.4 ± 8.0	11.6
Tarsus (mm)	28.16 ± 1.2	412	47.6 ± 2.0	59.1
Bill to feathers (mm)	12.59 ± 0.5	417	41.8 ± 2.0	30.1

At hatch, the tarsus is on average 59% of the average female tarsus measurements. The weight at hatch and the bill to feathers are much less well developed. It must therefore follow that the tarsus grows slower as opposed to the bill to feathers and the weight.

The relationship between fledging size and adult size is more difficult to calculate. Only a very few chicks have been captured that could fly or fly weakly. In particular, chick DN60089 was captured at fledging and was subsequently captured the following year as a breeder. This is an ideal case for studying the relationship between fledging size and adult size.

Table 4.3 The relationship between size at fledging and size at first breeding (1 year old)

	Fledging Redshank (DN60089)	1st year Redshank (DN60089)	% of adult measurements at fledging
Weight (g)	112	128	87.5
Tarsus (mm)	46	46	100.0
Bill/feathers (mm)	34	45	75.5
Bill/nares (mm)	26.5	35	75.7
Wing (mm)	126	160	78.7
Tail (mm)	53	56	94.6

During the research, 3 fully fledged (free flying) Redshank were captured using mist nets. Catching flying juveniles proved more difficult than anticipated, but the capture of 3 juveniles was considered a success.

Table 4.4 The relationship between post fledging size and adult size.

	Juvenile Redshank (n=3)	Estimated age (days)	Adult Redshank (female)	% of adult biometrics (1985)
Weight	118.3 ± 0.3	45-55	133 ± 6.8	88.7
Tarsus	47.6 ± 0.57		47.1 ± 1.9	100
Bill/to feathers	41.5 ± 3.5		41.9 ±1.9	99
Wing	163.6± 1.5		168 ± 4.0	97.3

By using mean female adult Redshank, the calculations of % adult measurements represent minimum values of development. Thus 45-55 days after hatching adult measurements have been reached for tarsus, bill to feathers and wing length. The weight is a minimum of 88% of adult weight.

In addition, the adult weights are all for incubating birds. In mid-July it is likely that adult weights are different from those of breeding pairs.

Feather development

Although rather variable, the development of the feathers and the loss of down is a useful age indicator. As can be seen from Figure 10 the emergence of pins, the eruption of the feathers, and full emergence of the feathers occur after 5, 9 and 12 days respectively. Individual positions on the young Redshank vary in the degree to which they may be used as ageing criterion. In particular, it is of note than an experienced person could age young Redshank from the state of feather development in the different body regions. This is, however, much less accurate than using exact measurements and as such should only be used when accurate ageing is not important (see Figure 10 for instructions).

Figure 10 Feather Development in Young Redshank

Instructions for use

Figure 10 is split up into three sections.

Section one is concerned with the emergence of feathers at the earliest stage of development in the different body regions. Early development is detected by the appearance of 'pins'. The pins are small wax covered sheaths which emerge from the young bird's skin.

Section two graphically highlights the time at which the feathers begin to emerge from the sheaths. When this occurs, the feather appears like the end of a small paint brush emerging from the waxy sheath.

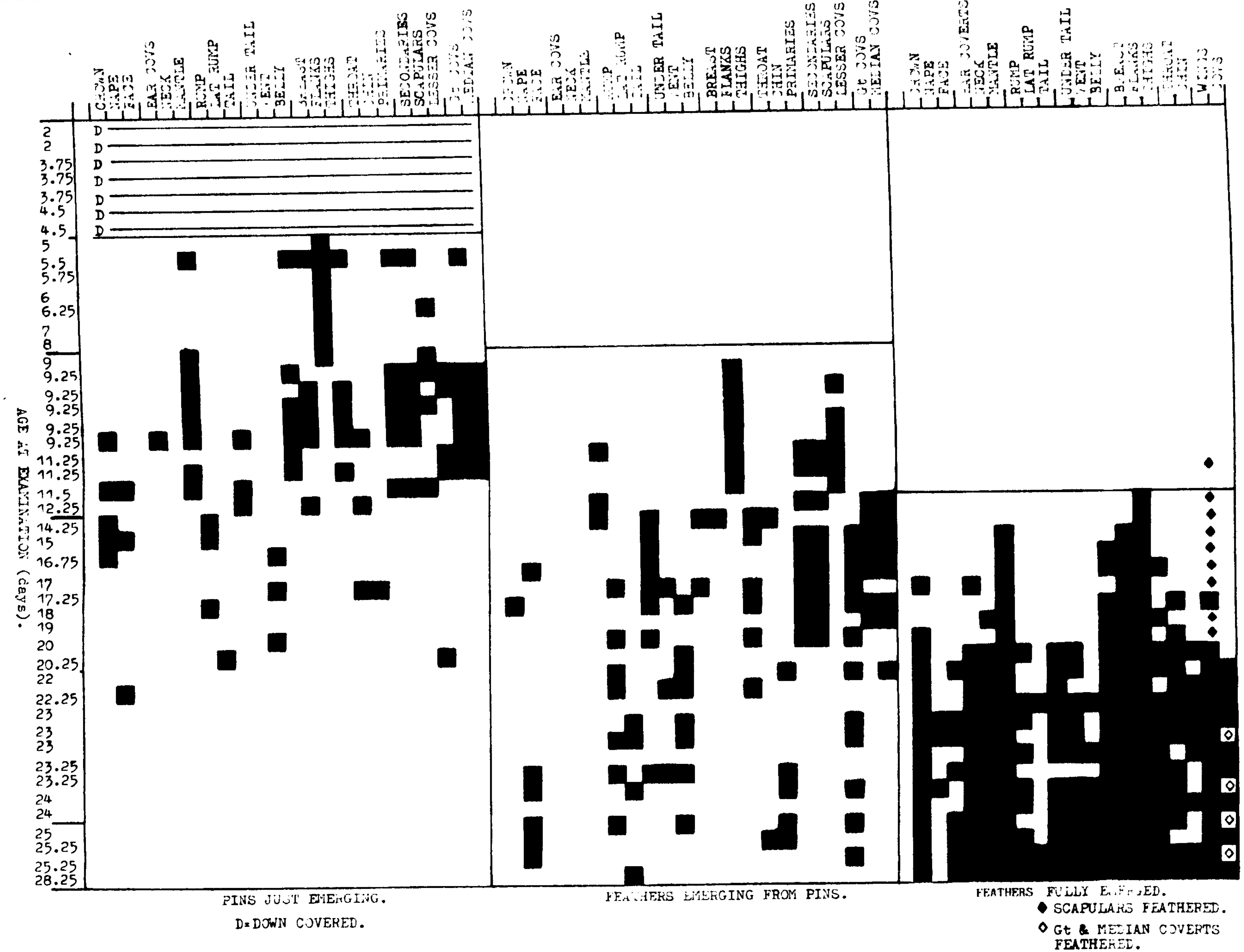
Section three indicates when the feathers have completely emerged from their sheaths. The time of complete feather emergence differs for the different body regions.

Body regions are labelled separately. By using a ruler, it is possible to determine at what age pin emergence, feather eruption and complete feather development occur in each body region.

The actual age of each chick examined is on the left hand side of the figure.

In all sections, the problem of individual variation in feather development highlights the dangers of using feather development as an ageing criterion.

FIG.10 THE GROWTH AND DEVELOPMENT OF FEATHERS IN YOUNG REDSHANK (in relation to chick age).



Chick growth

Chicks of known and unknown age were captured and measured in an attempt to monitor growth throughout the pre-fledging period. Primarily, every effort was made to ring chicks in the nest, thus enabling re-captured chicks to be aged exactly. Chicks first captured out of the nest were only useful in studying change over a given period of time.

Of those chicks ringed in the nest, re-captures were between one and six times. Of those chicks captured and ringed away from the nest, re-captures ranged from one to eleven times.

Figures 11 - 14 present the raw data plotted out for age versus weight, bill to feathers, tarsus and wing measurement.

Figure 15 presents the mean weights for the age classes of chicks re-captured (1-28 days old).

Fig.11. GROWTH DATA FOR YOUNG REDSHANK.

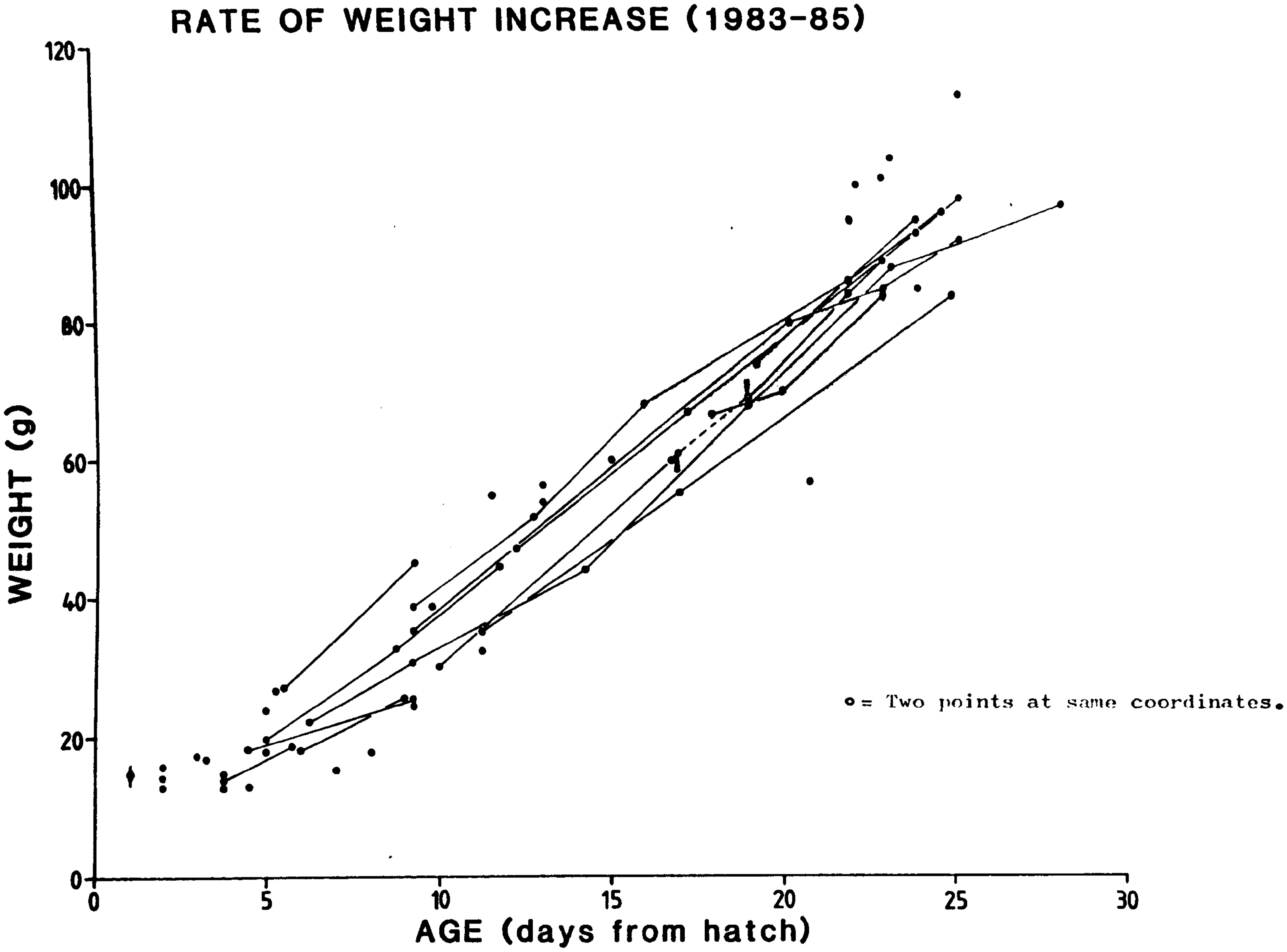


Fig.12. GROWTH DATA FOR YOUNG REDSHANK.

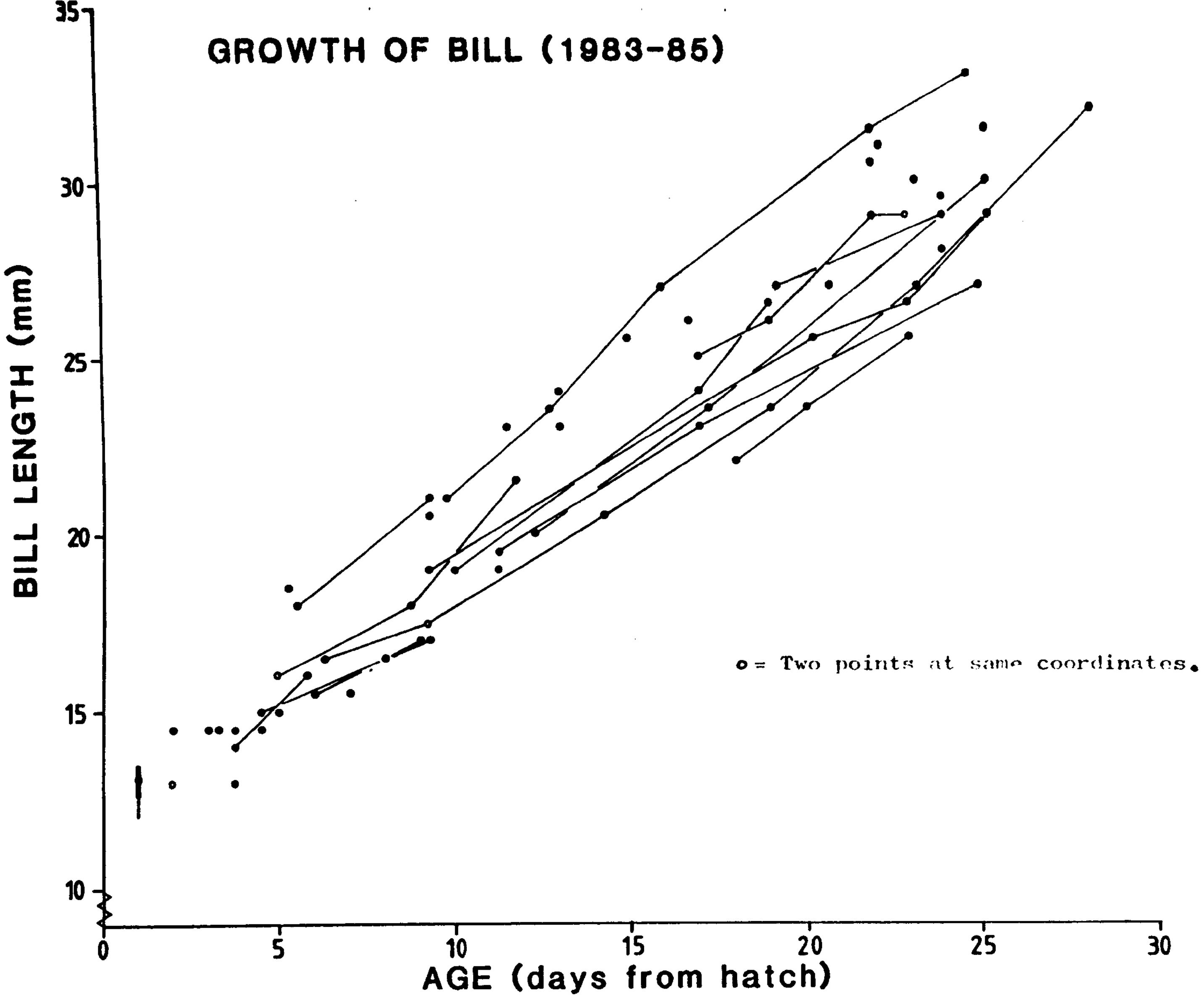


Fig.13. GROWTH DATA FOR YOUNG REDSHANK,

GROWTH OF WING (1983-85)

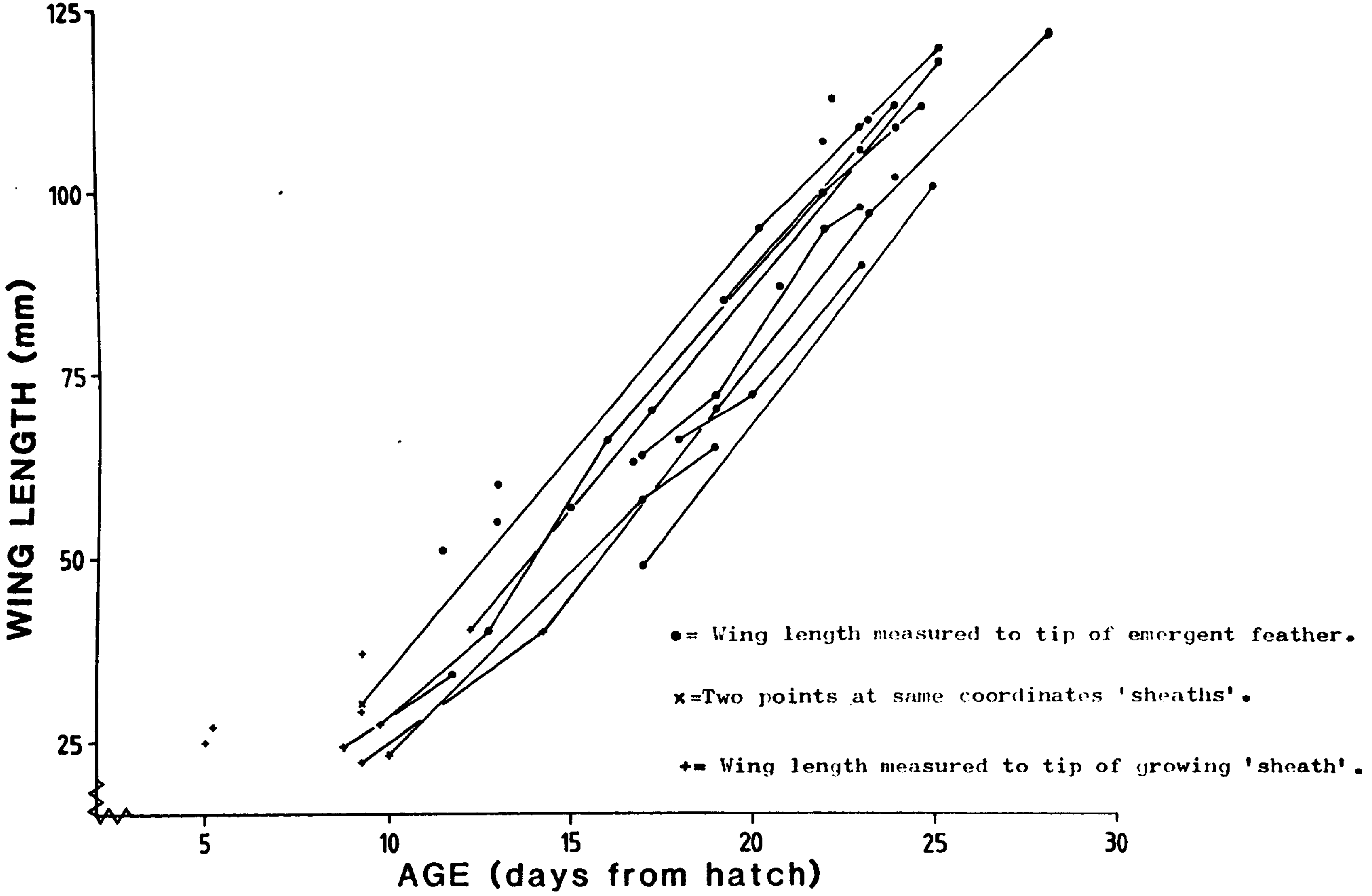


Fig.14. GROWTH DATA FOR YOUNG REDSHANK.

