The Breeding Ecology of the Lapwing at Seal Sands, Teesside:: with reference to Food, the Environment and three Neighbouring Species.

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by

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Abstract.

The breeding success of the Lapwing at the ICI Brinefields, Teesside, was studied in comparison to three other species - the Ringed Plover, Redshank and Skylark. Environmental data was recorded and pitfall traps were set up to study the available food.

Clutch losses were low in comparison with other studies for all four species, there being no significant difference between species. Predation accounted for most losses.

Growth rates of chicks varied widely between species. Lapwing chicks grew slowly - at a rate significantly lower than a study in Teesdale this year. Ringed Plover chicks grew slowly too, though at a slightly faster and more steady rate. The growth of the Skylark chicks was quick and unrestricted. Differences in growth rates were probably attributable to differences in the availability of food to the species. Many Lapwing chicks grew up by channel edges where their food was, although relatively easy to find, not very abundant. Dry weather and saline water may have caused the chicks to dehydrate. Brooding of Lapwing chicks was shown to decrease with age and be extremely rare in direct sunlight.

Lapwing chick mortality was very high - there being a calculated zero survival rate. Ringed Plovers faired much better, (54% of chicks fledging); Skylark chicks had even better survival rates. Predation was not thought to be the major cause of the Lapwing's low survival rate - partially because of the high survival of other species and partially because of the low clutch predation rate. The mortality of Lapwing chicks was positively correlated to their growth rates and this suggested that poor growth and the problems of dehydration were probably the major causes of mortality.

CONTENTS.

	Page
1.1 Introduction	1-3
1.2. Site Introduction	3-7
2. Methods	8-11
3. Results:	
3.1. The Breeding Season, Nests and Eggs	12-23
3.2. Growth and the Food of the Chicks	24-40
3.3. Survival and Mortality of Chicks	41-44
4. Discussion:	
4.1. Populations, Densities and Use of Habitat	45
4.2. Nest Survival	46-47
4.3. The Growth Rates of the chicks	47-53
4.4. Survival and Productivity	53-54

List of Figures:

Fig.1. The Study Site - a map.

Fig.2. Nest Sites - a map.

Fig.3. Skylark Territories - a map.

Fig.4. Nest Site Characteristics.

Fig.5. Lapwing Nesting Season.

Fig.6. Ringed Plover Nesting Season.

Fig.7. Predated Nests - a map.

Fig.8. Lapwing Mean Growth Curve.

Fig.9. Ringed Plover Mean Growth Curve.

Fig.10. Redshank Growth Curve.

Fig.11. Skylark Mean Growth Curve.

Fig.12. Lapwing Growth Curve - as used for regression.

Fig.13. Lapwing Growth in Teesdale.

Fig.14. Ringed Plover Growth Curve - as used for regression.

Fig.15. Skylark Growth Curve - as used for regression.

Fig.16. Growth in relation to Adult Weight.

Figs.17-31. Invertebrates caught at Pitfall Sites.

Figs.32-42. Relative Proportions of Invertebrates caught at Pitfall Sites.

Fig.43. Lapwing Brooding.

Fig.44. Ringed Plover Brooding.

Fig.45. Survival of Lapwings and Ringed Plovers.

List of Tables:

Table 1. Daily Nest Mortality and Survival Rates.

Table 2. Daily Survival Rates of Eggs in Other

Table 3. Probabilities of Egg Survival through Incubation.

Table 4. Seasonal Lapwing Nest Survival Rates.

Table 5. Seasonal Ringed Plover Nest Survival Rates.

Table 6. Successful and Unsuccessful Lapwing Nest Characteristics.

Table 7. Hatching Rates and Overall Survival Rates until after Hatching.

Table 8. Growth Rates calculated by Regression.

Table 9. Mean Growth Rates of Lapwing Chicks with Age.

Table 10. Mean Growth Rates of Ringed Plover Chicks with Age.

Table 11. Composition of Droppings from Lapwing, Ringed Plover and Skylark chicks.