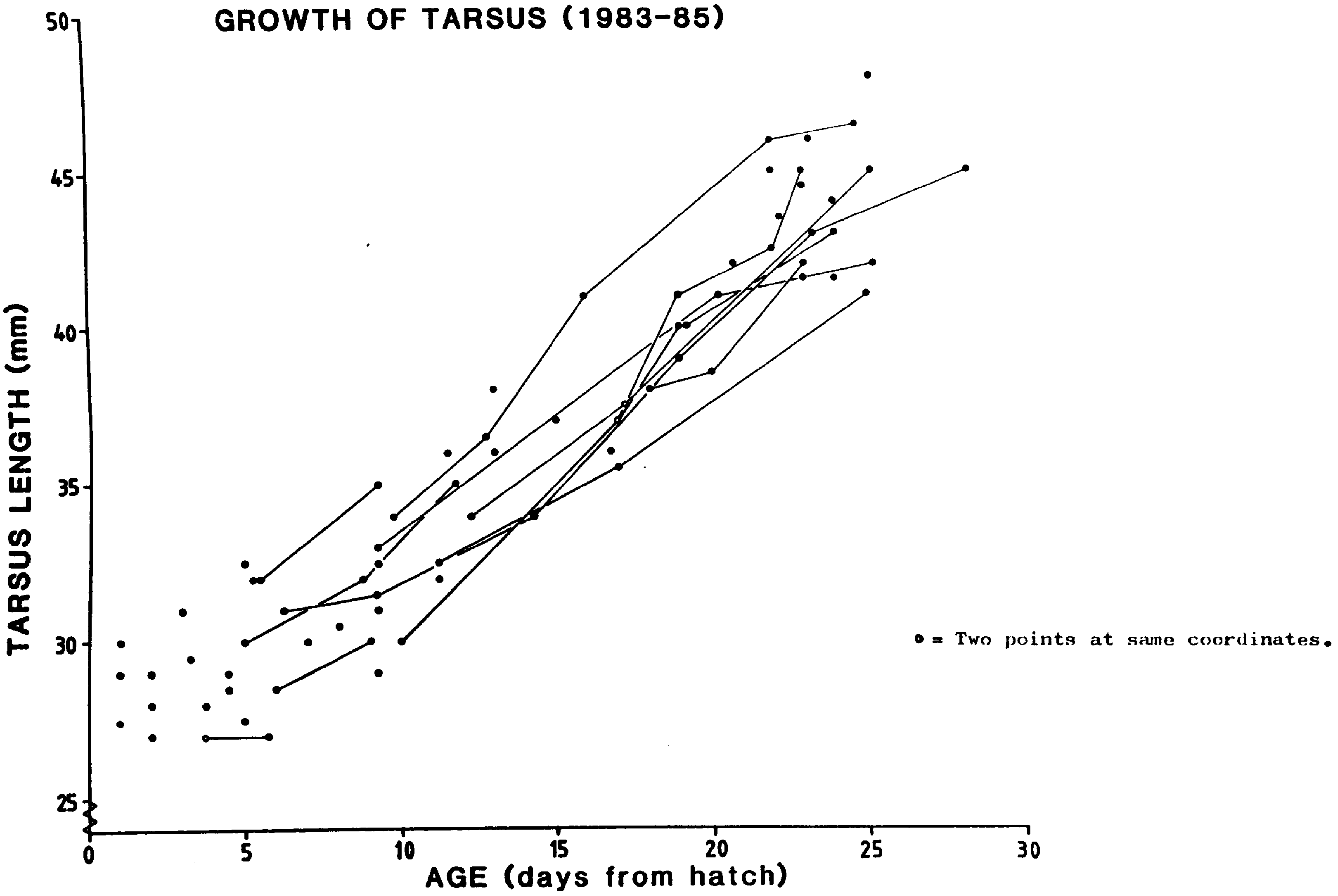
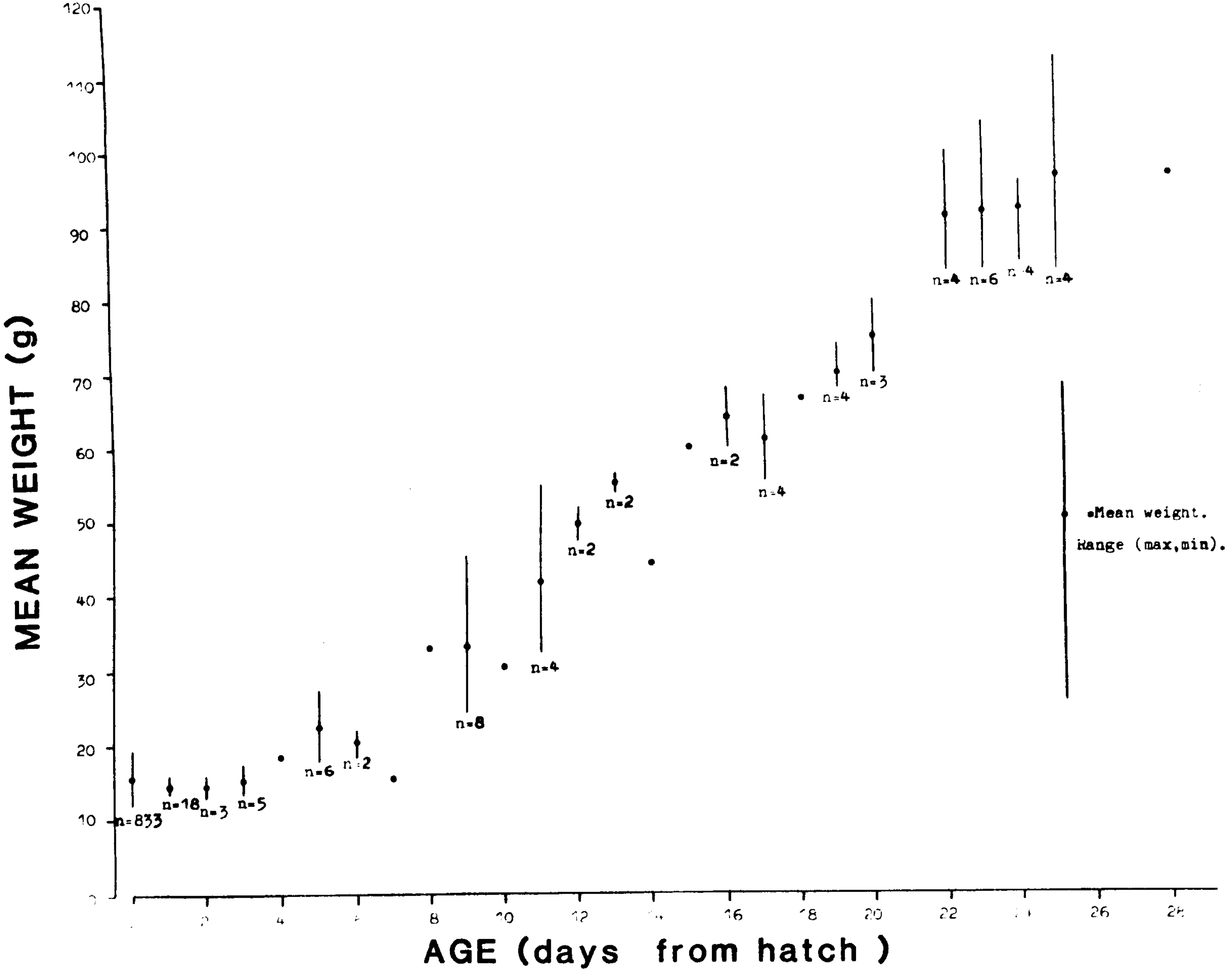


FIG.15 THE MEAN WEIGHT OF DIFFERENT AGED CHICKS



Observation of Figure 11 reveals an almost perfect relationship between chick weight and chick age. The correlation co-efficient calculated ($r = 0.97$) is highly significant ($p < 0.001$), indicating the very strong relationship that exists. Similarly, correlation values of $r = 0.95$ ($p < 0.001$) (age v tarsus) and $r = 0.96$ ($p < 0.001$) (age v bill to feathers) are equally of a high significance level. These figures suggest that there is little variation in growth rate between the chicks measured.

To determine the relationship between measurements and age, a multiple regression analysis was carried out. In this case both the age and measurements were known. However, it was intended that measurements could be used to predict age where this was unknown. Therefore, age was taken to be dependent variable. The independent variables were weight, tarsus and bill to feathers length.

Table 4.5 Beta values and F-ratios for the relationship between chick age and chick weight, tarsus and bill to feathers.

Dependent Variable		Independent Variables		
		Weight	Tarsus	Bill to feathers
Chick Age	Beta	0.626	-	0.354
	F	29.9***	n.s.	9.5***

Significance values associated with F-ratios (d.f. 2,74)

A total of 97% of the cumulative variance was explained

Thus, the best predictors of a chick's age are its weight and its bill length.

Further examination of the data set revealed that all parameters measured were highly correlated with each other. In addition, the bill measurements allowed a comparison of the different measuring techniques, thus enabling the relationship between bill tip to feathers, tip to rear nares and tip to front nares to be studied. As already mentioned, this has stirred considerable interest amongst ringers over the last few years.

Table 4.6 The relationship between the different chick parameters measured.

Pearson's correlation coefficients (r)

	wt.	tar.	b/f	wts.	wtf.	T
Chick weight						
Tarsus	0.979*** (77)					
Bill to feathers	0.974*** (79)	0.975*** (77)				
Wing: to tip sheaths	0.837*** (14)	0.797*** (14)	0.714** (14)			
Wing: to tip feathers	0.938*** (37)	0.892*** (37)	0.856*** (37)	n.v.		
Tail	0.930*** (16)	0.871*** (16)	0.888*** (16)	n.v.	0.948*** (16)	-

n.v. = not valid

All chick parameters measured are highly and significantly correlated with each other. In particular, weight, tarsus and bill tip to feathers are very highly correlated. Thus a very strong relationship exists between these three parameters.

The correlation analysis between the three different bill measurements resulted in the following co-efficients.

	B/f	B/rn	B/fn
Bill to feathers (B/f)	-	-	-
Bill to rear nares (B/rn)	(78) 0.995***	-	-
Bill to front nares (B/fn)	(66) 0.992***	(66) 0.996***	-

These correlation co-efficients indicate the very strong relationship and the similarity in growth patterns of the young

Redshank's bill.

Growth data were gathered for two main reasons.

(a) To produce an age estimating Formula which could be readily used to estimate Redshank age.

(b) To study the growth and development of young Redshank with an aim to determining any differ ential growth that may occur between broods, within broods, within the season and between seasons (see Introduction).

I shall deal with the ageing technique first.

As noted from the correlation co-efficients (Figs. 11-14), all chick parameters are highly correlated with chick age. Ageing could therefore have been done by using one chick parameter.

It was felt that by using two chick parameters, the resultant age estimate would be more likely to take account of any unsual variants and thus would be more accurate.

With this in mind, a stepwise multiple regression analysis was run on age versus weight, bill to feathers and tarsus. The analysis was terminated after weight and bill to feathers were regressed because tarsus did not regress significantly.

The Equation arrived at:

(1) age = 0.165 weight + 0.474 X Bill to feathers - 5.407 (n = 77)

For age versus a single parameter (weight) the following equation was produced.

(2) age = 0.255 wt + 0.264.

Using Equation 1, chicks of known weight and bill measurement could be aged.

In many of the chicks re-captured at one day old, only the weight was measured. These chicks were therefore excluded from the ageing formula as no bill measurements were obtained.

In the case of Equation 1, 97.4% of the cumulative variance is explained, which is marginally more than the 97.0% of the variance explained in the single parameter regression of age versus chick weight.

The use of tarsus and bill to feathers measurement on their own is less noteworthy. In each case only 95% and 96% of the cumulative variance is explained.

Figures 16 and 17 are concerned with the second aim of the chick growth work. Sample size of chicks handled of known age was very small (91 re-captures). To sub-sample this low sample inevitably meant that no detailed statistcial analysis could be carried out. The curves do, however, strongly indicate general patterns of growth.

Fig.16. INTRA SEASONAL GROWTH RATE DATA.

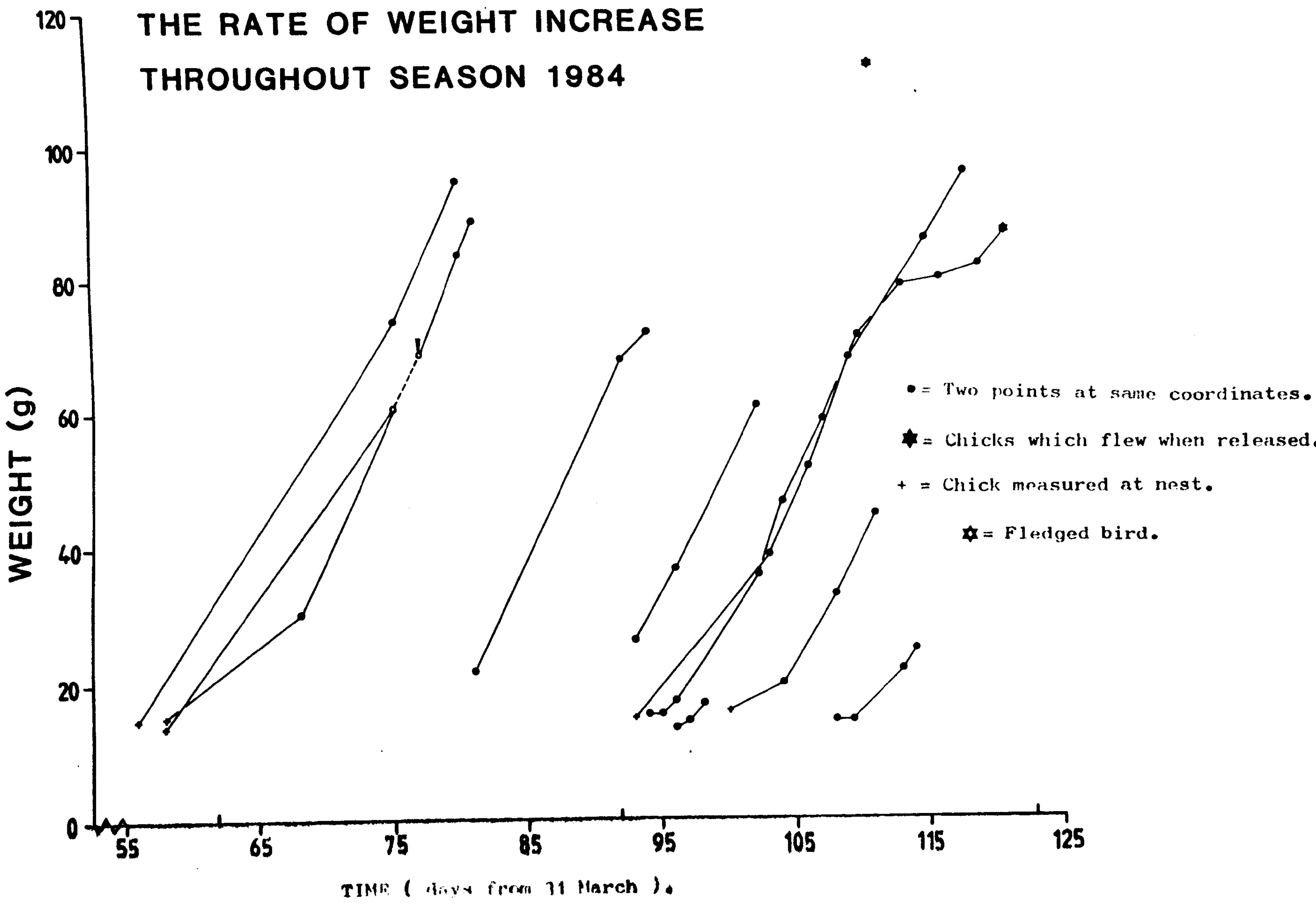


Fig.17. INTRA SEASONAL GROWTH RATE DATA.

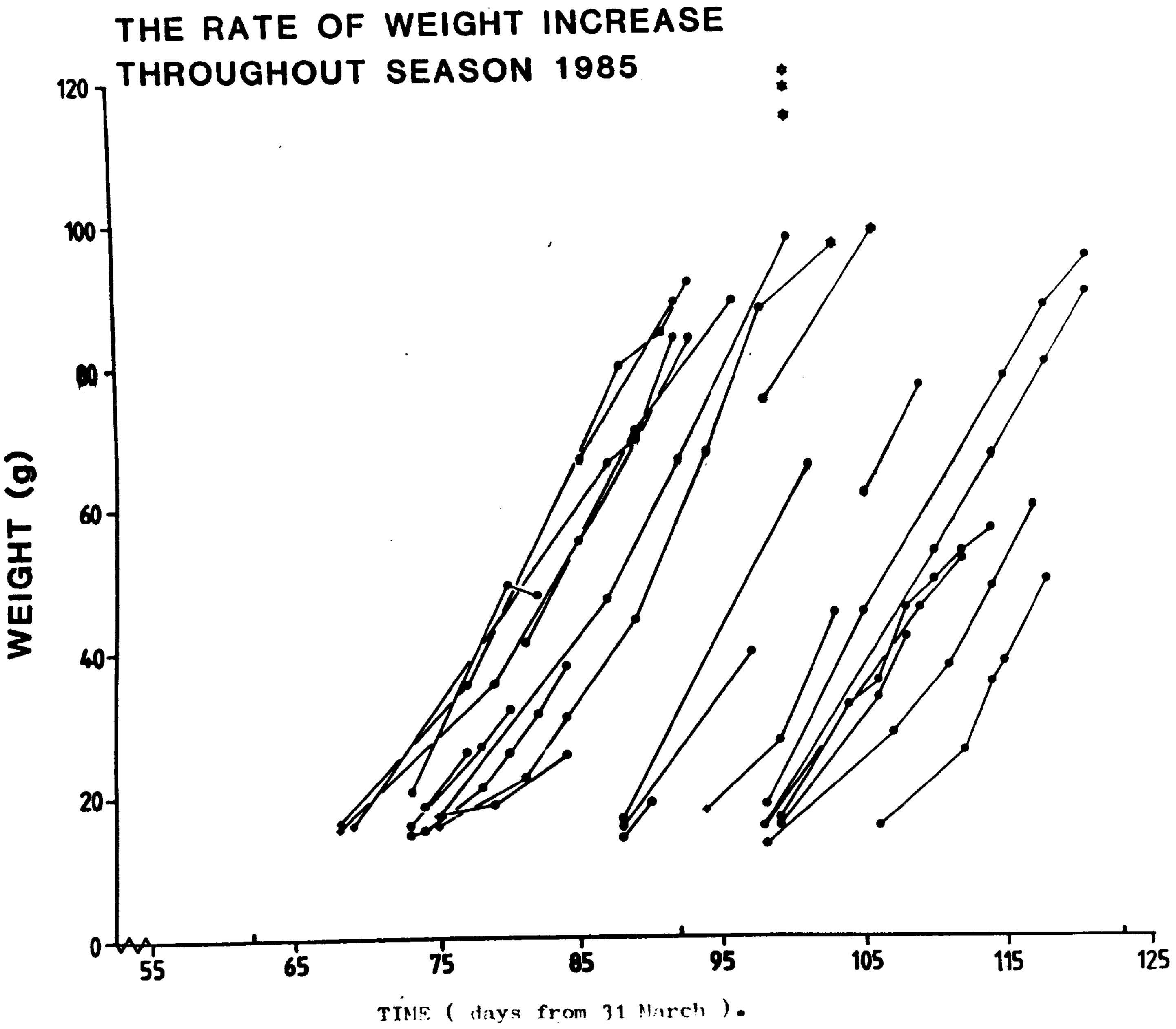
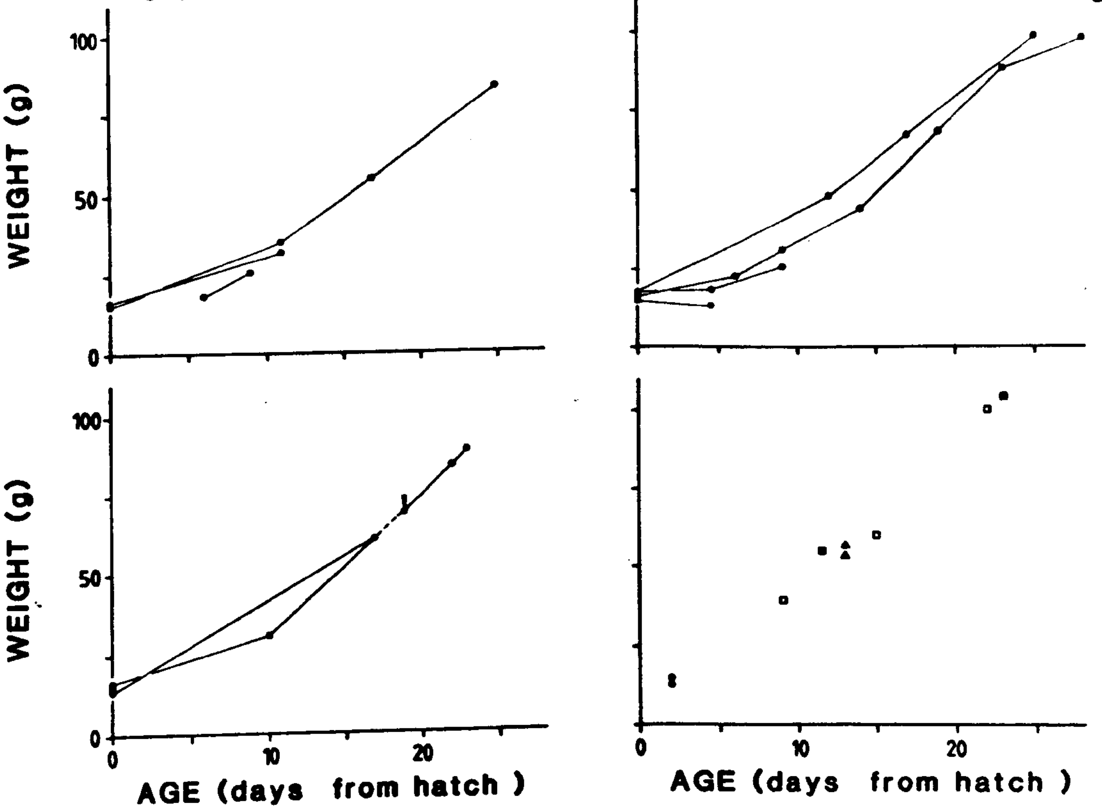
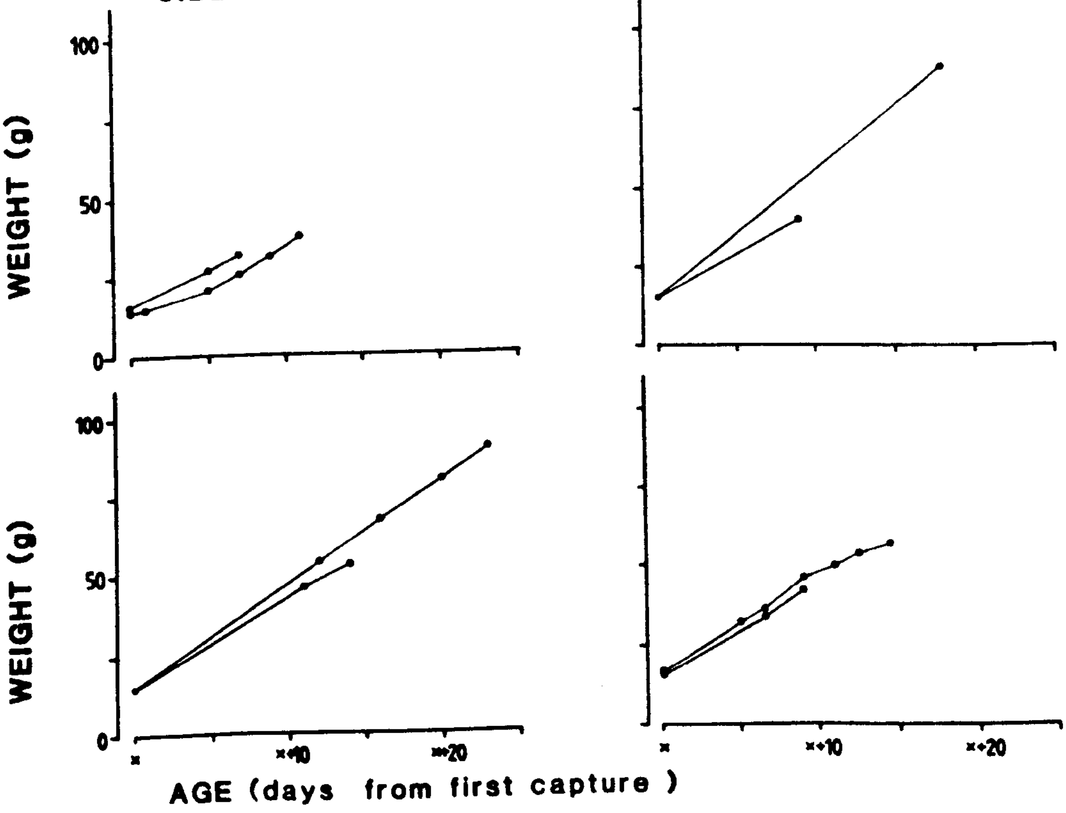


FIG.18

SIBLING GROWTH RATES (Chicks of unknown and known age).