Table 12. Prey items fed by Skylark parents to chicks in the nest.

Table 13. Use of Pitfall Sites by Young Waders.

Table 14. Growth Rates Of Chicks Surviving to 8 Days and those not.

Table 15. Wader Chick Survival Rates, (in chicks/day).

Table 16. Seasonal Lapwing Chick Survival Rates.

Table 17. Pullus weight increases in g/day during the fledging period.

1.1. Introduction.

The Lapwing, *Vanellus vanellus*, is one of the commonest and most widespread wading birds in Britain, there being an estimated 181,500 breeding pairs (Reed, 1985) and a large wintering population. As a breeding bird it is found in a variety of habitats, including saltmarsh and upland moor, though it is most commonly associated with pasture and arable farmland. In winter it forms large flocks often with 100 birds or more (Barnard and Thompson, 1985) and typically frequents farmland rather than coastal habitats. The species feeds largely on invertebrate prey, though it may occasionally also take seed or grain and vertebrate prey such as fish. Typical food includes earthworms (*Lumbricidae*), beetles and their larvae (*Coleoptera*), some *Hymenoptera* and their larvae, *Diptera* and their larvae and spiders (*Araneae*) (Cramp et al, 1983). They usually feed visually, running along a few paces and then stopping to sight prey on the ground surface in front of them, though they may also use a foot trembling technique to attract subsurface prey (Barnard and Thompson, 1985). The former technique, in particular, requires short vegetation so that the bird can see its prey and this is reflected in the choice of its breeding and wintering habitats.

This study investigates the breeding of Lapwings in a lowland coastal habitat consisting of a mix of pasture and tidal and freshwater pools. Here it was possible to compare the species' breeding performance and ecology with that of some other ground nesting birds, notably the Ringed Plover, *Charadrius hiaticula*, and the Skylark, *Alauda arvensis*, and also to a lesser extent the Redshank, *Tringa totanus*. The Skylark and Redshank are often found breeding together with the Lapwing, the Skylark preferring meadow, pasture and arable habitats and the Redshank the wetter meadows and marshes that are most often found in lowland coastal habitats. The Ringed Plover is predominantly a bird of the coast, nesting on shingle beaches, (though also on bare ground and stony flats elsewhere), and feeding, (with a similar technique to the Lapwing) on worms and other invertebrate prey on the shoreline (Nethersole-Thompson & Nethersole-Thompson, 1986). As a breeding bird it is not often found together with the

Lapwing and so this study, of the two plovers breeding together, should provide a useful comparison between the species.

Both the Lapwing and Ringed Plover lay their eggs on the ground in shallow scrapes, the Lapwing usually in short grass with some vegetation lining the nest and the Ringed Plover on shingle or stones. The Redshank and Skylark generally hide their nests much more, typically making nest-cups in tufts of grass, the Skylark lining this with straw and grass. The chicks of the Lapwing, Ringed Plover and Redshank are nidifugous, i.e. they are able to leave the nest shortly after hatching, (O'Connor, 1984), and as with most waders they feed themselves as soon as they are strong enough to move around. Their prey usually differs somewhat from that of the adults, Lapwing chicks preferring spiders larvae and smaller *Coleoptera*. Ringed Plover chicks also take smaller prey including flies, spiders and sandhoppers (Nethersole-Thompson & Nethersole-Thompson 1986). Skylark chicks are nidiculous and are thus fed in the nest by their parents - typically being brought larvae and spiders rather than the seed and grain that their parents also feed on (Green, 1978). All the species' young normally therefore take fairly energy rich and easily swallowed prey that allow a high intake rate and that give a quick growth rate.

Past studies of the breeding biologies of the four species have often looked at the importance of habitat and environmental factors in the degree and variation of breeding success. On a national scale, Shrubb (1990) has noted changes in Lapwing clutch sizes and success due to agricultural change, breeding success being generally higher on cereal and bare tilth land than in bare plough and upland grass areas. More locally, Baines (1988) has shown differences in Lapwing breeding success between agriculturally improved and unimproved pastures in Cumbria and Durham, whilst Jackson & Jackson (1975,1980) in their 8 year study of Lapwings in the New Forest, have helped to show the importance of weather in year to year variations. Pienkowski (1984b) has helped to show differences in the strategies and successes of two breeding populations of Ringed Plovers - one in Greenland and one on the Northumberland coast - as well as showing how the species' feeding ecology relates to behaviour and choice of habitat, (1983, 1984a). Green & Cadbury (1987) have helped to emphasize the importance of feeding ecology in the choice of habitat and local movements of breeding waders, whilst Green (1978) has also looked at the importance of feeding ecology in the choice of habitats of Skylarks.

As well as looking at differences in the species' breeding biologies, this study aims to further this investigation of environmental effects by trying to relate growth rates, mortality and fledging success to the quality of the habitat - for food and for shelter - and to the weather. The following main points will be covered:

1). Nest sites and the success of nests and eggs until after hatching.

2). Pre-fledging growth and feeding.

3). Mortality and fledging success.

The environment may affect all of these - poor weather for example prolonging incubation and decreasing hatching success, and also reducing the chicks' growth rates and increasing the chances of their mortality. This study investigates the nature of such effects and concludes by looking at the suitability of the area as a breeding habitat for each of the species.

1.2. Site Introduction.

The site studied - the ICI Brinefields at Seal Sands, Teesmouth - is just a small part of a formerly extensive area of grazing marsh and saltmarsh formed by the Tees estuary. Today the area has been much changed by the development of a petrochemical industry on the river, the Brinefields themselves being an area of reclaimed saltmarsh used by the ICI group for storing gas. Despite this it is still a good area for birds, with a large area of pasture, (used by cattle in summer), that supports both breeding birds and feeding flocks, and a set of tidal and freshwater pools. The pools are used by passage waders throughout the year - these including Dunlin (*Calidris alpina*), Greenshanks (*Tringa nebularia*) and Common Sandpipers (*Actitis hypoleucus*) - but they are particularly important as feeding sites for the breeding waders and wildfowl. Ditches and several areas of temporary standing water were also used by the birds and their young for feeding, (see Fig.1). The salinity of several of the pools is quite high - due to sea-water or the brine that is used for storing gas on the site - and this may restrict the food available.

The plant life of the site is dominated by grass, meadow and ruderal species. The grass species include *Festuca rubra*, *Deschampsia flexuosa*, *Holcus lanatus* and *Elymus spp* and the rush *Juncus articulatus*, whilst the meadow flowers and weeds include the Thistles *Cirsium arvense* and *C. vulgare*, the Nettle (*Urtica dioica*), Clovers (*Trifolium spp*), Ragwort (*Senecio jacobaea*), Hawkweed (*Hieracium murorum*) and the Meadow Buttercup (*Ranunculus acris*). Many of these species provide food for Skylarks, Linnets (*Acanthis cannabina*) and other seed eating birds.

The tidal and briny pool edges have a different mix of vegetation, including several saltmarsh species. Glasswort (*Salicornia europeaea*) is dominant, other species including Lesser Centaury (*Centaurium pulchellum*), Greater Sea Spurrey (*Spergularia media*) and Sea Aster (*Aster tripolium*). A plateau area to the east of the main site, which was also used by some of the birds, is typified by sparse dune vegetation including Marram grass (*Ammophila arenaria*), Birdsfoot Trefoil (*Lotus corniculatus*) and Hawkweed. (A fuller list of species is given in Appendix 1).

Pitfall traps were put down in 6 main areas to study the invertebrate fauna of the site. *Coleoptera* and *Arachnida* were particularly common across the site whilst some Sandhoppers and shore living worms (*Oligochaetes*) occurred by the tidal pools, together with *Diptera*. The characteristics of the pitfall sites are summarized below, whilst their locations are shown in Figure 1.