SIBLING GROWTH RATES



Growth differences within broods

In the majority of broods followed up, it was unusual to find any more than one surviving chick. In the few cases where more than one chick was caught (not necessarily on the same day), the rate of growth and stage of development could be compared.

In addition to chicks of known age being compared, chicks of unknown age could also be compared.

Figure 18 suggests that even where more than one chick survives within a brood then the growth rates will still remain fairly constant.

Figures 16 and 17 can be used to observe differences in growth between and within seasons and between individuals.

Without detailed analysis of the individual slopes, any conclusions must be carefully considered before they are accepted. The following statements were considered to be truly representative of chick growth.

(a) Growth rate is consistent throughout the season (mid-May to early August).

(b) Growth rate is the same for both years in which detailed work was carried out (1984, 1985).

(c) Growth rates are very similar for individual chicks, no matter what year and what time of the season they are monitored. Note that in this case I am not referring to differences in growth rate throughout the fledging period of an individual.

Referring to (a): No further comment can be made as to break up the data would further reduce the sample size.

In reference to (b): A simple bivariate regression analysis of the 1984 and 1985 growth data allows for the gradients of individual parameters to be studied (see Figure 19 and Table 4.7).

Fig. 19 The annual growth rates in young redshank of weight, tarsus and bill tip to feathers as shown by regression slopes. Data for year 1984 and 1985

(for sample size and actual gradient see Table 4.7)

Upper line (1) = 1984 data

Lower line (2) = 1985 data

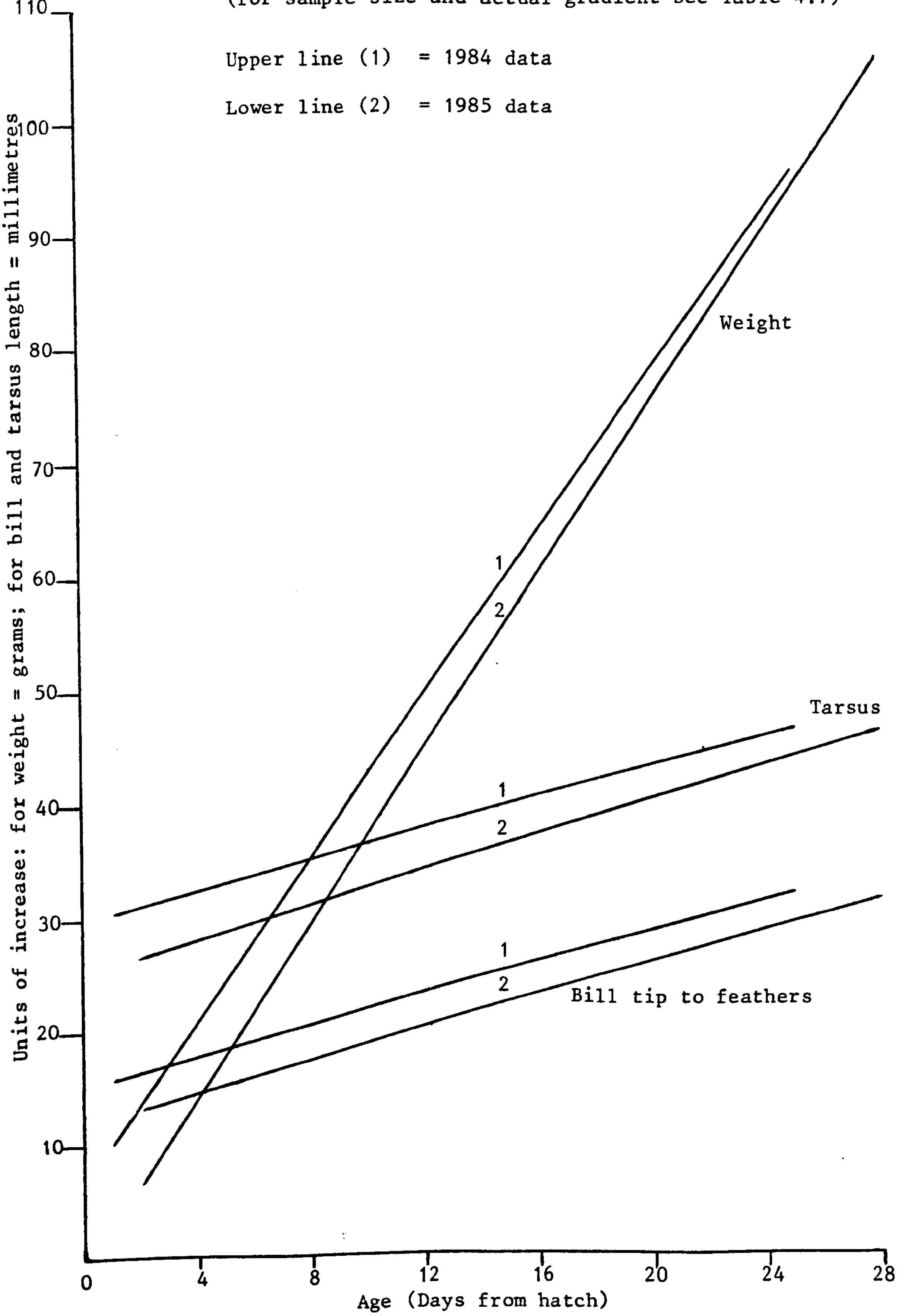


Table 4.7 The gradients calculated to represent rate of growth: weight, tarsus and bill measurements (1983-1985).

	Slope of regression							
Chick parameter measured	1983	(n)	1984	(n)	1985	(n)	Overall (1983-1985)	
Weight	2.98	21	3.5	23	3.79	47	3.49	91
Tarsus	0.77	11	0.65	19	0.75	47	0.68	77
Bill to feathers	0.96	12	0.67	20	0.70	47	0.68	79

From Table 4.7 it can be seen that the overall regression slopes have been affected by the small 1983 sample. The data do show the degree of similarity in rate of growth between 1984 and 1985 which could be drawn for all chicks of known age and re-captured in both years. Growth in both these seasons is similar as supported by Figures 16 and 17.

The largest degree of variation was found in the growth of individuals between broods. Thus, some individuals grew more rapidly and achieved a greater size than other individuals did over a given period of time (see Figure 11).

This results section finishes with several observations which are relevant to the Discussion which follows.

Redshank broods do not generally mix. Over the years several aggressive encounters have been witnessed between pairs shepherding their broods along the same ditch. These encounters were often quite violent and often involved both members of each pair. Secondly, an adult was observed on a ditch where it was known to have two chicks. On searching the ditch only one chick was found. A second adult (not attached to the first) on another ditch escorted a chick to the first ditch, where the chick joined the first adult. The second adult returned to its ditch whilst the first adult 'apparently furious' with the straying chick, flipped it over with its beak. Both adult and chick then ran down the edge of ditch one. A further search revealed two chicks now in the ditch (both ringed). A search in the second ditch revealed a much older chick which had not been previously ringed. Both broods were being tended by single adults. This demonstrates that birds do have the apparent ability to recognise their own chick and do have the ability to sort out a mix up, should one arise.

Chick mortality, although known to occur at a high level, is not easily quantified. The most common causes of chick death were predation (Kestrels and Herring Gulls) and low temperatures leading to death by lowering of body temperature. It is likely that many of those predated upon were already weakened in some way. A chilled chick is feeble and calls persistently, thus attracting predators. Other causes of death were hatching death (chick died during hatching) and crushing by cattle. In total, only a tiny percentage of chicks dying were probably ever found. The majority taken by predators were almost certainly removed from the study area.

The summer of 1985 was particularly cold, with June and July temperatures below average. It is therefore interesting to record that 62.5% of all chicks found dead were in 1985. Many of these deaths could, I feel, be attributed to low temperatures and subsequent increase in predation.

DISCUSSION

It is difficult to compare these results with others. Apart from studies on Redshank, the only others have been on Lapwing, Ringed Plover, Kentish Plover and Common Snipe. Therefore, no other Tringine Sandpiper has been subjected to a similar study of their young.

In many ways, Grosskopf's study of Redshank (1958a, 1963) led the way for further study. In the aspect of chick growth, however, the study is less intensive and offers no real break-through on wader chick growth. In fact the results in this part of Grosskopf's work (1958a) conflict more than any other with work carried out on the Ribble.

Grosskopf highlights the problem of chick re-capture and of the variable nature of chick weights. Fledging on the Wangerooge was considered to occur only between 28-33 days, with the latter length suggested as being more normal. This degree of variation is not so different from that encountered on the Ribble. The main differences concern chick weights. The variation in weight and state of development is understandable but the actual weights recorded by Grosskopf are very light. For example, 3 chicks at 20 days of age weighed, on average, 57.6 g (Grosskopf 1958a). On the Ribble, 7 chicks between 19 and 20 days of age averaged 69.6 g. Three chicks on the Wangerooge aged 25 days averaged 71.3 g (Grosskopf 1958a). A sample of 8 Ribble chicks, at 24-25 days of age, averaged 94.5 g. This is a clear and very surprising difference. The chicks caught on Wangerooge Island at 26 days of age, or more, were incredibly light and would suggest that something was very wrong with these Redshank, presumably related to their food supply.

Another point of interest fromGrosskopf's (1958a) paper concerns weight gain over a period of time. Over a period of 3, 5 and 6 days, young Redshank gained 1, 9 and 6 gms respectively. Similar time intervals for Ribble Redshanks give weight gains of 9.5 (average of 2 cases), 9 and 11 gms (average of 3 cases). It would appear that Grosskopf has discovered the tailing off effect which occurs in growth rate of chicks as they get older, but the weights at which these individuals are beginning to tail off (60,40 and 45 g) are way below the weights that the Ribble Redshank reach before they begin to slow in rate of growth.

Grosskopf's study does agree with this one in that he found the growth of siblings to be very similar (Grosskopf 1958a). Here we have two studies, carried out in different localities, but on a similar habitat type, the results being quite different. In their study of Lapwings, Jackson & Jackson (1975, 1980) found greatly protracted fledging periods and the chicks were lighter as a result of a very hot summer which dried up all the feeding places. Weather conditions can have an effect on growth rate, mainly by the effect on the food supply. Possibly, the Wangerooge chicks which seem to have been much lighter than the Ribble chicks were affected in a similar manner.

Young Redshank reared in captivity had a very similar growth rate to Redshank on the Ribble. After 1 week the young birds averaged 27.5 gms; after 2 weeks 60 gms; after 3 weeks 97 gms; and after 4 weeks 105 gms (Goss-Custard, Wilkins & Kear 1971).

At hatching, young Redshank are feeble. Within a few hours the chicks are dry and strong and are almost ready to leave the nest. An examination of the ratio of chick measurements to adult measurements reveals that in one measurement (Tarsus length) the chicks are particularly well developed at birth. The chicks therefore are born with very well developed legs, which are presumably important for movement through vegetation to feeding grounds, and running from predators. Shorter-legged individuals may be less quick and may find some of the longer vegetation difficult to pass over. I would suggest that this may be particularly important when the chicks leave the nest as young Redshank have to pass through the deep grass that surrounds their nest until they reach the shelter of the feeding grounds. Many parents took their broods on long journeys (up to 1 km), but then settled in an area. The feeding grounds were normally the interior of ditches where movement was much easier. Movement in the ditch was still important as often the tide came in very fast, putting chicks in danger of drowning. Young Redshank tended to hide in their feeding ditch rather than run away. But it is likely that strong legs were just as important here as they often hid on the side of deep edges and also pushed themselves into tiny cracks and holes half way up the ditch edge.

I conclude that long legs may be important for running through grass and debris and that they may also be important for climbing steep banks and for pushing a threatened chick into a hiding hole. Similar thoughts on the role of a long Tarsus are discussed in Kalas (unpubl. thesis 1982) and in Pienkowski (1983).

At birth, the bill length is just under one-third of the adult bill length. Little is known about the feeding patterns of young Redshank as most feeding on the Ribble takes place within the confines of a ditch. It is probable that initial feeding effort is directed at almost anything that moves. This pattern of indiscriminatory pecking has been witnessed in young Ringed Plover (Pienkowski 1983); and in young Lapwing (pers. observation). The main problem here is that pecks may be directed at objects so small that no swallowing motions would be detected, even if it were successful.

If the Redshank egg is a compromise between resources invested in the egg, and resources lost from the female, then it would appear that the state of development of the chick at hatch ought to be near optimum. With this in mind, one would expect body appendages to be of a similar state of development. If the bill was much longer at hatch, the directional and manipulative skills would be greatly reduced, possibly resulting in a decreased survival potential. One must therefore assume that bill length at hatch is the best length for catching small prey whilst standing on long legs. The long legs themselves are difficult to coordinate and it is not unusual to see a small chick tripping and stumbling while attempting to run away. The actual growth rates are therefore very different for the different appendages. At the time of fledging, the young Redshank has a near-full adult tarsus measurement and tail length.

The wing length, bill length, and weight, are still only 75-87% of the adult measurements. Growth therefore still occurs after fledging until the adult measurements are reached.

Full adult size is reached, for most young birds, probably between 40-45 days (but see weight and wing length). The fledglings caught in this study were of unknown age; these birds were assumed to have hatched at the time of the first nests known to hatch. I would therefore expect that the predicted ages are slight overestimates. Apart from weight, most fledgling measurements were the same as the adults. Juveniles do not reach adult weight until much later. A study in the south Camargue revealed that juveniles did not reach adult weight until November (see Glutz et al 1977).

The development of feathers in young Redshank was studied in considerable detail in 1985. Studies in 1984 indicated that the appearance of pins, eruptance of sheaths, and the full emergence of feathers may be a useful indicator of age. Feather development begins in different body regions at different times. By observing the different body regions, and scoring for state of development, it was possible to study this aspect of development.

The results indicated that a very arbitrary ageing could be carried out, but this could never be very accurate. There was a considerable degree of variation in state of development in any one body region. Ageing may be done on this basis, but care should be taken when interpreting results.

The disappearance of down and the emergence of the tail feathers was of particular interest. Every chick caught was completely downy until the age of 4.5 days. After this age, pins normally began to appear on the flanks and scapulars. Even at fledging the vent and lateral rump were often downy and the underside of the wings bald. Those areas which were normally covered by feathers of the wings were last to be covered in feathers of their own. Feather development takes place first in those areas most important for (a) insulation (flanks, belly, breast and mantle); and (b) flight (wings, tail). The development of the tail is particularly late in beginning. This could be a mechanism whereby early fledging is delayed as controlled flight is impossible without the use of a well developed tail.

The only wader study to have used feather development in a useful manner was that carried out by Lessells on the Kentish Plover. In this case, brood care was studied in broods of estimated age (the broods were aged according to feather development). (For further details see Lessells 1984). I stress again that I would tend to be wary of such a technique as the range in state of feather development is larger for chicks of any one age.

The data on chick growth represent an enormous amount of effort.

To some extent the return per unit time spent searching is very low, but in an aspect of biology where so little is known, every datum point can be an important contribution to our understanding of wader growth patterns.

The data analysis has been kept simple and the growth curves not transformed in any way. Although a log transformation would benefit the data, the overall aim has been to (a) highlight difficulties associated with wader chick work; (b) gather as large a set of data as possible; and (c) to arrive at an easy to use yet relatively accurate age determining formula.

With the initiation of the B.T.O.'s latest scheme to determine wader survival and natal philopatry, many ringers have become involved with capturing and measuring young waders. It is important that contributing ringers are able to understand and relate to findings if their interest is to be maintained. In Chapter 3, I have outlined the lack of knowledge in wader fledging and subsequent confusion in determination of natal philopatry. If our knowledge is to be increased in these and other aspects it is vital that the enthusiasm and diligence of amateur ornithologists is maintained. The over-riding need to gather and understand such data has also been described in Chapter 3.

If ringers cannot understand and relate to findings, subsequent interest will greatly decrease. I therefore suggest that at this stage at least, analysis of chick growth and survival are kept as simple and as intelligible as possible.

The first and most important finding relating to the B.T.O. scheme is that both weight and bill measurements are useful ageing criteria. Concerning the measurement of the bill, three measurements were taken (see Methods). The relationship between the three different measurements was such that any one could be reliably used as a representative of bill measurement. All bill measurements were made using a dividers and 15 cm ruler. The use of dividers in this case is considered unnecessary and probably no more accurate. Once again the simplicity of measurement would not deter an amateur ornithologist from taking measurements of any chicks caught. I would agree with the B.T.O.'s choice of age determining measurement (bill to feathers). Weight can be difficult to record on very windy days and may be liable to fluctuate more on a daily and hourly basis.

From Figure 15 a very interesting pattern emerges. There is a slight drop in weight from birth to 2 days of age, after which weight begins to increase. This drop in weight after birth has been recorded by Nethersole-Thompson & Nethersole-Thompson (1979), Redfern (1983), Soikkeli (1967) and Yates (unpubl. thesis 1982). Surprisingly, no such decline in weight was observed in a study of Lapwing chicks in the New Forest (Jackson & Jackson 1980).

At the end of the developmental period, just prior to fledging, the rate of weight increase begins to decrease. Thus the growth curve shows a gradual levelling out at the time of fledging. This is as found by Green (1985); Stiefel and Scheufler (1984); Tuck (1972); and Williamson (1960).

Growth rates of sibling Redshank are considered to be fairly constant, as found by Grosskopf (1958a) and Yates (unpubl. thesis 1982). Presumably, as chicks are reared together in the same ditch, then the rate of growth reflects the level of food availability. In ditches of poorer quality, the possibility of inter-sibling competition cannot be overlooked. It is possible that this is one reason why broods of more than one chick are so rarely encountered on the Ribble.

The growth curves suggest that rate of growth is the same in the early and late part of the season. In the early season there tended to be fewer broods (especially in 1983, 1985); and presumably less competition and aggressive encounter over use of given ditches. Thus feeding should have been fairly easy. Environmental temperatures were, however, lower in late May and early June, and subsequent heat loss would have been greater. The tidal cycle was also such that some disturbance of feeding occurred in early June. In the latter half of the season environmental temperatures were higher, so heat loss was not a problem. The ditches did tend to dry out, however, causing a scarcity of the moist areas for preferred feeding. In addition, more broods were present at this stage, resulting presumably in more competition for favoured feeding ditches. The end result of these, and no doubt other unknown factors, was a similar rate of growth throughout the season.