Site 3 - Meadow, long grass (100% cover and 30cm grass in July).

a - near a drying ditch

b - 3m above b

Site 2 - Meadow, medium length grass (100% cover and 20cm grass in July); grazed in summer.

(a and b)

Site 1 - Short grass / bare ground (10% cover, 2cm grass) by briny pool progressively silting up.

c - near pool

d - 3m further away

(a and b flooded and unused)

Channel Sites - by Pools to east of site; varying salinity.

1 - some *Salicornia* (15% cover, 5cm high);

65.4ms/cm Conductivity (SE = 0.4; n = 6).

2 - little vegetation (10% cover, 1cm high);

93.8ms/cm Conductivity (SE = 0.5; n = 6).

3 - dense *Salicornia* (40% cover, 15cm high);

18.7ms/cm Conductivity (SE = 0.1; n = 6).

Compound Site - fenced off area of machinery, huts and gravel (2.5% cover;

SE = 1.7; n = 6; 3.7cm vegetation; SE = 0.8; n = 6).

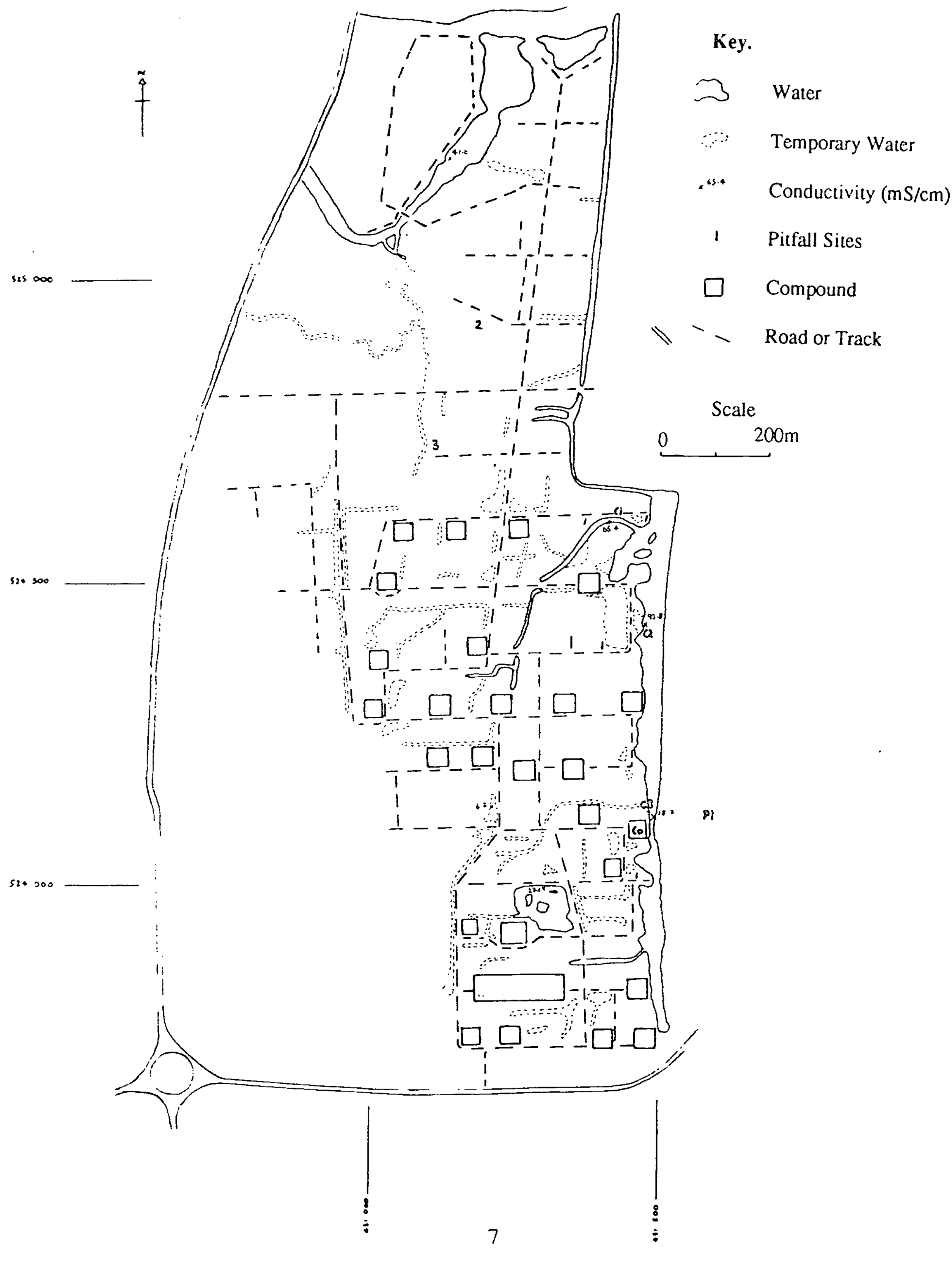
Plateau Site - an area to the east of the site with sparse dune vegetation