Chick ditches offer shelter (from extremes of hot and cold), abundant feeding areas, shelter from predators, and relatively easy movement. The vegetation surrounding ditches makes movement slow and difficult for the chicks. It is thus not surprising that ditches were favoured as feeding grounds. Very large ditches were only rarely used, presumably because of the exposure to predators and weather conditions and the nature of the very soft substrata which Redshank chicks appeared to find difficulty in crossing.

The growth rates between seasons appear constant. This was particularly so for 1984, 1985 (the data set for 1983 was too poor to warrant inclusion). This suggests that there was sufficient food in both years to allow similar rates of growth. In both years chicks have been caught both on and off the study sanctuary area. The quality of the feeding ditches are presumably slightly variable; but as little is known about the time spent feeding it is very difficult to determine if the achieved growth rate is the result of a constant or variable feeding rate between seasons and ditches. What can be said is that some Redshank stick to the same ditches, whilst others wander over the marsh using several different ditches in which to rear their chicks. Repeated catching attempts seemed to move some broods, whereas in other cases broods would remain in the same ditch even when being caught regularly. One other point concerned the initial movement of broods. A brood would often move a long distance (1 km), passing many ditches before finally settling on one ditch. Those broods often then stuck to the chosen ditch until fledging.

The bivariate regression slopes calculated from the 1984 and 1985 data set indicate that the rate of growth is more or less constant between the two years. The 1985 chicks do, however, appear to have started from a smaller size. The mean egg volumes of eggs 1-4 are in fact smaller in 1984 than in 1985. In addition, mean chick tarsus lengths are significantly smaller in the 1985 nestlings than in the 1984 chicks. There are no differences in chick weight and bill to feather measurements in nestlings from 1984 and 1985.

This difference in growth rate does seem to be a very real difference. Actual reasons are rather obscure. Obviously the fact that smaller eggs, and thus smaller chicks, were produced in 1984 does in some way explain the variation. However there are surely other factors involved.

We do not know if older more experienced birds are more successful at the chick-rearing level. We do know that in some years Redshank take their young to the same areas of the marsh (even the same ditch on some occasions), but it is not known how extensive this pattern is. Similar brood rearing site fidelity is documented in Greenshanks (Nethersole-Thompson & Nethersole-Thompson 1979).

The difference in growth rates between individuals from different broods is interesting but not surprising. I would expect some ditches to be of much higher quality than others and as a consequence chicks may benefit by satisfying their energy requirements relatively easily. In poorer ditches food would be less available and consequently foraging time would have to be increased. It is also probable, though not proven, that more experienced adults may control their young more efficiently, thus allowing for more efficient movement in and to the feeding grounds. Another major unknown factor concerns sex differences in growth rate. It is possible that the smaller chicks were in fact young males and the larger chicks young females. The data set is too small to test this.

Levels of predation were examined but very few firm conclusions can be reached. The mortality observed gave an indication of how death occurred, but the levels of death that must occur clearly indicate that only a tiny fraction of dead chicks are ever recovered.

In my own opinion, the majority of mortality occurs in the first four days. I would suggest that in most cases death is brought about by low environmental temperature which brings about a fall in body temperature. Of course if the chick is brooded then body temperature may be increased. Once they have left the nest the chicks separate out, in order to minimise risk of total loss of the brood. Once apart, brooding is more difficult as the chicks have to be drawn in from several points. At this very early stage chicks require regular brooding, especially when environmental temperature is low and when wind and rain are prevalent. A lack of brooding at this stage will result in a rapid deterioration of body condition and possible death.

Chick mortality may also occur when a brood becomes fragmented. When an adult is moving a brood rapidly to a ditch (perhaps up to 1 km away) there is a possibility that some chicks will get left behind. I would suggest that this is a time when brood reduction could occur. There are several documented cases of young waders being brooded by parents of different pairs. In those cases chicks have apparently been left behind and their brooding cries stimulated other birds to brood them (see Hakansson 1978; Hildén 1977; Thin 1942).

The evidence for rapid brood movement at an early stage of life is also well documented (see Hale 1955; Nethersole-Thompson & Nethersole-Thompson 1979; and Thompson 1982). I therefore conclude that mortality arises due to brood movement and fragmentation resulting in weaker chicks falling behind, chilling, and becoming feeble. As already stated, feeble chicks call persistently, thus attracting predators. Some predation of broods would take place as broods move across the marsh surface from the sanctuary of one ditch to another. At this stage adults are particularly attentive. However, they are not as effective at evicting predators as are the Common and Arctic Terns. In the presence of Terns, Redshank thus gain, as many large Gulls and Kestrels are forcibly ejected from the study area.

The only other major source of chick mortality is flooding. Again this is unquantifiable, but the largest tides will certainly be responsible for drowning some young Redshank, or at the most chilling them. When floods occur at night the potential for brood separation, and thus chick mortality, is even greater.

The survival of a young wader to fledging is very much an unknown quantity. If we are to learn more about populations and recruitment, then it is vital that all aspects of biology are fully understood.

Studies of plover chicks have progressed over the last few years; but sandpiper studies are sadly lacking, almost certainly due to the difficulty of chick capture. The overall aim should be to increase our knowledge and understanding of brood survival in order that reasoned arguments may be advanced about an area's productivity and general importance. Once this aspect of wader biology has been studied in greater detail, it may perhaps be possible to estimate productivity much more accurately. Where this can be achieved, the implications of land use change can be more readily quantified and more meaningful conservation measures can be taken to ensure that populations do not enter an irreversible decline.

Chapter 5

Redshank survival, mortality and population size on the Ribble Marshes

Introduction

From its inception in 1973, the Ribble Redshank project set out to study several aspects of Redshank biology. One of the main aims of this project was to determine how long Redshank live. Other objectives were to determine accurately the population of Redshank breeding on Banks Marsh and to attempt to discover what limits and regulates the population.

From the beginning, Redshank were colour ringed with several colour rings making each bird individually recognisable. In 1974 individually numbered metal rings, supplied by the British Trust for Ornithology, were placed on all birds captured. The use of colour and numbered rings allowed all birds recaptured in subsequent years to be individually identified. This formed the basis of the capture - recapture study which has continued up to the present date. Redshank have therefore been captured, marked and recaptured over a period of 14 years.

In all 14 years, Redshank have been captured on Banks Marsh. Unfortunately, the study area has not been the same in every year (due to problems of grazing cattle). The capture - recapture study is therefore confined to that area of Banks Marsh where work was carried out in every year. This area is known as the Restricted Area (see Yates, unpubl. thesis 1982). Yates estimated the study area as being 2 km^2 and the restricted area 1.04 km^2. The restricted area, however, is the area in which most nests are found.

All birds first captured and recaptured in the restricted area are included in the capture - recapture analysis. Birds which were first marked outside or were recaptured out of the restricted area are not included in the capture - recapture analysis.

Since 1973, 1156 Redshank have been ringed with B.T.O. metal rings. In the years of this study (1983-85) a total of 743 adult Redshank were caught, 271 of these being unringed. Where unringed birds were caught, these were ringed. Birds caught, which already carried a ring, had their number recorded. Thus, at the end of each season some birds had been caught for the first time whilst others had been caught in previous years.

Mortality/survival estimates

The method of Jolly (Jolly 1965) was used to estimate mortality and survival. This method requires several marking occasions (in this study an occasion = a year) and several chances of recapture. Where marked individuals are being considered, only the most recent date of capture is included in the analysis. Thus, each marked individual in the day i sample contributes only one mark (its most recent) to the total number of marked individuals caught on day i. The number of marked animals at risk in the day i population (M_i) means the number of marked individuals at risk in this case.

A summary of terminology used in Jolly's stochastic model (1965)

n_i = The number of individuals caught in year i.

m_i = The number of marked individuals caught in year i.

r_i = The number of marked individuals released in year i. (In this study $r_i = n_i$).

m_{ij} = The number of individuals caught in year i which were last caught in year j. (e.g. the number of females caught in 1984 which were last caught in 1981 = 5).

y_i = The number of individuals marked and released on year i and caught again in subsequent years.

z_i = The number of individuals marked before year i, not caught on year i, but caught in a subsequent year.

M_i = The number of marked individuals at risk in year i.

$$M_i = m_i + Z_i \frac{(r_i)}{(y_i)}$$

N_i = The population size in year i

$$N_i = M_i \frac{(n_i + 1)}{(m_i + 1)}$$

S_i = The chance of an individual surviving from year i to year i + 1.

$$S_i = \frac{M_{i+1}}{M_i - m_i + r_i}$$

Where survival is known, the life expectancy can be calculated.

Life expectancy = $\frac{-1}{K}$ where K = survival. $\log_e$

B_i = The number of additions to the population between year i and year i + 1.

$$B_i = N_{i+1} - S_i N_i$$

$\frac{m_i}{n_i}$ = The proportion of new unmarked birds captured.

$\frac{n_i}{N_i}$ = An estimate of the proportion of the population captured in any one year.

For further details on terminology see Jolly (1965) and Begon (1979).

The raw data from 1975-85 are shown in Tables 5.1 and 5.2. For the purposes of this study, males and females have been separated thereby allowing a calculation of male and female survival. All estimations are shown in Tables 5.3 and 5.4.

The use of Jolly's method requires that several assumptions are adhered to. These assumptions are briefly reviewed.

Assumptions of the Jolly stochastic method (1965)

For the Jolly method to operate accurately, several assumptions must be upheld. Many of the assumptions considered in this section have actually been considered in Chapter 3 on breeding site fidelity.

The first assumption is that all marks were permanent and noted correctly on recapture.

In this study, rings made of the hard alloy 'monel' were used. These rings have been found to show much less wear than the old type, softer metal rings. Rings were normally legible even on the oldest birds (13 years). In cases where rings were considered to be showing some sign of wear, the ring was replaced. It is probable that where the ring is attached to the bird above the knee then ring wear will be negligible.

I know of no case where a ring was discovered to have been mis-read.

All individuals, whether marked or not, had an equal chance of being caught.

Because females are less site faithful after a 'divorce', they are therefore probably less likely to be recaptured than males. For this reason, the survival data have been separated for both males and females (see Chapter 3, Table 3.11 and Tables 5.3 and 5.4). Within this period of study, all birds marked within the restricted area are considered as having an equal chance of recapture.

The capturing, handling and marking one or more times of an individual had no effect on its subsequent chance of recapture.

This assumption was upheld by Yates (unpublished thesis 1982), who noted that only the early years of the study could be used because in these years unringed birds were as likely to be old as they were young. In the latter years, unringed birds caught for the first time were more likely to be first years. Thus, in the later years, it proved difficult to separate age effects from first marking effects. The analysis of Yates (unpublished thesis 1982) indicated that being caught for the first time did not affect the chances of recapture significantly.

The capturing, handling and marking one or more times had no effect on an individuals chances of dying or emigrating.

This could not really be tested, but since all marked individuals have been shown to be equivalent, irrespective of the number of captures, it is reasonable that this assumption is held (Yates, unpublished thesis 1982). See also Table 3.4 and analysis in Chapter 3.

The age of birds did not affect their chance of recapture.

From Tables 3.3 and 3.6 in Chapter 3, it can be seen that young inexperienced birds appear to be less likely to be recaptured. In the main, I consider that this is because young birds are probably slightly less site faithful (see Chapter 3). It would therefore appear that this assumption is not upheld. Seber (1973) stated that if survival was independent of mark status and probability of capture is independent of age, then the Jolly method will not be greatly affected by age-dependent mortality.

Sampling periods were short in relation to the total time.

The average length of sampling (trapping) period between 1974-81 was 60.5 days. This is approximately 16.5% of the entire year and is considered as an acceptably small proportion of the total time.

The assumptions have therefore in the main been upheld.

Results

Table 5.1 The capture - recapture raw data of adult males for analysis by the method of Jolly (1965).

Year of release of marked Redshank (j)

Year i	n_i	r_i	1974	75	76	77	78	79	80	81	82	83	84	85
				Recapture marks M_{ij}										
1974	66													
1975	68		13											
1976	82		6	20										
1977	51		5	9	12									
1978	75		8	6	17	15								
1979	69		1	1	8	6	21							
1980	96		0	2	4	3	16	30						
1981	97		1	2	1	0	7	9	37					
1982	74		1	0	0	3	0	2	3	24				
1983	101		0	0	0	0	1	2	6	18	30			
1984	110		0	0	0	0	2	2	4	1	9	44		
1985	75		0	0	0	0	0	1	0	1	2	10	44	

Table 5.2 The capture - recapture raw data of adult females for analysis by the method of Jolly (1965).

Year of release of marked Redshank (j)

Recaptured marks M_{ij}

Year i	n_i	r_i	1974	75	76	77	78	79	80	81	82	83	84	85
1974	66													
1975	66		7											
1976	68		8	16										
1977	51		6	4	6									
1978	77		5	2	12	17								
1979	64		0	4	3	3	18							
1980	91		3	2	1	3	16	23						
1981	96		0	1	1	0	5	8	31					
1982	67		0	1	0	1	0	0	5	22				
1983	103		0	0	2	0	2	0	4	18	28			
1984	112		2	1	0	0	0	1	3	5	9	38		
1985	69		0	0	0	0	1	0	0	0	2	8	33	

Table 5.3 The calculation of the male capture - recapture data by the method of Jolly (1965).

Year i	n_i*	Y_i	Z_i	m_i	M_i	N_i	S_i	B_i	m_i/N_i	m/n_i
1974	66	35	-	0	0	-				
							0.764	-		
1975	68	40	22	13	50.4	248.4			0.27	0.19
							0.914	68.9		
1976	82	42	36	26	96.3	296			0.28	0.32
							0.815	-2.0		
1977	51	27	52	26	124.2	239.2			0.21	0.51
							0.662	1.2		
1978	75	47	33	46	98.7	159.6			0.47	0.61
							0.795	60.1		
1979	69	46	43	37	101.5	187			0.37	0.54
							0.901	39.9		
1980	96	50	34	55	120.3	208.4			0.46	0.57
							0.722	46.3		
1981	97	44	27	57	116.5	196.8			0.49	0.59
							0.649	96.4		
1982	74	41	38	33	101.6	224.1			0.33	0.45
							0.688	18.3		
1983	101	54	22	57	98.1	172.5			0.58	0.56
							0.683	53.1		
1984	110	44	14	62	97	170.9			0.64	0.56
1985	75	-	-	58	-	-				0.77
								Mean	0.41	0.51

* Note $n_i = r_i$ in this study

Overall S = 0.759

Life expectancy = 3.63 years

Table 5.4 The calculation of the female capture - recapture data by the method of Jolly (1965).

Year i	n_i^*	Y_i	Z_i	m_i	M_i	N_i	S_i	B_i	m_i/N_i	m/n_i
1974	66	31	-	0	0	-	0.880	-		
1975	66	31	24	7	58.1	486.6	0.925	-160.2	0.14	0.11
1976	68	25	31	24	108.3	289.9	0.663	116.7	0.23	0.35
1977	51	24	40	16	101	308.9	0.642	-14.3	0.16	0.31
1978	77	42	28	36	87.3	184	0.873	90.4	0.42	0.47
1979	64	32	42	28	112	251	0.696	18.7	0.25	0.44
1980	91	43	26	48	103	193.4	0.651	70.4	0.47	0.53
1981	96	45	23	46	95.1	196.3	0.662	87.6	0.49	0.48
1982	67	39	39	29	96	217.6	0.804	28.6	0.31	0.43
1983	103	46	24	54	107.7	203.6	0.614	56.4	0.50	0.52
1984	112	33	11	59	96.3	181.4			0.62	0.53
1985	69	-	-	44	-	-				0.64
								Mean	0.36	0.44

* Note $n_i = r_i$ in this study

Overall S = 0.741

Life expectancy = 3.34 years

All birds included in the results in Tables 5.3 and 5.4 were captured and recaptured within the restricted zone.

Tables 5.3 and 5.4 show the calculated estimates of M_i N_i S_i and B_i. In addition, the proportion of new birds and the proportion of the population caught annually is estimated.

In the last three years the number of marked individuals as a proportion of all Redshank caught was an average of 0.63 for males and 0.56 for females. Thus during the period of this study an annual average of 37% of males and 44% of females caught were caught for the first time. Over the period that the project has been running, the proportion of new birds annually caught has ranged from 36%-89% (for females) and 33-81% (for males).

In each year the proportion of the population captured varied. In the last two years it is estimated that 61% of males and 56% of females were caught. Overall, 41% of males and 36% of females were caught each year from the existing population. This is not a very good average as less than half of the birds present were actually being caught.

Annual estimates of survival from year n to year n+1 are shown in Tables 5.3 and 5.4. No estimates of standard error have been calculated as the use of these in this context is now questioned. Begon (1979) suggests that calculations of standard error should only be used with extreme caution. Begon also points out that some workers, notably Manly (1971) and Roff (1973) have stated that the estimates of standard error appear to be correlated with estimates themselves, thereby giving cause for concern (Begon 1979).

For these reasons I have rejected the use of standard errors but must accept that the population and survival results can only be used with extreme caution.

From the tabulated results it can be seen that survival fluctuates considerably from one year to the next. This is perhaps not surprising as there is considerable differences in winter weather conditions between years which may presumably have an effect on overwintering levels of mortality. There may also be annual fluctuations in the level of breeding season mortality. For example, the number of Redshank found dead during the breeding season has varied from one to four over the last four seasons. It is likely that a fairly high percentage of birds which are killed or die are never actually found. Similarly, after the very cold winters of 1981-82 and 1984-85, six marked Redshank were recovered dead by members of the public. In other winters, when the climate was more favourable, fewer or no Redshank were recovered. If one accepts that only a proportion (probably small) of dead birds are ever actually found, then clearly in some years the level of overwinter mortality may be high as highlighted by Davidson and Clark (1985).

The overall survival calculated for males is 0.759. Thus, mortality (1-S) = 0.241.

The overall survival for females is calculated at 0.741. Thus female mortality is 0.259.

The life expectancy for a male is 3.63 years and for a female 3.34 years.

The slight differences in male and female survival and thus life expectancy may arise because males are slightly more site faithful (see Chapter 3) and because females may suffer a heavier rate of mortality during the breeding season (five out of nine Redshank found dead on the breeding grounds in the last four years were females). In two cases, females had died/were killed whilst preparing to lay eggs. It may be that at egg laying time females are cumbersome and lethargic and are therefore more likely to be predated.

An overall estimate of adult survival = 0.75. Thus the annual adult mortality (including birds leaving the study area but still alive) is estimated at 0.25 and life expectancy is estimated at 3.48 years.

No direct estimate of juvenile mortality can be made from this study. However at this stage two facts based on this study can be advanced:

(a) Of these birds recovered or controlled away from mainland Britain, 42% were juveniles, thus supporting the idea of Hale (1973) that younger birds generally move further south during winter.

(b) The majority of birds recovered from the south and south-west of Europe have been shot. Thus by inference, young birds may be more likely to be shot.

According to Boyd (1962) estimates of juvenile mortality are in the range of 1.2 to 2.5 times as high as the annual adult mortality. For the purposes of this study I shall use the mean given by Boyd of 1.6 (Boyd 1962). Juvenile mortality is therefore estimated as being 1.6 times higher than adult mortality. Juvenile mortality is therefore estimated as 0.40. Therefore, approximately 40% of Redshank fledglings will die in their first year of life.

Populations

As a result of the capture recapture study, the population of Redshank within the restricted area may be estimated and population density calculated. In six out of ten years the female population has been estimated as being larger than the population of males. This is probably as a result of the lower breeding site fidelity exhibted by females (see Chapter 3).

Over ten years the male population ranged from 170 birds to 296 birds. The female population ranged from 181 birds to 487 birds. If we accept these population estimates then we can say that the number of birds in the restricted area has declined from 735 birds to 352 birds. This represents a decline over nine years of 0.52 or 0.058 per annum.

To remain stable, the population required a recruitment of 0.25 to balance the loss of breeding birds. As the population was declining by 0.058 per annum, then the annual recruitment required would be 0.19 (= 0.25 - 0.058).

This level of annual recruitment would ensure that the population would only decline by 5.8% per annum.

Since 1975, the estimated population of males has fallen from 248.4 to 170.9 in 1984. This represents a decline of 0.31 or an annual decline of 0.03.

Annual male recruitment = 0.22 (= 0.25 - 0.03). I have not attempted to estimate the annual recruitment of females because I feel that the level of breeding site fidelity exhibited is such that an accurate estimate could perhaps not be achieved.

Recruitment in the Banks Marsh populations of Redshank appears to be in the region of 19-22% per annum.

Before advancing further with these findings I must first say that the above caculations over simplify a very complex and natural dynamic system. Nonetheless, for the benefit of this study the results give a workable estimate which may be used further.