(17.5% cover; SE = 5.3; n = 6; 5.3cm vegetation; SE = 2.5; n = 6).

The breeding bird community is dominated by pasture and marshland species notably Lapwings, Skylarks, Redshanks and Meadow Pipits (*Anthus pratensis*). A few pairs of Mallards (*Anas platyrhynchos*), Moorhens (*Gallinula chloropus*), Partridges (*Perdix perdix*), Yellow Wagtails (*Motacilla flava flava*), Sedge Warblers (*Acrocephalus schoenobaenus*) and Reed Buntings (*Emberiza schoeniclus*) also bred on the site. One pair of Snipe (*Gallinago gallinago*) and one other drumming male were seen, but were not thought to have bred. Coastal bird species included Ringed Plover, one pair of Oystercatchers (*Haematopus ostralegus*) , two or more of Shelduck (*Tadorna tadorna*) and a small colony of 24 pairs of Common Terns (*Sterna hirundo*) - all these occurring near the pools.

Predators included one pair of Kestrels (*Falco tinnunculus*), a pair of Magpies (*Pica pica*) and several Carrion Crows (*Corvix corone*), all of which regularly hunted the site. Herring Gulls (*Larus argentatus*) and Black-headed Gulls (*Larus ridibundus*) were particularly numerous, whilst Herons (*Ardea cinerea*) were occasionally seen on the pools. A family of foxes (*Vulpes vulpes*) also used the site, one individual being seen on 27 April and another younger one being killed by a truck on 1 June. There was no evidence of Stoats (*Mustela erminea*) or Weasels (*Mustela nivalis*) occurring on the site.

Fig.1. The Study Site.



2.1. Methods.

The study site was visited an average of 3 times a week from 23 April until the start of August. The initial part of the fieldwork involved finding and mapping nest sites and territories and recording the numbers of Lapwings, Ringed Plovers, Skylarks and Redshanks. The numbers of predators seen on each date was also noted. A vehicle was used for observations, nests being found by looking for the sitting birds or by watching for exchanges at the nests. Apart from their location, the number of eggs at each nest on each visit was recorded as well as the following nest site characteristics: Average Vegetation Height; Tuft Height; Percentage Vegetation Cover and Nearest Neighbour Distance, (during that nest's incubation). Dates of predations, desertions and hatchings were also noted as well as the number of successfully hatching eggs. (N.B. Visits to nests do not increase the chance of their eggs' predation - see Galbraith, 1987).

The chicks of each species were individually ringed for identification and later in the season some Lapwing and Ringed Plover chicks were colour-marked using coloured tape on the rings. This meant that individual chicks could be identified, at a distance, once flying. The numbers of chicks in each brood, their location and whenever possible their weights, were recorded on each visit. Weights were recorded using a Pesola spring balance and were measured to the nearest 1g. Bill length measurements, which can often be useful for estimating chick ages, (P.S.Thompson, pers comm.), were not used here as the ages of most of the chicks were exactly known; (most individuals were ringed at or near the nest). As wader chicks leave the nest soon after hatching, not all were located on every visit. In some cases, the presence of anxious adults in the vicinity of previous captures was enough to suggest that at least one chick was still alive. As well as measuring the above variables, Lapwing and Ringed Plover broods were also watched for 50 minute spells to investigate how the proportion of time that they were brooded was related to age, temperature, direct sunlight and the time of the day. The number of chicks being brooded and the length of the period of brooding were recorded.

The feeding locations and prey of adults and chicks were also studied. Pitfall traps (7cm in diameter at the top and 8cm deep) containing a mixture of 4% formalin and a little teepol were placed in the ground at the main feeding locations from 27 April. These were emptied and reset at fortnightly intervals. Other pitfalls were added later in the study as new feeding areas were used. The invertebrates caught were preserved in 70% Alcohol and identified to Family level. Droppings from young Lapwings, Ringed Plovers and Skylarks were also obtained when handling chicks. This allowed a study of the actual, as opposed to just the potential, prey. The droppings were broken up in alcohol with a pair of fine tweezers and prey remains identified, (where possible), to Class level. The number of fragments of each different invertebrate type, in each dropping, were recorded.

The following weather data - which were used to study growth and mortality rates - were recorded at 1200BST on each visit: Temperature (^{o}C) at 1m; Temperature (^{o}C) at chick level, i.e. c.5cm; Wind Direction and Speed and Cloud (in octas). The occurrence of rain through the day, the state of the soil moisture and the state of the water levels (in pools, ditches and any areas of temporary standing water) were also recorded. Temperatures at 1200BST and the occurrence of rain were taken from newspapers from a Newcastle Weather Station for the days between visits. (All the weather data recorded is shown in Appendix 8).

Water salinity in some of the pools was also recorded, measurements being taken in terms of the water's Conductivity (in mS/cm). Conductivity in water increases with the level of salt and so can be used to show the relative level of salinity between different areas of water. Measurements were taken from sample jars of water taken from the pools.

2.2. Statistical Methods.

The initial numbers of each species on the site were investigated using nearest neighbour distances and densities. Nearest neighbour distances were calculated for the nests of each species separately, the neighbouring nests having to overlap in timing for at least one day. Densities of nests were calculated for the whole 93ha of the site, or for the habitats favoured by species within the site.

Clutch survival, egg survival and chick survival were calculated using the Mayfield method (Mayfield 1975). This looks at only the observed survival and mortality, treating each as a function of time. The number of clutches surviving in n nest-days gives a daily survival rate, (mortality being the inverse of this). Individual eggs may be lost from clutches that otherwise continue to survive and a daily egg survival rate can also be calculated from the number of eggs lost in n egg-days. The survival rate until hatching of clutches, or of individual eggs in otherwise surviving nests, was calculated by p^I, where p is the daily survival rate and I the incubation period. Multiplying the survival rate of clutches until hatching with that for individual eggs in otherwise surviving clutches, gave the probability for an individual egg surviving until hatching in any nest. A hatching rate was also calculated, (by the number of eggs hatching from n eggs present at the start of hatching), and this, combined with the above survival rate, gave the probability of an individual egg surviving incubation and then hatching successfully. Chick survival rates were calculated similarly, the rates given being calculated from the number of chicks surviving in n chick-days.

Two problems of the Mayfield method are investigated in the discussion: firstly the use of a constant daily survival rate and secondly the assumption that each clutch has an equal chance of predation.