For an estimation of pre-fledging survival, Yates proposed a model which accounted for juvenile mortality, the proportion of inexperienced birds in the population and the hatching success of experienced and inexperienced adults (Yates, unpublished thesis 1982). With certain stipulated assumptions it is considered that this model does give a realistic estimate of juvenile mortality/survival.

The mean number of chicks surviving to breed per adult = SP

$$SP = HP \times PF \times FY$$

HP = the number of chicks hatched per adult

$$= \frac{(A_1 \times P_1)}{BP} + \frac{(A_2 \times P_2)}{BP}$$

BP = Breeding Population

PF = prefledging survival

Fy = juvenile survival

A_1 = the proportion of 'inexperienced' breeding adults. (These are first time breeders = recruits).

A_2 = the proportion of 'experienced' breeding birds. (These are birds known to have bred before = controls).

P_1 = the chick production of 'inexperienced' birds

P_2 = the chick production of 'experienced' birds. In this study SP = A_1.

In the above, the prefledging success is the only unknown.

Fy = C.60 (Boyd 1962)

A_1 = 0.19 - 0.22

A_2 = 0.78 - 0.81

P_1 (Inexperienced first time breeders) = 0.98

P_2 (Experienced breeders) = 1.29.

The figures for P_1 and P_2 have been calculated from the data gathered in 1983 and 1984. At any one nest the breeding experience of the female was calculated and taken as an index of the experience of the pair. Although not technically absolute, this is better than summing the years of breeding experience found at any one nest. The figure obtained for the number of eggs hatched per pair was then halved to give an estimation of the number of chicks hatched per individual. The first two years of this study were sufficiently different as to be the best and worst year over the three year period.

$$\text{The prefledging survival} = \frac{SP}{HP \times Fy}$$

Where $A_1 = 0.19$ and $A_2 = 0.81$: Where $A_1 = 0.22$ and $A_2 = 0.78$

then $PF = 0.26$ then $PF = 0.30$

Therefore the fledging success varies between 26-30%, depending on the level of recruitment that is accepted.

The level of recruitment accepted has been based on the estimated decline of the population. There is, however, a possibility that the population has not actually declined but in fact has remained relatively stable. The observed trend of a decline in population may therefore be interpreted as an estimate which is becoming more accurate. A review of Appendix 8 shows that the number of nests found within the restricted area has ranged from 116 to 173 nests. There is no indication of an overall decline. However, it should be stressed that search effort may not have been constant between years. This was almost certainly true of 1982 when only one person walked the study area regularly. In 1985 the lower number of nests was attributed to an increased level of overwintering mortality. Mortality was thought to have been high during the winter of 1984-85 as a result of severe weather conditions (Davidson and Clark 1985).

The previous estimates of pre-fledging success were based on the assumption that the Redshank population in the restricted area declined over a number of years. If, for the purposes of estimating pre-fledging success, the population is considered to have remained stable, then a different estimate may be calculated.

Where A_1 is considered to be 0.25 and A_2 is 0.75 then PF (pre-fledging survival) = 0.34 (34%).

Thus, even when the population is considered to have remained stable, a fledging success of 34% is high enough to maintain numbers.

All estimates of pre-fledging success (26-34%) are encouragingly close to the field estimate of 32%

These are very interesting results which deserve further discussion. Before discussing these in full several problems and assumptions must be highlighted.

(a) The model assumes that juveniles enter the populations from the same area from which adults are caught (the adult catchment area). The results discussed in Chapter 3 indicate that a large percentage of chicks which return do so from the adult catchment area.

(b) The model assumes that hatch success is the same in all parts of the study area from where adults are returning. (This was found not to be so by Yates (unpublished thesis 1982)).

(c) Juveniles are as likely to move into the study area as they are to move out. If the ungrazed marsh is more attractive to site selecting Redshank, then juveniles may be more likely to move into the sanctuary rather than to move out.

(d) Although hatch success has been quantified for 'inexperienced' and 'experienced' birds we do not know if 'inexperienced' birds are less successful in aspects of brood care. In addition, we do not know if chicks are more or less likely to fledge in the grazed and ungrazed marsh.

I feel that the only real problem with this model concerns the estimates of P_1 and P_2. The higher the estimation of P_1 and P_2 then the lower will be the estimate of PF. The main problem here is that if there is competition between broods, chick mortality may be density dependent. Although I do not think this is likely to occur, some results do at least suggest that chick production may be less when the population is at its highest (see Ashcroft, unpublished thesis 1978).

All these factors make the use of a simple model appear very inadequate. However, when these points are all considered it is probable that the model gives a reasonable estimate of pre-fledging success.

This model therefore suggests that the Pre-fledging mortality is in the region of 66-74%. The estimate of mortality from field observations was 67.9%. Thus the field based estimated compares favourably with the theoretical estimate.

From both field and theoretical calculations it therefore appears that between 26-34% of chicks which hatch actually fledge. For the purpose of the following section mortality shall be 70%.

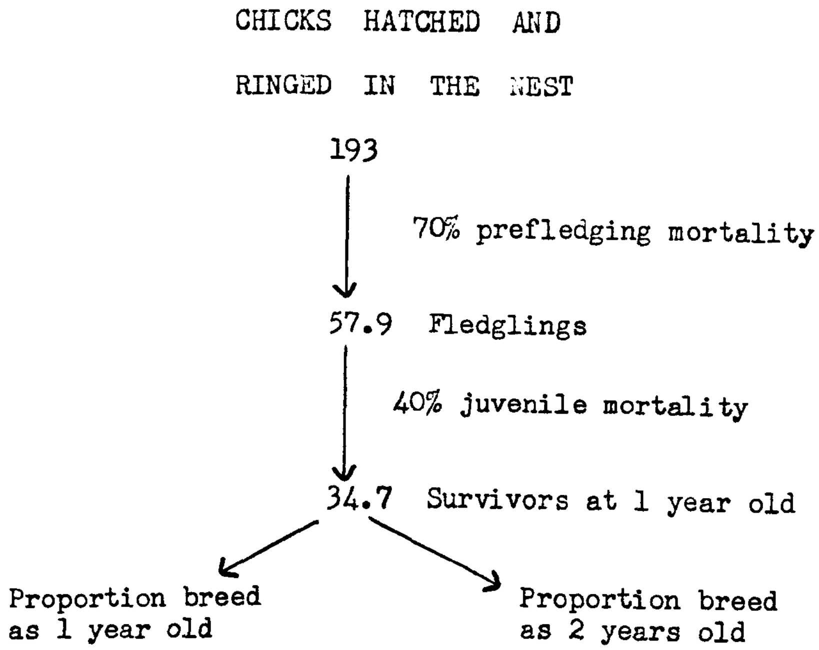
Of the chicks which fledge, 40% will die over their first winter period. This will leave a stock of Redshank which will be recruited to their population of origin. Of those birds which enter the population some will breed whilst others will not breed. The reasons for breeding or not breeding in the first year have already been discussed in Chapter 2.

From the information on breeding age of birds ringed as chicks the following statement can be made. Fifty percent of the chicks which returned to breed did so in their first year. A further 32% of all these returning were caught breeding for the first time as two-year olds. The remainder of chicks which returned and bred did so in their third year. Even if some birds bred but were not captured, the data suggest that at least some birds breed for the first time as two-year olds. Indeed Grosskopf (1964) suggested that most birds bred for the first time as two-year olds. Thus, it would appear that not all young Redshank nest in their first year. Of those that breed in their second year, the stock would be further reduced by a second year of overwintering mortality.

In the simplest form, the data may be used to examine the level of natal philopatry which exists.

If the first year of the study is taken (1983), the following figures may be advanced.

Year 1983



At the very simplest level, one can determine that from a cohort of 193 chicks, all of the same age, 34.7 could be expected to be alive at one year old (after pre and post fledging mortality). Of these chicks, 8 returned to breed and therefore must have survived to one year old. Thus a minimum of 23% of these birds likely to have survived have returned to breed. As already stated in Chapter 3, when the losses from pre and post fledging mortality are taken into consideration it would appear that natal philopatry is very high indeed.

DISCUSSION

Many different workers have attempted to assess mortality and population size with varying degrees of success. In an early paper, Grosskopf examined the mortality and mean age of some waders. In particular, Grosskopf reviewed the various methods of assessing mortality (Grosskopf 1964). Lack (1954) proposed a method by which life expectancy and mortality of birds could be estimated based on the number of recoveries of ringed birds. For the analysis, Lack used the data from the large number of ringing studies which had been undertaken in western Europe. This method was later modified by Haldane (1955) and used extensively by Boyd in a classic paper on mortality in European Charadrii (Boyd 1962).

In the Boyd method, there are several drawbacks which mean that mortality is always overestimated. Some of these problems are briefly outlined below.

(a) Birds recovered dead have often been shot. As already suggested, younger inexperienced birds appear more likely to be shot.

(b) Birds of different status (experienced, inexperienced) may overwinter in different regions, thereby affecting their chances of mortality and perhaps recovery.

(c) Ring loss raises the mortality compared with the actual mortality rate. Obviously if rings do fall off then ringed birds are less likely to be discovered. This is no longer a problem with the advent of more resistant, stronger, monel rings.

For the reasons discussed, it was generally considered that mortality and thus life expectancy was assessed accurately by the Boyd method.

The second method used to assess mortality is based on the frequency of return of marked individuals to a breeding or wintering ground. In this method, a number of individuals are given permanent marks. All individuals are captured in a specified area and their return to the area of marking is monitored over a given period of time. In addition, the number of unmarked birds are assessed.

The data may then be subjected to capture - recapture analysis using the model considered to be most appropriate. In this case, the method of Jolly (1965) was considered to be best. The Fisher - Ford method assumes the survival rate to be both constant and age-independent (Fisher & Ford 1947). In the case of the Redshank, there is evidence to suggest that survival, or at least recapture, is not age-independent (see Chapter 3, Table 3.4). The Manly and Parr (1968) method requires a large extensive sample for each year. It was considered that this could not be fulfilled, so the use of Jolly's stochastic model was considered to be most suitable.

As a general condition, all birds (males and females; experienced and inexperienced) must show a high degree of site attachment (either breeding or wintering site) to the site in which they are marked. Where birds are alive but no longer present on the site of marking then mortality is likely to be overestimated.

The above are the main ways by which annual survival can be estimated.

Estimates of mortality therefore vary depending on the method of calculation. Boyd (1962) has estimated the annual mortality of Redshank based on ringing studies in several European countries. The results of his findings are shown in Table 5.5.

Table 5.5 Estimates of annual mortality in Redshank based on the recovery of ringed birds in several European studies.

Annual mortality (%)	Country of ringing study	Authority
41	Great Britain (up to 1958)	Boyd (1962)
32	Sweden (up to 1956)	"
57	Denmark (up to 1956)	"
41	Other European (up to 1953)	"
44	West Germany	Grosskopf (1964)

The mean mortality is 43%.

From studies carried out on the breeding grounds, Redshank mortality has been estimated. The results of these studies are shown in Table 5.6.

Table 5.6 Estimates of Redshank mortality based on breeding and passage studies.

Annual mortality (%)	Study area	Type of study	Authority
18	Amagar, Denmark	Passage	Boyd (1962)
25	West Germany	Breeding	Grosskopf (1964)
17	N.W. England	Breeding	Ashcroft (1978)
23	N.W. England	Breeding	Yates (1982)
25	N.W. England	Breeding	Thompson (1986)

In this case, the mean adult mortality is estimated as 21.6%. Thus the estimation of Redshank mortality is half the estimated mortality calculated from ring recoveries. This would appear to highlight the problem of overestimation of mortality by ring recovery methods.

Some additional mortality estimates were calculated by Boyd for some other waders.

Table 5.7 Estimates of mortality based on the recovery of ringed birds (for selected waders).

Species	Mortality	Authority
Calidris alba	44 ± 11.3%	Boyd (1962)
Calidris canutus	32.4 ± 3.2%	"
Philomachus pugnax	47.6 ± 3.6%	"
Gallinago gallinago	51.9 ± 5.4%	"
Limosa lapponica	29.5 ± 7.9%	"
Numenius phaeopus	30.8 ± 9.1%	"
Tringa glareola	46.4 ± 10.2	"

The majority of these mortality estimates are very high. For reasons already mentioned, mortality is almost certainly overestimated in most of the above species. It is therefore apparent that estimations of the above type probably represent a maximum level of mortality which occurs.

The results shown in Table 5.8 have been gathered by research workers who have concentrated their efforts on one particular species in one particular area. In most of these studies, mortality is estimated purely on a percentage returning bird basis. Under these circumstances, the most accurate estimate would be achieved after a long term rather than short study. Unfortunately it is very often difficult to determine the time period over which the mortality estimated has been calculated.

Table 5.8 Mortality estimates of selected waders based on the return of adults to their breeding grounds.

Species	Mortality	Authority
Calidris pusilla	43.2%	Gratto, Cooke & Morrison (1985)
Calidris mauri	46.8%	Holmes (1971)
Calidris temminckii	19%	Hildén (1978)
Calidris minutilla	46%	Miller (1983)
Calidris alpina	25%	Soikkeli (1970b)
Micropalma himantopus	47%	Jehl (1973)
Scolopax rusticola	39%	Kalchreuter (1975)
Limosa limosa	36.9%	Glutz *et al* (1977)
Numenius arquata	28%	Glutz *et al* (1977)
Actitis hypoleucos	19%	Holland *et al* (1982)
Actitis macularia (female)	31.6%	Oring *et al* (1983)
Arenaria interpres	22.2%	Bergman (1946)

Note: Estimated levels of mortality have not been made for Red-necked phalaropes or Grey phalaropes *Phalaropus fulicarius*. These birds exhibit variable but often low breeding site fidelity making estimates based on the frequency of return completely worthless.

From Table 5.8 several points may be highlighted. Firstly, short studies such as Gratto, Cooke & Morrison (1985), Holmes (1971b), Jehl (1973) and Miller (1983a) have very probably overestimated mortality. In order to assess mortality in a breeding study over a short period of time, all breeding birds must be caught, marked and then recaptured over at least two seasons. Obviously a more accurate assessment is gained over a number of years as this is more likely to account for annual variation in survivorship.

Some of the more detailed long term studies, such as Bergman (1946), Hildén (1978a), Holland *et al* (1980), Oring *et al* (1983) and Soikkeli (1974), are probably good estimates of annual survival.

Finally, mortality levels are high in the Common Snipe and Woodcock Scolopax rusticola because these are game birds.

The annual mortality levels found in Redshank as a result of breeding studies are comparable with the annual levels estimated in some other waders. Hildén's study of Temminck's stints (Hildén 1978) and Soikkeli's study of Dunlin (Soikkeli 1970b) have both been detailed studies which were conducted over a considerable number of years. Since the beginning of Hildén's study in 1963 until the present day, Temminck's stint mortality has been estimated between 19 and 24%. As a result of the length of the study, Hildén discovered than an individuals mortality was related to its age and sex. In the Dunlin, Soikkeli showed that mortality was in the region of 25%.

In the North American Spotted Sandpiper, Oring et al (1983) discovered that female sandpipers exhibited a greater degree of breeding site fidelity than males. Where this occurs, and males are erratic in their fidelity, it is difficult to accurately assess annual mortality in relation to sex. As a result of their findings, Oring et al felt that only female mortality could be accurately estimated (in this case female mortality was 31.6%).

It is therefore of note that breeding site fidelity must first be estimated before annual mortality is estimated. If birds are not returning to their breeding grounds research must determine if these birds have died or have moved elsewhere to breed. Where birds are found to move from one area to another to breed then it is likely that mortality could not be accurately estimated from a breeding study. An individuals mating systems may be a reasonable predictor of the degree of breeding site fidelity likely to be exhibited. In the promiscuous, polygynous and polyandrous birds, breeding site fidelity may be very difficult to determine. In the case of polygyny, males move throughout a general area attempting to mate with as many females as possible. In the case of the White-rumped Sandpiper, the male never incubates so is presumably more difficult to catch (Parmelee et al 1968). In polyandrous birds such as the Phalaropes and the Dotterel, the females are constantly on the move laying clutches of eggs for one or more males. In this case, females may be difficult to catch therby making estimation of mortality very difficult (Nethersole-Thompson 1973; Schamel & Tracy 1977; Reynolds 1984). In lekking species such as Ruff and the Buff-breasted Sandpiper Trygnites subruficollis, males compete for females which do all the incubating and care solely for the young. In this sort of mating system it is likely that there would be a sex bias in mortality rates as it is generally agreed that females are more numerous than males. Where males return to the same lek on consecutive years, mortality could be estimated but if some birds tend to move around a general area then it is likely that male mortality would be overestimated.

Finally, a number of birds maintain a monogamous bond in one region and are polyandrous in other regions. The sanderling may be monogamous, sequentially polyandrous, or may even produce a clutch of eggs for her mate and a clutch for herself (Parmelee 1970; Pienkowski & Green 1976). Under such circumstances it is very important to know which mating system is generally prevalent in an area before accurate estimates of mortality can be made.

In the case of Temminck's stint, Hildén discovered that each male mated with two separate females and each female mated with two separate males (Hildén 1975). In this case, known as successive bigamy, both sexes incubate making estimation of mortality more straight forward.

It would seem that an individuals mating system will be closely related to the degree of breeding site fidelity exhibited and that breeding site fidelity in the large determines whether mortality may be estimated or not in a breeding study.

The Redshank is generally monogamous, with both birds sharing incubation and brood rearing duties. To a large extent, the degree of breeding site fidelity is fairly well understood making the estimates of mortality an accurate statement.

The data gathered on population size are therefore probably a good index of the real population within the restricted area. If the population of males is considered, it is apparent that the population fluctuates from one year to the next. Such population fluctuations have also been observed in Greenshanks (Nethersole-Thompson 1951; Nethersole-Thompson & Nethersole-Thompson 1979; Thompson et al 1986). The reasons for a fluctuation in numbers from one year to the next are by no means certain.

Some authors have suggested that density dependent competition for food, nesting space, or even mates, may regulate bird populations over a period of years. In Redshank there was a suggestion that the number of chicks hatched may be negatively related to the number of breeding females. When tested this was found to be non-significant.

In reality, competition between broods was rarely seen. Even in the best year (1984) broods never occupied even half of the available feeding ditches. It would also seem highly unlikely that food could ever be a limiting factor to Redshank breeding on the Ribble marshes. The area of mudflats are extensive, offering a rich supply of food in close proximity to the breeding grounds. Although a detailed study of the feeding patterns and distribution of Redshank has not been made, it is known that at least some birds use the intertidal flats when available.

Without detailed experimental work it would also seem to be impossible to say that availability of nest sites could ever limit the Redshank population on the Ribble. It is possible that this could occur early in the season when the growth of grass is slow, but it is very difficult to believe that nesting habitat is limiting later in the season when the growth of grass is so rapid.

It is possible, however, that the lack of nest sites may limit the population of Redshank on the grazed marsh. In many areas of the grazed marsh the grass remains very short offering no real scope for concealing a nest. In those parts of the grazed marsh where nests are built, reproductive success may be less as a result of the predation of poorly concealed nests.

Under certain conditions there may be density dependent competition for mates and for nest sites. It also seems likely that the spring tides are able to act in a density dependent way to reduce reproductive success. Redshank select the channel edges to nest on as these are higher and drier than much of the other green marsh. As a result of the drier substrata, the covering vegetation grows much faster providing early suitable cover for nest sites. Birds arriving later and birds nesting later often position their nests away from channel edges. This is probably because grass of a certain length is most attractive to site selecting Redshank. After a period of time the grass on the channel edges becomes very long and possibly is no longer as attractive as grass growing in other areas which are not as dry.

When Redshank breeding density is greatest, birds are found nesting in almost all suitable areas (both on and away from the channel edges). At such a time, a high spring tide may flood and destroy all those nests found in the lower lying areas of the green marsh. In most cases, higher tides destroy more nests because they encroach upon more of the saltmarsh.

When breeding density is lower, such as at the beginning of the season, fewer nests (proportionally) are lost to spring tides because the majority are positioned on channel edges. The tidal cycle is therefore able to reduce reproductive success in a density dependent manner.

In 1977 the spring tides were so high that almost all Redshank nests found were destroyed. As a result of the flood water only 17 young Redshank hatched and were ringed. In 1983 and 1986 two periods of high tides destroyed many nests, thereby greatly reducing the final number of chicks hatched. In other years the tides were less severe with the result that potential reproductive success was much better.

In those years when reproductive success was very high a large number of broods could be present on the marsh at any one time. Where this occurred, it is possible that some competition between broods may take place for the best feeding ditches. Therefore, there could be density dependent competition for ditches and the food and shelter that ditches offer. Although aggressive encounters were rarely seen between pairs with broods, there is still a possibility that this may occur. In those years where hatch success was high and many ditches held a brood, the weather could exert a density dependent effect in conjunction with the tides. When the water level rises broods are forced out of ditches onto the top of the marsh, thereby increasing the chances of predation and chilling. In the larger ditches broods could normally find refuge in side channels. Therefore under extreme weather conditions (very hot or cold and windy) brood mortality may increase where many brood rearing ditches are occupied.