Growth rates of chicks were investigated using regression analysis. The regression equations calculated used only a single measurement for each individual, rather than every reading. Where individuals were caught more than once, a single measurement was chosen at random. This method was used for several reasons: firstly, there is a need to retain independence amongst the values used; any second weighing from an individual is likely to be dependent on the first. Secondly, there is a need to avoid bias to those chicks caught on a number of occasions. Thirdly, and lastly, the technique often reduces the variation caused by underweight, (or overweight), individuals and thus more accurately represents growth. Both methods were initially used to investigate the differences in their results and it was found that the method using just single weighings for individuals was, on average, the more accurate. Analysis of the data on the growth of Lapwing chicks at the Brinefields showed that the average growth rate, for different age classes, was significantly positively correlated with the number of times that a chick had been caught:

For 0-5 days of age: $r = +0.49$; $df = 33$.

For 5-10 days of age: $r = +0.53$; $df = 17$.

Regression analysis, using all the weighings for each individual, would, if used, be biased to those caught more often and thus give a falsely high growth rate. Additional data collected in Teesdale also highlighted the problems of using all weighings, the regression equation explaining only 35% of the overall variation, ($r^2 = 0.35$).

Growth was also studied by looking, for different age classes, at the growth of individual chicks. As with the regression technique, only one reading was used, within each age class, for each individual.

The survival of chicks was calculated by expressing the number of chicks surviving each day as a percentage of an initial known number. In addition, Mayfield daily survival rates were calculated for individual chicks, (and, in the case of the Skylark, for whole broods too). Productivity was calculated as the mean number of chicks raised per pair.

Stepwise regression was used to analyse the causes of variation in the brooding of Lapwing chicks. A logarithmic function was used to describe the percentage of time that chicks were brooded, this best fitting the data.

The numbers of invertebrates at each pitfall site were graphed to show the variations of Family abundance through the season. Graphs of the relative proportions of invertebrates caught, helped to show which invertebrate groups were the most important or dominant at each site.

3. Results.

3.1. The Breeding Season, Nests and Eggs.

Populations and Densities.

There were 25 pairs of Lapwings on the site, each of which attempted to nest at least once and which at the height of the season had nests at an average Nearest Neighbour Distance of 66m apart, (SE = 9m; n = 24). There was a mean density of 0.27 pairs/ha over the site. Densities of 0.6 pairs/ha (n = 18) were found on the saltmarsh areas where the habitat was most suitable for nesting; here they often overlapped with Ringed Plovers. Thirty of a probable 34 Lapwing nests, (25 first clutches and 9 replacement clutches), were found. There were 45 Skylark territories on the 93ha of the site, a mean density of 0.48 territories/ha. Redshanks and Ringed Plovers nested at lower densities. There were 10 pairs of Ringed Plovers on the site, which nested during the earlier part of the season an average 119m apart, (SE = 20m; n = 7). Most nests were along the shorelines of the pools, where there was a mean density of 0.5 pairs/ha (n = 9). 13 of a probable 19 nests, (13 first clutches and 6 second clutches), were found. 8-10 Redshank pairs nested on the site, though, as only some of the nests were found, no density could be calculated. The following maps, (Figs. 2 & 3), show the location of all of the nests and replacements found and the Skylark territories.

Nests, the Breeding Season and Incubation.

Nest site characteristics are summarized in Fig.4 (and Appendix 2). Ringed Plovers nested in the open on stones or bare ground with an average 0.2cm (SE = 0.1cm; n = 13) of vegetation and 16% cover (SE = 6%). Lapwings, Redshanks and Skylarks all nested in grass, usually with tufts immediately around their nests. The vegetation around the Lapwing nests' was low, averaging 3.5cm, (SE = 0.6cm; n = 27), whilst Redshank and Skylarks nested in taller grass that averaged 8cm (SE = 0.9cm; n = 10) and 10.4cm (SE = 1.9cm; n =11) respectively.

The numbers of Lapwing nests peaked early in the study, calculations from the nests found giving a mean date of 18 April (SE = 2.4 days; n = 24) for the completion of first clutches, incubation starting a day or two earlier. There was a mean of 3.92 eggs per nest

(SE = 0.06; n = 24), the species typically laying 4 eggs. The female incubated for most of the time (of 137 observed sitting birds 108 (79%) were females; SE = 3.5%), the male typically standing guard nearby. Replacement nests had an average 3.857 eggs (SE = 0.143; n = 7), a value insignificantly lower (t = 0.654, df = 22) than the mean of 3.941 (SE = 0.059; n = 17) for first clutches. The nesting season is shown diagrammatically in Fig.5, this showing the peak of nesting in early May and the restriction of the numbers of replacement clutches later in the season.