Population regulation is unlikely to take place on the wintering grounds. Winter conditions can, however, substantially reduce bird numbers such that the number of available breeders is reduced the following spring. During the winter period of 1984-5, Redshank mortality was recorded as being higher than normal. Several Ribble Redshank and many other Redshank were found dead on the south coast of England. Those birds were thought to have died because their food items were not accessible (the mudflats had frozen over). (Davidson & Clark 1985).

In a review of the available shorebird literature, Goss-Custard found no direct evidence to suggest that offspring production was related to the number of breeding pairs. He does, however, point out that the exclusion of some potential breeders by the breeding stock could lead to overall chick production being density dependent (Goss-Custard 1981).

In an analysis of 14 years of breeding Greenshank data, Thompson et al showed that the population of breeding females was smaller following a cold June two years previously (Thompson et al 1986). The suggestion was that weather conditions two years previous reduced the survival of chicks and therefore the recruitment to the population in the following years. A similar finding was shown by Soikkeli in a study of Dunlin (Soikkeli 1970b). In this study, Soikkeli showed that the breeding density was affected by the number of young Dunlin produced two years previously.

Thompson et al also found that mean fresh clutch weight was inversely related to the number of breeding females present on their study area (Thompson et al 1986). However, this study also found that the number of chicks hatched was directly related to the number of breeding females. Unfortunately it could not be tested to see if these chicks were less likely to survive. Generally, lighter eggs produce smaller chicks which may have less yolk reserve and therefore may be less likely to survive. If this were the case, then the density-dependent effect on clutch weight could result in a density-dependent effect on offspring survival.

In a review, Evans and Pienkowski (1984) suggested that shorebirds may never reach the utopian levels of the carrying capacity of their habitats because adverse weather acts unpredictably to cause mortality on the breeding and wintering grounds. To an extent this may hold true for some populations but I am inclined to feel that future research will increasingly show the importance of density dependent regulation in wader populations.

I should like to finish this chapter by examining breeding density and estimating the overall population of Redshank on the Ribble Marshes. The restricted area was calculated as 1.04 km^2 (Yates, unpublished thesis 1982). In 1984 it was estimated that within this area there were approximately 175 breeding pairs of Redshank. This gives an overall density of approximately 168 pairs per km^2. Although not as high as the estimate of Yates (unpublished thesis 1982), both estimates clearly indicate that Redshank are nesting at very high densities on the ungrazed saltmarsh. Grosskopf's population was approximately 90 pairs per 18 hectares. This extrapolates to a population of 500 pairs per km^2, but of course in a species which nests semi-colonially in clusters or groups it is not valid to extrapolate. This is clearly demonstrated when one considers the density of 300 pairs per hectare published by Zhmud (1983). In this case I can only assume that the author was working on a group of Redshank in a small area. Although these birds were almost certainly nesting at high density, it is quite apparent that the study area was well below one hectare.

Nesting densities achieved in moorland and rough pasture are very much lower, although on occasion quite large groups (normally 15-20 pairs) may be found nesting in a small area of apparently suitable habitat (Sharrock 1976).

An assessment of the overall Ribble marshes population is made all the more difficult because of the lack of information on the grazed greenmarsh. From Crossens to Hesketh Outmarsh the area of saltmarsh is estimated as 8 km^2. Of this area, 2 km^2 is an ungrazed sanctuary. The remainder of the Nature Reserve greenmarsh is grazed by cattle.

I would estimate that approximately 250 pairs nest in the ungrazed portion of the Reserve. In the grazed marsh, densities may be up to a third less than the more favourable ungrazed areas. I would therefore tentatively suggest that there may be 250 pairs of Redshank nesting on the grazed greenmarsh. This gives an overall estimate of 500 pairs of Redshank within the boundary of the National Nature Reserve.

It must be stressed that this is a rough estimate. A more accurate estimate could be obtained if the breeding density of Redshank in the grazed marsh was known.

Saltmarshes, because of the proximity of an abundant food source and the luxurious cover of vegetation, are good breeding sites for Redshank. In this context it is therefore vitally important that as many areas of saltmarsh are conserved (both large and small). On a national level, saltmarsh is very much a threatened habitat with many areas being drained and reclaimed for agricultural development.

The Ribble Marshes N.N.R., totalling 2302 hectares, is therefore a site of national importance because of the plant and animal communities which have been conserved.

It is now vitally important that management is undertaken or at least the plant communities monitored in order to check that grazing (by cattle and wildfowl or non summer grazing (in the study sanctuary) is maintaining the vegetation in an ideal condition for breeding birds (notably Redshank and Common Terns) and wintering wildfowl. If the interests of both the wintering and breeding birds can be protected, then the Nature Reserve will be all the more valuable. If, as some suggest, lack of grazing in the summer is destroying the integrity of the saltmarsh plant community (F. Mawby pers. comm.) then research will have to be undertaken to determine how best this problem can be solved.

The densities of breeding Redshank, Black-headed Gulls and Common Terns demand that at least part of this area is managed with these species in mind. To manage this area with any other objective would almost certainly mean a large scale decline in Redshank breeding numbers and the possible loss of what is now a healthy population of Common Terns.

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APPENDIX 1 (a)

NEST DATA SHEET

Nest No.................

Ring No. Male...........

Female.........

Date found................. 1986

Time........................

Est. stage of Incubation......

Contents when found...........

Clutch......................

Final outcome anddate.........

....

Eggs (laying order)	1	2	3	4	5
Length (mm)					
Breadth (mm)					
Volume (cm^3)					

Date & Time	Nest contents	Date & Time	Nest contents

Date hatched...................

Incubation period..............

Hatching order of eggs	1	2	3	4	5
Hatching order of chicks	1	2	3	4	5
Ring No.					

APPENDIX 1 (b)

CHICK DATA RECORDING SHEET

CHICK BIOMETRICS 1985

CHICKS RINGED IN NEST

Nest No................. Clutch size............. Brood size..........

Date & Time of Ringing

Ring No.

Egg & hatch order

Egg tooth

Weight

Tarsus length

Bill 1. (to ff.)

Bill 2. (rear nares)

Bill 3. (front nares)

Notes

CHICKS RINGED AWAY FROM NEST

No. caught (& ringed)

Date & Time of ringing

Ring No.

Est. Age (egg tooth?)

Weight

Tarsus length

Bill 1. (to ff.)

Bill 2. (rear nares)

Bill 3. (front nares)

Wing length (to sheaths if present)

W-L (to ff. tips when erupted) & P. Score

Notes

CHICKS RETRAPPED

Date & Time	Ring No.	Posn.	Last caught	Age	Wt.	T	B_1	B_2	B_3	W_1	W_2 (+ P. Score)

APPENDIX 2

BIRD DATA SHEET

Date.............. 1986

Species REDSHANK Nest No.........

Trap No............

Time ....

New................

Ring No............

Control............

Sex.................

Age (tick)

First summer ....

1 year Old ....

Colour Rings

Left leg Right leg

Removed (tick)

Wing Tag

Left Right

(Col)

(Stripe)

(Symbol)

(Removed)

Biometrics

Weight................... (g)

Wing Left............. (Right............. (mm)

Tail : To feathers............ **(mm)**

Bill To feathers............... (mm) to Nares.............. (mm)

Tarsus Length................. (mm)

Tarsus Width.................. (mm)

Softparts (colour)

Tarsus............ Bill: Base............

Plumage

Mantle.....................

Breast....................

Scapulars Left............. Right.........

Secondaries Left........... Right.........

Primaries abraded (tick)

Juv. I.M. Coverts retained (tick)

Notes

APPENDIX 3

A list of the outcome of all nests indicating the main source of nest failure.

1983

Marsh nest(s)		%	Field/enclosure nest(s)	
Hatched	78	39.39	5	
Deserted due to trapping	19	9.59	-	
Deserted	4	2.02	-	
Flooded	71	35.86	-	
Predated	9	4.54	1	
Addled/nest failed/ collapsed	7	3.53	-	
Not completed	8	4.04	-	
Crushed by cows	2	1.01	2	
Unknown	-	-	1	
	198		9	= 207

1984

		%		
Hatched	166	84.26	2	
Deserted due to trapping	13	6.6	-	
Deserted	2	1.01	-	
Flooded	6	3.05	-	
Predated	1	0.51	1	
Addled	1	0.51	-	
Not completed	8	4.06	-	
Crushed by cows	-	-	4	
	197		7	= 204

1985

		%		
Hatched	106	64.24	5	
Flooded	26	15.76	-	
Deserted due to trapping	14	8.48	-	
Deserted	6	3.64	—	
Predated	1	0.61	3	
Crushed by cows	2	1.21	4	
Collapsed*	5	3.03	-	
Not completed	5	3.03	-	
	165		12	= 177

* collapsed nests due to very heavy rainfall

APPENDIX 4

A Comparison of the Breeding Biology of Redshank and Greenshank

	Redshank *Tringa totanus*	Greenshank *Tringa nebularia*
Male biometrics:		
Weight (g)	126.3 ± 6.5 (118)	163.3 ± 11.3 (12)
Wing length (mm)	166.5 ± 3.1 (118)	189.5 ± 3.7 (10)
Bill to feathers (mm)	40.6 ± 1.9 (118)	53.9 ± 2.1 (10)
Tarsus length (mm)	46.9 ± 2.0 (118)	60.7 ± 2.7 (9)
Female biometrics:		
Weight (g)	134.4 ± 8.0 (101)	199 (3)
Wing length (mm)	169.5 ± 4.2 (101)	189.7 ± 3.5 (12)
Bill to feathers (mm)	41.8 ± 2.0 (101)	55.8 ± 2.5 (11)
Tarsus length (mm)	47.6 ± 2.0 (101)	60.4 ± 2.0 (11)
Mean clutch	3.82 (533)	3.91 (389)
Fresh egg weight (g)	22 (80)	31 (171)
Egg length (mm)	4.501 (101)	5.143 (100)
Egg breadth (mm)	3.182 (101)	3.480 (100)
Mean clutch weight as a percentage of mean female weight	62.5	60.9
Factors affecting timing of laying	(a) Arrival date on breeding ground. (b) Cold spring delays start of laying. (c) In coastal Redshank, laying often timed to begin just after a sequence of spring tides.	(b) Arrival date on breeding ground. (b) In northern areas, laying occurs after snow has melted. (c) Laying occurs earlier in Scotland when latter half of April and early May are mild.

	Redshank	Greenshank
	(d) Bird age: older birds breed earliest.	(d) Older birds breed earliest.
	(e) Pair fidelity: faithful pairs nest earlier than new pairs.	(e) Laying may partly be under genetic control.
Laying intervals (hours)	38 (10)	44 (26)
Incubation	Occasionally begins on laying of the 3rd egg. Clutches of 1 and 2 eggs have been incubated to hatching.	Typically begins on laying of 4th egg but occasionally begins between 3rd and 4th egg. Incomplete clutches may be covered at night or during severe weather.
Incubation period (days)	The mean incubation period ranged from 25-26.3 days for three field seasons (193). Seasonal and annually variable. Longer periods due to disturbance or incubation by one adult only.	24.3 (36) Annual variation occurs.
Share of incubation	Incubation shared, male and female incubating for approximately equal times. Brooding spells shorter than in Greenshank.	Incubation shared, male and female incubating for approximately equal times. Males mainly incubate at night.
Egg chipping intervals (hours)	Ranged from a mean of 81-88.5 over three field seasons (191).	92.2 (19)
Eggshell disposal	Variable. Some birds remove all shells, others none. Removed shells often carried and dropped in the air from a height into pools and ditches.	Variable. Some birds remove all large shell fragments whilst other birds less vigilant. Shells carried an average

	Redshank	Greenshank
	Time of hatch and weather conditions may be important. Nests hatching at night or during bad weather often do not have shells removed. Damaged eggs often removed.	of 150 m and then dropped, often into a pool. Damaged eggs known to be removed. Some adults hide shell fragments under nest lining.
Length of time chick in nest (hours)	10.2 (104) Weather and hatch synchronicity affect time chicks remain in nest.	Ranges from 4-25. Weather affects time chicks remain in nest.
Breeding success: % nests hatching	62.5 (560) Annually and locally variable.	78.4 (111) Annually variable.
% eggs hatching from successful nests	88.7 (335)	92.2 (87)
Re-lays	Up to 2 repeat clutches produced (brood replaced if lost at early stage).	Up to 3 repeat clutches produced. Regional variation in ability to re-lay.
Time to produce re-lay (days)	If pair remain faithful, 12.4 (8). If pair split up, 13.2 (8)	13 (15)
Chick weight (g)	15.6 (833)	21 (74)
Chick size at birth as a % of adult size		
Weight	11.6	10.5
Bill to feathers	30.1	?
Tarsus length	59.1	?
Egg chick correlation at hatch	Egg volume v chick weight Pearson's $r = 0.729$, $p < 0.001$ (142)	Egg weight v chick weight Pearson's $r = 0.556$, $p < 0.01$ (13)

	Redshank	Greenshank
Brood care	Both sexes initially attend brood. Later in pre-fledging period one adult often deserts. Occasionally pair accompany fledged young.	Both sexes initally attend brood. Female often deserts brood in early half of season. Occasionally male deserts brood. Both members of pair sometimes accompany fledged young.
Brood rearing areas	Some areas known to be used by specific pairs in different years. In coastal birds, tidal patterns may affect areas used for brood rearing.	Traditionally, pairs take their young to the same area each year. Male leads female and chicks to feeding grounds. Much singing at this stage. Weather may cause variation. In some years pairs leave one area for same area to be occupied by another pair.
Brood mortality	Mortality is heaviest in first few days after hatch.	Mortality is heaviest in first few days after hatch.
Fledging success	Variable between years and localities. On Ribble marshes (England), overall fledging success estimated at 26-34%. In Wangerooge (Germany) fledging success estimated at 50%.	In Spey Valley (Scotland), 31.9% chicks fledged from 47 young which left nest.
Fledging period (days)	26.5-35	25-31
Breeding habitat	Wet meadowland, rough pasture, moorland and coastal saltings.	Blanket bog, stone-littered wet moorland; and forest marsh in Spey Valley and northern Europe.

	Redshank	Greenshank
Nest site	In tussock of grass, sedge or heather. Canopy normally conceals eggs from above.	Nests situated beside stone or rotting timber. Very rarely nest placed beside no obvious structure.
Breeding density	On Ribble marshes up to 115 pairs/km^2. On smaller marshes, density ranges from 1-12 pairs/ha. Locally, populations may reach very high density.	Ranges from 0.01-2.5 pairs/km^2. Locally there is large differences in density, with large numbers in very good areas.
Mating system	Monogamous. Polyandry and polygyny occasionally recorded.	Monogamous. Polygyny occasionally recorded.
Age of first breeding	1 and sometimes 2 years.	2 years, but breeding attempt may occur at 1-year old.
Age related breeding variations discovered	Older birds arrive back earliest, lay earliest and produce largest eggs. Old birds are more likely to breed successfully and as a consequence are more likely to return in later years.	More experienced birds complete clutches earliest, laying lighter eggs. Older birds are more likely to return and breed successfully than young birds.
Mate fidelity	One pair together for a minimum of 5 consecutive years. A second pair were together 5 times over a period of 9 years. 46% of birds returning in 3 consecutive years mated with the same partner. Some birds change mates every year.	Thought to remain faithful to partner from one year to the nest. Quantifiable data not available.
Nest site fidelity	Same nest scrape only rarely used on consecutive years.	Each nest scrape used for an average of 2.6 ± 0.09 years (117).

	Redshank	Greenshank
Breeding site tenacity	Age and success in previous year important. Males more likely to return than females.	Age and success in previous year important. Older successful birds more likely to return.
Breeding site dispersal	Sex differences exist. After nest failure pair more likely to split up. Males remain site faithful whereas females are more likely to disperse after failure resulting in mate separation. Within season dispersion similar to between season dispersion.	Faithful pairs less likely to disperse. Effects of success and mate separation uncertain.
Natal philopatry	High. A large percentage of chicks which fledge and survive the first winter return to breed in area of birth. No sex bias.	Probably high.
Natal dispersal	No sex bias in dispersal distance. Both males and females return to within 600 m of their birthplace (20).	Unknown. A ringed male nested within 1000 m of its birthplace.
Voice	For detail comparison study Sonagrams (Appendix 5).	
Song flight:		
Function	Mate attraction.	Attract mate, advertise presence and space out breeding pairs.
Height of delivery (m)	Approx. 10-50.	Normally 50-200. Rarely very low (10m) and up to c 300m.

	Redshank	Greenshank
Period of delivery	Most frequently in early morning and late afternoon/evening. Mainly prior to laying and particularly after large number of nests lost.	Early morning and evening. Particularly before laying and then before hatching. Unmated bird may sing at any time and with great vigour.
Nest relief	Not particularly elaborate. Later stages often conducted in silence.	Ritualised nest change. Wary birds take longer to change over. Generally very noisy, using rapid *'chip chip'* calls. Functions uncertain but may serve to indicate continued presence of breeding pair through incubation period (Nethersole-Thompson, *pers. comm.*).
Alarm calls	Noisy in latter stages of incubation and with young. In early season, nest and general area often left silently. Displacement song may be used at times of stress. A variety of special calls are used to silence chicks in nest.	Very demonstrative in latter stages of incubation and with chicks. Male may sing over hatching nest when disturbed. Alarm calls serve to call up off-duty bird when danger threatens. A variety of special calls are used to control chicks in egg and nest.
Brood care	A number of calls are used to control and comfort chicks. May be individual and sex differences in calls used. Once chicks have left nest,	A wide variety of calls are used to comfort chicks. Once chicks have left nest controlling calls may be detected as

	Redshank	Greenshank
	control calls are more subtle and may only be detected at close range. Adults respond to alarm calls of chicks, sometimes going 'frantic' and hovering over individual in trouble.	changes of pitch from normal alarm calls. May become aggressive and demonstrative when brood in danger.
Contact calls	Used when moving across breeding ground and when arriving at feeding ditches and pools.	Used when moving from one feeding area to another. When silent, may sometimes encroach on another bird's territory. If discovered, usually evicted.
Anti-predator strategy	Nests in high numbers, locally at high densities. A group of birds may join together and hover over enemy. Whilst hovering, the legs are dangled and a number of confusing 'shrieking' calls are used. Will attack aerial predators such as Herring and Lesser Black-backed Gulls and Kestrels. Benefit in some areas by associating with Lapwings (Rankin 1979) and Common and Arctic Terns (this study).	Aggressive when threatened. Will use low rapid flight and 'shrieking' calls to frighten predator. Will strike predators such as Crow <u>Corvus corone cornix</u>, Kestrel, and ground predators such as Stoat <u>Mustela erminae</u>. Large ground predators such as Red Deer <u>Cervus elaphus</u> may be forced away by diving flight, whereas Red Foxes <u>Vulpes vulpes</u> may be led away by a distraction display. Young children reacted to in a different way from older people. Anxious birds with young have struck humans.
Breeding distribution	Breeds in Continental middle latitudes, mainly in temperate and steppe but overlapping into	Broods in west Palearctic across Continental upper middle latitudes

	Redshank	Greenshank
	boreal and Mediterranean zones. Within oceanic regions extends into subarctic and marginally into low arctic (Cramp & Simmons 1983).	south of tundra, through taiga and forest zone to fringe of steppes, and also extending to boreal oceanic regions (Cramp & Simmons 1983).
Area studied	Ribble Marshes, N.W. England and N. Lancashire. Wangerooge Island, West Germany.	Northern and north-west Scotland, Scaninavia and Soviet Union.

Redshank - Greenshank Review

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APPENDIX 5

A Sonographic Comparison of Selected Calls of Redshank and Greenshank

This Appendix compares a few of the more important calls used by Redshank and Greenshank during their breeding season. It is hoped that in the very near future a much more detailed and thorough comparison may be made. For a full review of Voice in Greenshank see Nethersole-Thompson and Nethersole-Thompson (1979). A detailed description of Redshank voice is published in The Birds of the Western Palearctic (Cramp & Simmons 1983).

A total of 8 Redshank and 6 Greenshank Sonagrams are exhibited. Whilst this is only a fraction of the calls which could be represented, it is hoped that this small selection gives an impression of the degree of similarity and difference which exists between the two species.

Ideally I would have liked to compare calls of all the shanks, but in reality this is beyond the scope of this work.

Sandpipers (in particular the 'shanks'), are vociferous and sufficiently numerous and accessible to make recording on the breeding grounds fairly straightforward to the dedicated sound recordist. Sandpipers therefore offer excellent opportunities for understanding and interpreting functionally avian communication. It is also possible that detailed analysis of voice could lead to meaningful discussions on the relationships between different species. Finally, at the species level, comparisons of individuals could be made with an aim to highlighting differences and in particular dialects, as has been done for some passerine species. Certainly, from my own experience of two Redshank nests, there was considerable variation in the breeding calls of adults. Unfortunately, the sexes of the two individuals involved were unknown so it is possible that the difference in calls was sex based.

The standard way of illustrating and analysing calls or song is the Sonagram(Sound Spectrogram) providing a three-dimensional representation of sound (see Cramp & Simmons 1983). Periodic changes in air pressure produce bird sound waves differing over time, in amplitude and frequency (number of cycles per second, Hertz). Birds hear variations in sound waves in terms of loudness and pitch respectively.

In the Sonagram, the horizontal axis gives information about time (seconds), the vertical axis information about frequency (kilo hertz) i.e.how high or low the sound is pitched. The density of shading indicates relative loudness (anplitude). Generally, Sonagrams give a reliable graphical representation of sound produced.

Redshank calls graphically represented in Sonagrams

A Male song A repeated 'Tu Tu' used by male whilst carrying out switchback flight. Function: mate attraction.

B Male song on ground 'Taweeo-Taweeo' followed by copulation calls which consist of a series of rattling calls which are given prior to and during copulation.

C Chick calls In absence of adults, chick used a short 'peep-peep-peep-peep' call, unlike the more typical disyllabic call 'bsi-bsi' shown in Sonagram D.

D Adult returning to brood in nest Adult gives slow rhythmic 'chip-chip' calls. Chicks call prior to and after adult calls; 'Bsi-bsi'.

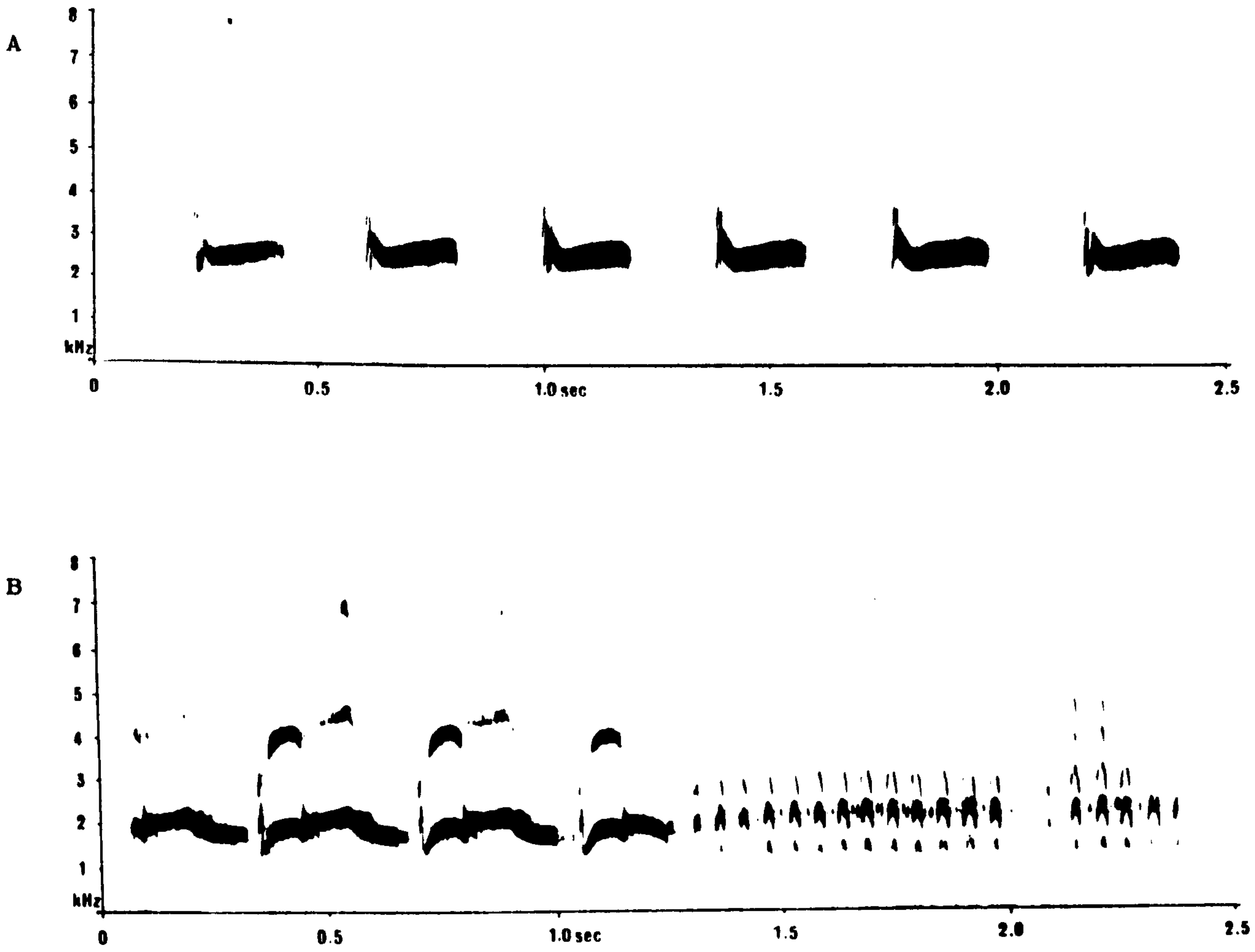
E Adult approaching brood in nest Now very slow chipping calls used. Chicks call in response to approaching adult.

F Adult arrives at nest Adult gives explosive calls - a series of 'Kok-kok' or Qwak-Qwak' as it arrives at the scrape. Chicks call in response.

G A very excited squealing call used by brooding adult; 'Kumeer-Kumeer' or Kemeer-Kemeer'.

H A second call used by a brooding adult whilst in attendance of a brood. A series of bubbling type calls rendered as 'oo-rooh-oo-rooh-oorooh-ooee-ooh'.

Selected Redshank calls.



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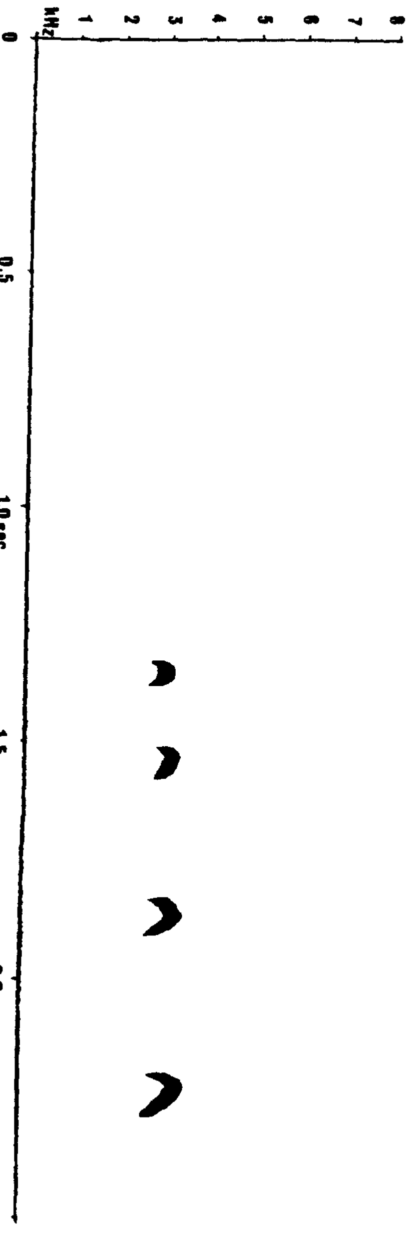
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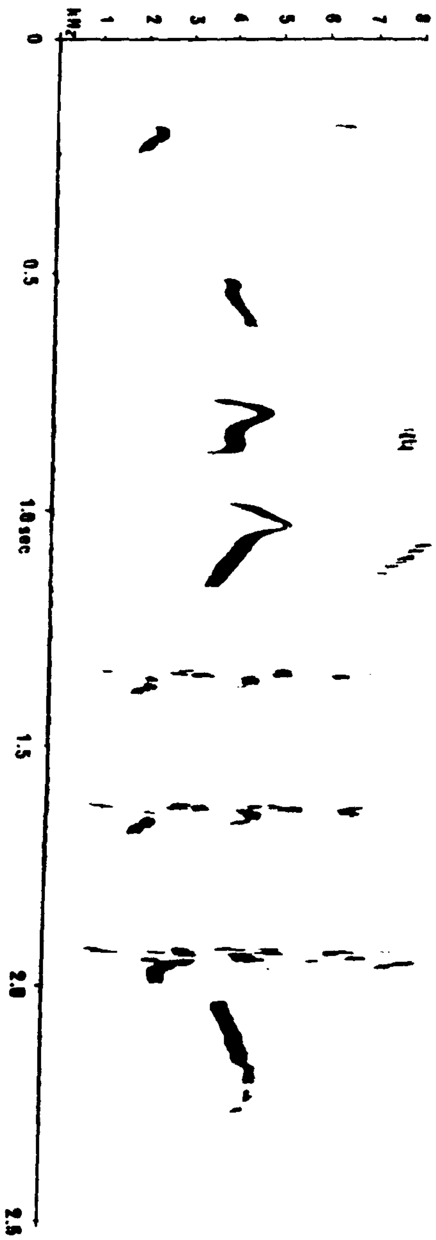
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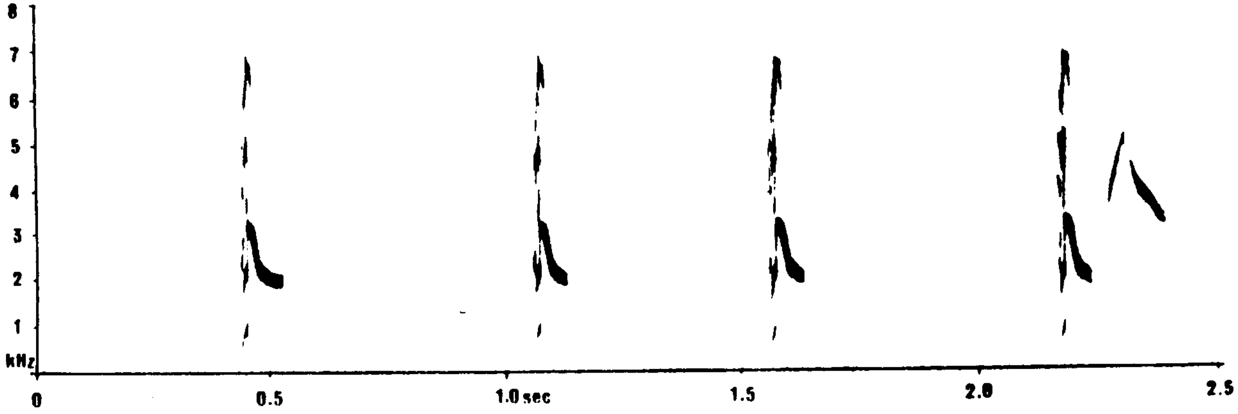
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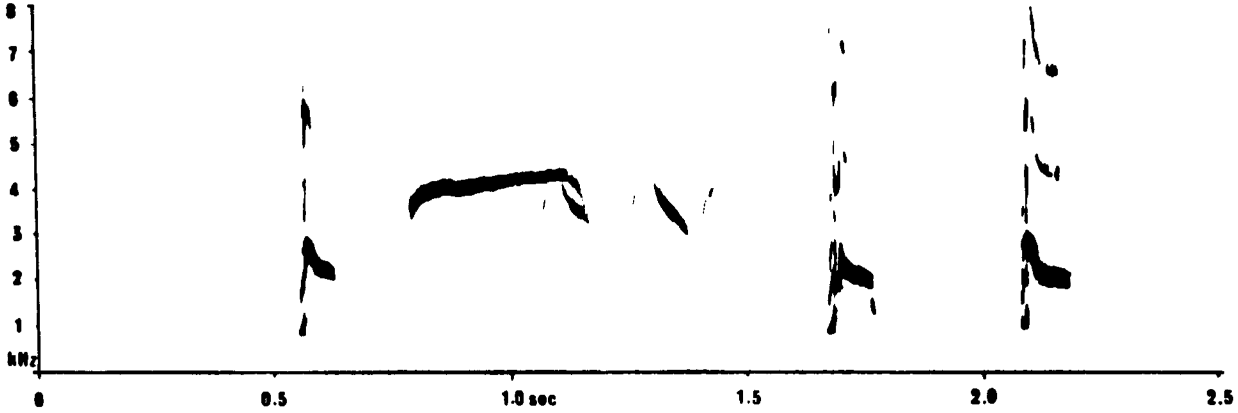
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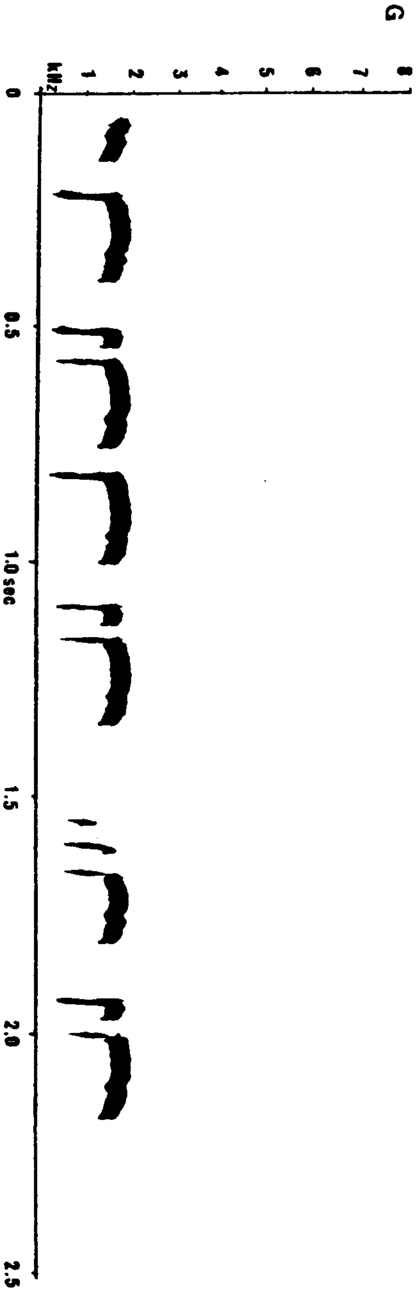

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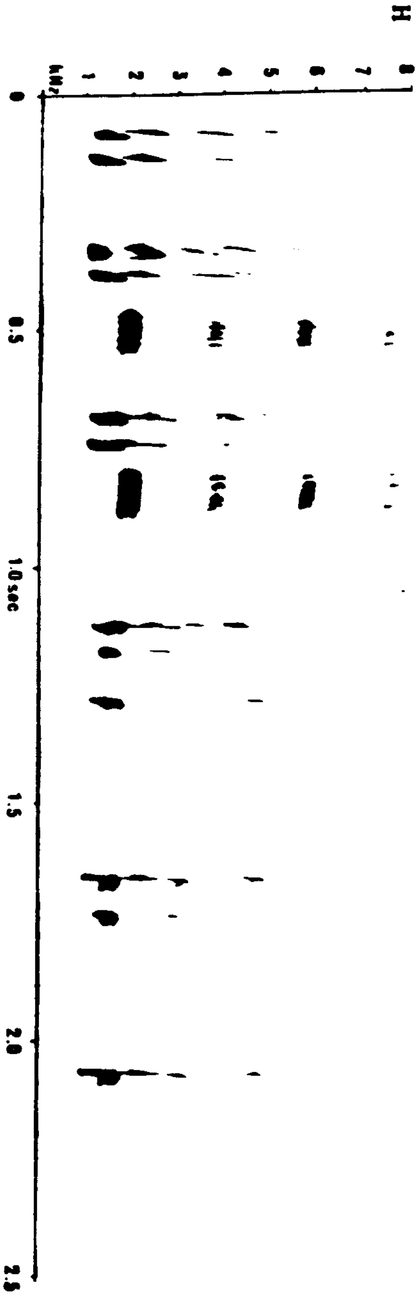

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Greenshank calls graphically represented in Sonagrams

A Male song A repeated 'Tew-Hoo, Tew-Hoo, Tew-Hoo', given whilst carrying out switchback flight. Function: spacing, mate attraction.

B Male copulation call A rattling/grating call given at a period of intense excitement as the male approaches and then copulates with a mate.

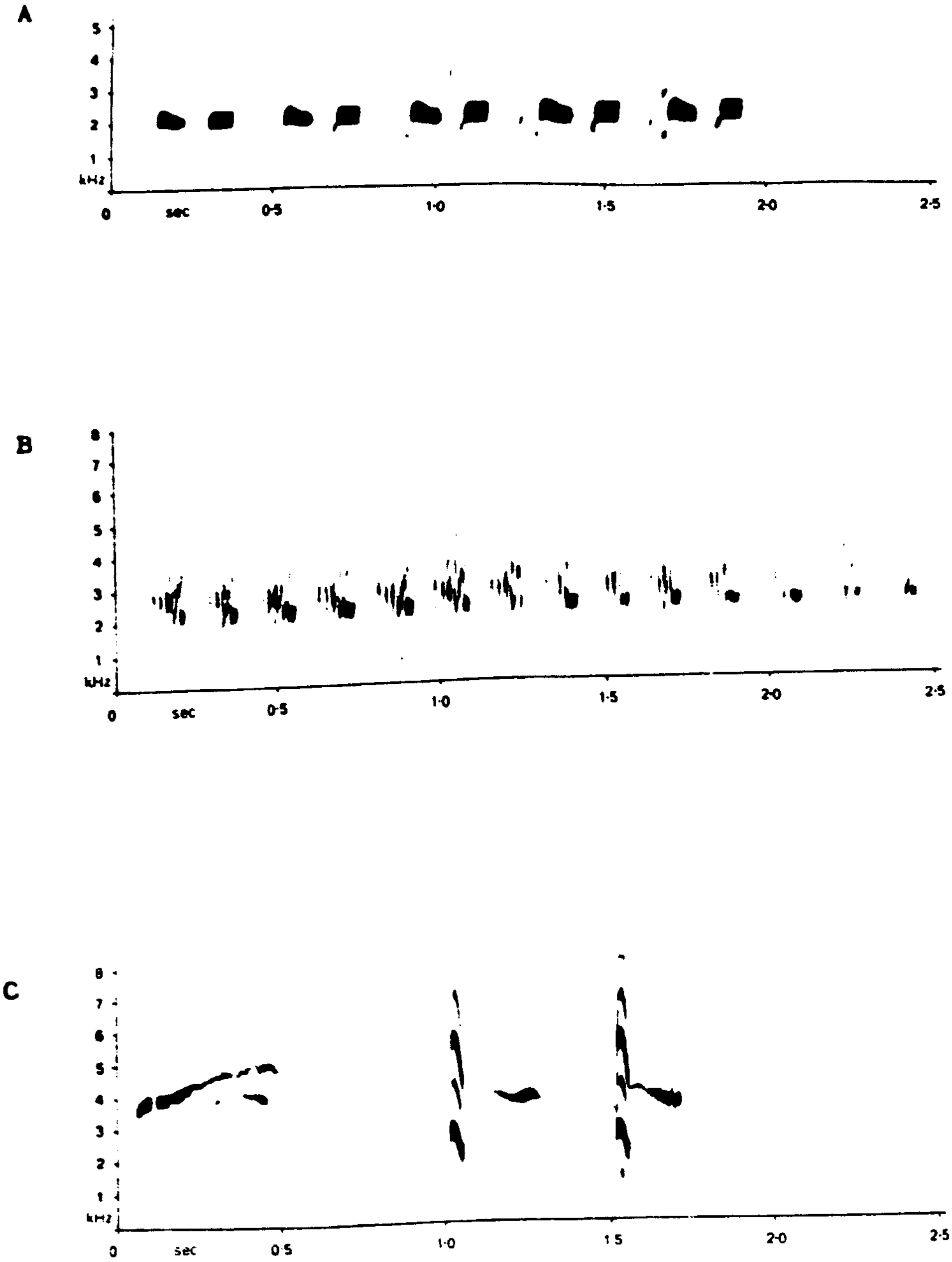
C Female calls Just before she reaches the nest. Rendered 'Kluk' or 'Klook'. Chicks call in the background.

D Female standing beside nest Gives very loud and harsh 'Kwak' calls. Chicks call prior to and after adult calls.

E Chicks calling in nest 'Pee-peep', followed by harsh 'gruff' call of adult. In this case there were 14 'Peep-peep' calls given by chicks and on 13 occasions these were answered by the 'gruff' call of the brooding adult.

F Chicks calling in the nest in the absence of an adult. This is a slightly more stressed 'peep-peep' call.

Selected Greenshank calls.



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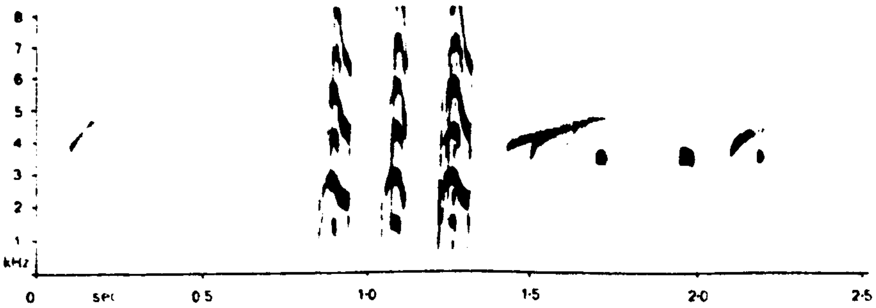
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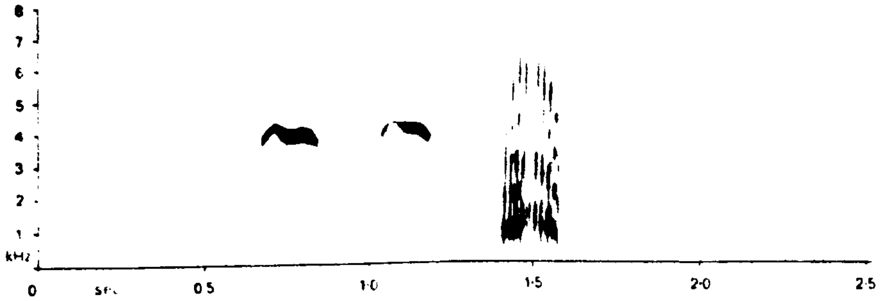
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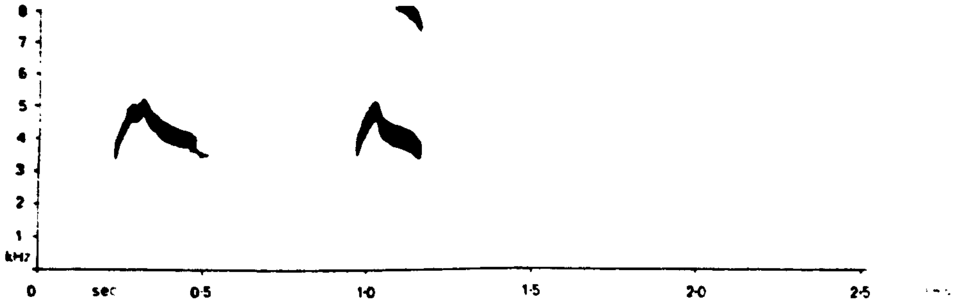
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A Comparison of Selected Calls used by Redshank and Greenshank

The song of the Redshank is less obvious than the display flight of the Greenshank. The Greenshank is a highly territorial bird (Nethersole-Thompson and Nethersole-Thompson 1979), and as such proclaims its territory from a great height in the sky. The Greenshank display also serves to attract a mate from the available birds. Greenshank song may be heard at a distance of several miles. The Redshank display is less loud and normally carried out from much lower in the air. The main purpose is to attract a mate.

In both species a rattling call is used prior to and after copulation. The wings are held above the head and are vibrated at great speed both before and during coition. The sonographic analysis indicate that the rattling call is more rapid in the Redshank but occurs over a similar frequency range as in the Greenshank.

The chick calls in Redshank and Greenshank are both disyllabic whistles. They are basically very similar in both species.

Adult 'chipping' calls are uttered both prior to returning to eggs and in the presence of chicks. All Sonagrams showing 'chipping' have been made from birds attending young.

In the Redshank section, Sonagrams d, e and f show a bird moving up to a nest with chicks. In every one, chicks call at one stage. The 'chip' calls of Greenshank occupy a similar frequency band as do the 'chip' calls of Redshank.

The calls of the adults as they arrive at the nest are very similar (see Redshank f and Greenshank C).

The calls of adults brooding chicks are quite different in both species. In the case of Greenshank, the brooding adult uses a harsh 'gruf' call to control chicks.

Redshanks have been found to use a variety of calls in the act of brooding young. The function of these calls is not certain. The general level of excitement of brooding adults appears to be very high. In the case recorded, one egg hatched whilst recording was taking place - the excitement registered may therefore relate to the appearance or the sounds of the newly hatched young.

APPENDIX 6

The relationship between female weight and wing length with egg length and breadth.

Specific name	Female Weight	Female Wing Length	Mean egg Length	Mean egg Breadth	(n)	Authority
T. erythropus	157	170	4.700	3.280	100	D.A.B.
T. totenus	134	163	4.501	3.182	101	P.S.T.
T. stagnatilis	76	142	3.900	2.700	75	B.W.P.
T. nebularia	194	193	5.143	3.480	100	F.C.R.J.
T. melanoleuca	185	193	4.890	3.300	53	A.C.B.
T. flavipes	84	163	4.200	2.890	51	A.C.B.
T. solitaria	49	136	3.600	2.550	68	D.A.B.
T. ochropus	85	146	3.910	2.800	100	F.C.R.J.
T. glareola	73	129	3.834	2.640	100	F.C.R.J.
Xenus cinereus	75	137	3.863	2.664	80	F.C.R.J.
Actitis hypoleucos	50	112	3.640	2.627	100	F.C.R.J.
A. macularia	51	109	3.200	2.300	88	A.C.B.

A correlation analysis to examine the relationship between female size and egg size.

Pearson's correlation coefficients (r)

	Mean egg length	mean egg breadth
Female weight	0.966***	0.959***
Female wing	0.959***	0.939***

Authority:		
	D.A.B.	D.A. Bannerman 1961
	B.W.P.	Birds of the Western Palearctic 1983
	F.C.R.J.	Francis C.R. Jourdain
	A.C.B.	Arthur C. Bent

APPENDIX 7. Factors associated with timing of breeding in waders

SPECIES/ FACTORS ASSOCIATED WITH LAYING DATE	MATING SYSTEM	NO. CLUTCHES AND RELAYS	NATAL PHILOPATRY AND BREEDING SITE FIDELITY	INCUBATION; FLEDGING PERIODS	STUDY AREAS	SOURCES
1. OYSTERCATCHER (<u>HAEMATOPUS OSTRALEGUS</u>)						
Food during pre-laying period and timing of tilling and sowing. Inland and coastal populations differ. Age appears to be unimportant.	Monogamous. Sometimes bigamy by male. Incubation shared; female takes largest part	Single brooded. Relays of 11% nests predated in Scotland	Low natal philopatry; breeding site fidelity strong, especially in male. Highly mate faithful.	24-27; 28-32 days	Aberdeenshire; Skokholm, Wales	Harris 1967 1969, 1970; Heppleston 1972; Briggs 1984
2. RINGED PLOVER (<u>CHARADRIUS HIATICULA</u>)						
In Arctic, breeding is delayed when snow clearance is late. Further south (e.g. U.K.), is related to decreasing risk of egg predation. Nests at higher altitudes and latitudes are latest. Timing does not coincide with most abundant food for chicks. Weather in temperate areas may be unimportant. No evidence for age effects.	Monogamous. Bigamy recorded rarely. Incubation shared.	Rarely double brooded. Relays frequent (up to 5 recorded)	Moderate natal philopatry and breeding site fidelity. No sex differences. Mate faithful.	23-25; 19-25 days	Greenland; Northumberland, England.	Bub 1962; Glutz *et al.* 1975; Green *et al.* 1977; Pienkowski 1984 a, b
3. MOUNTAIN PLOVER (<u>C. MONTANUS</u>)						
Cold and wet weather delays breeding. Very hot weather terminates laying season. No evidence for age effects.	Rapid multi-clutch system. Male incubates first, and female second, clutches. Second clutch not always fertilized by same male.	Relays readily	Moderate natal philopatry and breeding site fidelity. Male more faithful than female.	28-31; 33-34 days	N.E. Colorado, U.S.A.	Graul 1974, 1975, 1976.
4. DOTTEREL (<u>C. MORINELLUS</u>)						
At high altitudes and latitudes laying determined by snow melt. In temperate regions breeding is earlier when air temperature (May) is high. Laying season condensed in late years. Effects of age unknown.	Monogamous and sometimes polyandrous. Incubation generally by male. Female may lay for several males and shares incubation towards hatching.	Single brooded. Female sometimes relays for male losing first clutch.	No data; low breeding site fidelity. One female recorded in same area for 5 years.	24-28; 24-30 days	Norway; Finland; Scotland	Rittinghaus 1962; Pulliainen 1970 1971; Watson & Parr 1973; Nethersole-Thompson 1973; Kalås & Byrkjedal 1984; DBAT & PST unpubl
5. GOLDEN PLOVER (<u>PLUVIALIS APRICARIA</u>)						
Delay in breeding following many days of snow. Soil and habitat affects food quality and laying date. Large areas covered by snow results in high nest predation in early breeders. No relationship found with food for chicks, or between arrival date and age or hatching date.	Monogamous. Bigamy rare. Incubation shared.	Single brooded. Readily relays (up to 2 recorded)	Moderate natal philopatry, higher breeding site fidelity. Mate faithful (divorce recorded)	27-34; 25-33 days	Norway; Britain	Ratcliffe 1976; Byrkjedal 1978, 1980; Parr 1979, 1980

6. LAPWING (VANELLUS VANELLUS)						
Pre-laying period is shortest when food most available. In central Scotland lay approx. 5 days earlier in arable than in rough grazing; however, laying season is almost a month shorter in arable fields. Lay earliest in mild springs. Lunar cycle and social stimulation may be important. Effects of age unknown.	Monogamous. Bigamy occasional. Incubation shared; female takes greater share.	Single brooded. Many relays.	Moderate natal philopatry and breeding site fidelity. Some notable exceptions.	25-34; 29->42 days Incubation period shorter towards end of season. Very long fledging periods if summer very dry.	Central Scotland; Hampshire, England; Sweden.	Hogstedt 1974; Jackson & Jackson 1975, 1980; Galbraith 1985.
7. KNOT (CALIDRIS CANUTUS)						
Prolonged snow cover can prevent breeding. Pre-laying period is long if food is scarce. Timing of nesting may be affected by early spring weather; hatch appears to coincide with peak emergence of chironomids. Age effects unknown.	Monogamous. Incubation by both, male takes larger share	Single brooded. Relays?	?	21-22; 18-20 days	Ellesmere Is; Vrangelya Island, Siberia; N.E. Greenland.	Flint 1972; Hobson 1972; Nettleship 1974; Green et al. 1977.
8. SANDERLING (C. ALBA)						
Timing of snow melt important. Considerable habitat variation. Age effects unknown.	Monogamous. Sometimes polyandrous. In some years rapid mult-clutch system in Bathurst: Female lays two clutches, first incubated by her and second by male. (both fertilized by same male?). Incubation shared when single clutched.	Single brooded	?; some records of breeding fidelity (especially in males).	24-27 (31); = 17 days	Bathurst Island; N.E. Greenland	Parmelee 1970, Parmelee & Payne 1973; Pienkowski & Green 1976; Green et al. 1977.
9. SEMIPALMATED SANDPIPER (C. PUSILLA)						
Arrival earliest when weather is mild. Weather highly unpredictable. More experienced birds lay earlier.	Monogamous	Single brooded. Relays?	Moderate natal philopatry and high breeding site fidelity. Latter most marked if previous breeding attempt is successful. Mate fidelity?	20; 16 days Manitoba,	Barrow, Alaska; Hudson Bay, Canada.	Ashkenazie & Safriel 1979 Gratto et al. 1983
10. WESTERN SANDPIPER (C. MAURI)						
Early snow melt correlates with early nesting. Chicks hatch during the first major emergence of insects. Effects of age unknown	Monogamous	Single brooded. Relays when nest predated	Moderate natal philopatry and high breeding site fidelity. Some birds use same nests in consecutive years.	21; 17-18 days	Kolomak River (Sub-Arctic) and Barrow, Alaska.	Holmes 1971, 1972,.

11. TEMMINCK'S STINT (C. TEMMINCKI)						
Early laying if feeding conditions on coastal tidal flats are favourable. Hatch coincides with mass emergence of chironomids. Effects of age unknown	Rapid double-clutch system. Successive bigamy. Each male fertilises 2 clutches in his territory, and incubates first. Each female lays 2 clutches on separate territories and incubates second.	Double brooded. Female may relay for male losing clutch?	Moderate natal philopatry and high breeding site fidelity Males, especially older birds, show strongest tendencies. Pair bond is weak	21-22; 15-18 days	W. Finland	Hilden 1975, 1978, 1979.
12. LEAST SANDPIPER (C. MINUTILLA)						
Early breeding when spring is warm and food is available. Most experienced birds and faithful pairs nest earliest.	Monogamous	Single brooded. Relays	?; breeding site fidelity strong in males but data not available for females. Strong mate fidelity.	20-21; ? days	Sable Island, Nova Scotia, Canada	Miller 1979, 1983
13. DUNLIN (C. ALPINA)						
Arrival time varies slightly with weather; old birds arrive first. In far north snow melt affects laying season; further south nesting timed for chicks to hatch around peak emergence of chironomids. Older and mate faithful pairs breed earliest. Age effects unknown.	Monogamous. Sequential bigamy in females recorded. Incubation shared.	Single brooded, though doubles recorded. Relays frequent in some years and rare in others	Moderate natal philopatry and strong breeding site fidelity, especially in males. Females show strong nest site tenacity when mated with same males. 44-80% of pairs reform in 4 years	21-22; 18-20 days	S. Finland; Barrow, Alaska.	Holmes 1966a, b, 1970; Soikkeli 1967, 1970, 1974; Green et al 1977
14. STILT SANDPIPER (MICROPALAMA HIMANTOPUS)						
In wet and cold years food is less available and nesting delayed. Older birds and established pairs breed earliest.	Monogamous	Single brooded. Relay if clutch lost early in season.	Moderate natal philopatry and breeding site fidelity. Mate fidelity high.	19.5-21; 17-18 days	Churchill, Manitoba	Jehl 1973.
15. REDSHANK (TRINGA TOTANUS)						
Nesting is delayed by cold and wet weather in early spring which affects vegetation growth. Coastal compared with inland birds breed earlier and have longer laying seasons. Lunar cycle and spring/neap tides may be involved. Older and mate-faithful birds breed earliest.	Monogamous. Bigamy rare. Incubation shared.	Single brooded. Relays occur if nests lost. Some lay replacement clutches after loss of brood in first few days.	Moderate natal philopatry; breeding site fidelity strong especially in males. Birds most faithful to site if breeding was successful in previous year. Divorce related to breeding failure; occurs within and between seasons.	2[illegible]-31; > 26.5 days. Incubation period shorter towards end of season.	Wangerodge, W. Germany; Ribble Marsh, N.W. England; Soviet Union.	Grosskopf 1958a, b, 1959, 1963, 1970; Hale 1980; Hale & Ashcroft 1982, 1983; Stiefel & Scheufler 1984; P.S.T. unpubl. Zhmud 1983.

16. GREENSHANK (*T. NEBULARIA*)						
In Lapland, laying season related to snow cover. In U.K., nest earlier in years when April and May are warm Older females breed earliest. Some individuals are consistently early, others late. Territories bordering rivers contain earliest clutches. Rainfall and snowfall in early spring, and weather in June, have no effect	Monogamous. Bigamy recorded occasionally: Incubation shared	Single brooded. 3% relays recorded	Moderate natal philopatry; very high breeding site fidelity. 24% nests used by same female at least twice. Hatch success does not affect breeding site fidelity.	23-26; 25-31 days	Lapland; N.W. Scotland	Nethersole-Thompson 1951; Nethersole-Thompson & Nethersole-Thompson 1979; Thompson *et al.* 1986; D.N-T. *et al.* unpubl.
17. COMMON SANDPIPER (*ACTITIS HYPOLEUCOS*)						
Nesting may be earliest when early spring is mild and food is abundant. Little published on timing of laying season. Rainfall and habitat differences may be important.	Monogamous. Sequential polyandry recorded. Incubation shared	Single brooded. Relays occur	Moderate natal philopatry and breeding site fidelity. In N. England 91% males and 77% females returned to same territory in consecutive years. Divorce between seasons occurs.	21-22; 18-20 days	N. England; N.W. Scotland	Holland *et al.* 1982; Nethersole-Thompson & Nethersole-Thompson 1979; D.N-T. unpubl.; Jones 1983
18. SPOTTED SANDPIPER (*A. MACULARIA*)						
Nest earliest when food most abundant in early spring. First clutches coincide with first peak in food supply; hatching occurs when food is most abundant for chicks. Previous breeders nest earliest. At high densities aggression results in delayed breeding.	Polygamous and occasionally monogamous. Serial polyandry and resource-defence polyandry common. Considerable variations attributable to habitat. Incubation shared in monogamous pairs; otherwise male incubates first clutch and female shares in last clutch	Variable. Up to 5 clutches recorded. Each male incubates one clutch; female lays clutches for several males and may share incubation of one. Relays follow clutch loss.	Moderate natal philopatry; high breeding site fidelity. 80% males and 75% females return to same or adjacent breeding sites. In chicks, females more highly philopatric	21-22; 18-21 days	Great Gull Is., New York; Pelican Is., Itasca State Park, Minesota, U.S.A.	Hays 1972; Oring & Knudson 1972; Oring & Maxson 1978; Maxson & Oring 1980; Oring & Lank 1982; Oring *et al.* 1983
19. TURNSTONE (*ARENARIA INTERPRES*)						
Early snow melt results in early breeding. Social stimulation may be important as nesting is highly synchronous. Most hatching coincides with peak food supply for chicks. Effects of age unknown	Monogamous. Both sexes incubate, though female more consistent.	Single brooded. Relays recorded	?; high breeding site fidelity. Mate faithful ≥ 1 year	22-24; 19-21 days	Ellesmere Island, North West Territory, Canad.; N.E. Greenland	Vuolanto 1968; Nettleship 1973; Green *et al.* 1977.
20. RED-NECKED PHALAROPE (*PHALAROPUS LOBATUS*)						
Nest earlier if early spring is mild, and food abundant. Arrival and laying coincides with peak abundance of chironomids. Most experienced birds arrive and breed earliest. Evidence for heritability of laying date.	Polyandrous (sequential and to a lesser extent simultaneous). Only male incubates.	Single brooded. Male incubates one clutch; female may lay two fertilized by different males.	Moderate natal philopatry and breeding site fidelity. Sex bias and annual variations in natal philopatry exist. Nesting success may influence breeding site tenacity.	16.5-20.5; =20 days	W. Finland; N. Sweden La Perouse Bay, Manitoba, Canada.	Hilden & Vuolanto 1972; Raner 1972. Reynolds 1984.

APPENDIX 8

The total number of nests found on Banks Marsh and the number of nests found within the restricted area.

Year	Total nests found	Nests found in restricted area
1974	142	140
1975	192	165
1976	182	169
1977	203	164
1978	203	147
1979	185	145
1980	171	127
1981	206	173
1982	143*	116
1983	198	169
1984	197	161
1985	165*	122

In 1982 and 1985 the number of nests found was well below average.
In 1982 the majority of nest finding was carried out by a single person.
In 1985 adverse weather conditions over the winter reduced the breeding stock, such that fewer birds appeared to breed.

APPENDIX 9

Oldest birds caught

Year of recapture (No. of birds caught)

Date of ringing	1983	1984	1985	1986
1971	1	0	0	0
1972	0	0	0	0
1973	1	1	2	1
1974	7	12	10	6
1975	15	11	6	3
1976	14	9	7	3
1977	9	11	7	7
1978	17	18	11	8
1979	11	15	6	6
1980	17	11	12	6
1981	24	17	13	5
1982	27	19	17	5
1983	-	21	21	15
1984	-	-	32	15
1985	-	-	-	13

Oldest birds caught during the period of study

1983	DR36319	Ringed 10.8.71 (Juvenile)	c 12 years old
1984	DR13891	Ringed	c 12 years old
1985	DR13891	Ringed c 13 years old. DR52720 Ringed 13 years old	
1986	DR52720	Ringed 14 years old	

Age at capture (in years)

The oldest bird found alive on the study area was fourteen years old.

APPENDIX 10

A method for the recording of Redshank leg colour in a standard manner.

After the 1983 field season, it was felt that Redshank leg colour may be a useful determinant of an individuals age. To test this idea, a recording method was devised which allowed leg colour to be recorded in a standard and meaningful way.

Prior to the 1984 field season, six colours were selected which were thought to reflect the range of leg colour likely to be observed. In order that the method was repeatable, colours were selected from a Pantone colour marker selector booklet. Selected colours were cut out and stuck on a card. the card was then enclosed in a plastic wallet.

PANTONE 1 116M/F	PANTONE 2 123M/F	PANTONE 3 137M
PANTONE 4 150M	PANTONE 5 Orange 021M/F.	PANTONE 6 165M/F

The colours were ranked from one to six.
1= pale yellow.
6= bright red.
The above numbers represent the actual Pantone colours.

METHOD

When a bird was caught, a leg was washed and then held against the card. The leg was compared against each colour. The colour most similar to the actual leg colour was then recorded by rank on the bird data sheet.

APPENDIX 11

The number of summer plumage feathers found on four body regions of Redshank. The data are for 1984 only.

	MALE (n=116)		FEMALE (n=116)	
	Mean	s.d.	Mean	s.d.
Mantle	6.46	5.57	7.00	5.34
Breast	8.55	7.23	7.95	6.08
Right scapulars	2.51	2.44	2.96	2.26
Left scapulars	2.49	2.27	2.78	2.14
Right secondaries	0.21	0.52	0.34	0.78
Left secondaries	0.14	0.45	0.22	0.63