Ringed Plovers had a much longer breeding season than the Lapwing, (see Fig.6), with 6 of the 10 pairs having second clutches. The first pair started the incubation of its first clutch on 23 April, the first clutches on average being complete on 4 May, (SE = 3.8 days; n = 8). Second clutches were on average laid 19 days after the first had hatched, (SE = 7.6 days; n = 4). As with the Lapwing, the species typically lays 4 eggs, the mean clutch size being 3.75, (SE = 0.18; n = 12). Replacement clutches had an average of 3.5 eggs (SE = 0.473; n = 4), this being insignificantly different from the mean of 3.86 eggs (SE = 0.143; n = 7) for first clutches.

Skylarks had a long breeding season, lasting from mid-April to late July, with most pairs probably nesting twice, some probably thrice. Two pairs were proved to have had second clutches in this study, one laying 11 days after the first had hatched and the other 33 days after. A mean of 3.6 eggs was found per nest (SE = 0.25; n = 5), these being incubated exclusively by the female. The Redshanks had a much shorter season, nesting mainly from late April to early June with a mean of 3.71 eggs per nest, (SE = 0.29; n = 7).

Losses and Survival Rates.

Clutches failed to reach the hatching stage due to three main reasons - predation, desertion and trampling. Predation accounted for most of the nests that failed, 13 Lapwing nests, 4 Ringed Plover nests, one Skylark nest and two Redshank nests being lost in this way. Only one case of predation was actually witnessed, a Magpie taking a Redshank egg on 16 May. The pulled out lining of a Skylark's nest, whose clutch was taken on c.19 May and that of a Lapwing's nest, whose clutch was taken nearby on c.10

May, suggest that they were taken either by a fox or a Carrion Crow. Foxes were responsible for the destruction of the eggs and young in the Common Tern colony on the site at the start of July.

The locations and dates of all the predations seen are plotted on a map in Figure 7. This shows that there does not seem to be any "edge effect" to the predations - i.e. that nests that are close to hedges and fences, that predators may use as look-out perches or places to hide and watch, seem to be no more susceptible to predation than those in the centre of the site. The high number of other look-out perches, that were available to Magpies and Crows throughout the site, probably reduces the importance of any such edge effect here.

The map does though show that on two occasions, two nests were taken on the same day and thus perhaps by the same predator; (a Lapwing nest and a Ringed Plover nest 120m apart, being probably both taken on 5 May, and two Lapwing nests 100m apart being probably both taken on 22 May).

Only one clutch was deserted: a Redshank clutch with 4 eggs on 12 May, which had been incubated for at least 8 days; the pair subsequently laid again nearby. Two nests were trampled on: a Redshank nest by a worker in early May and a Skylark nest with recently hatched young that was trampled by cattle on 29 May. Some 70 cattle grazed the top 30ha of the site from 29 May, (a stocking rate of 2.3 cattle/ha), these being moved down to the southern 60ha at the start of August.

The Daily Nest Survival Rates (in Nests/Day) found by the Mayfield method for each species are shown in Table 1 below:

Table 1. Daily Nest Mortality and Survival Rates.

	Days with losses	Observed Nest-Days	Daily Survival Rate (a)	SE	95% conf. intervals
Lapwing	8	326	0.976	0.009	0.017
Ringed Plover	4	167	0.976	0.012	0.023
Skylark	1	27.5	0.964	0.036	0.067
Redshank	2	89	0.978	0.016	0.031

Individual eggs may be lost during incubation due to predation, or they may be broken and subsequently removed by adult birds. Ringed Plovers were twice noted to have done this, single broken eggs being removed from clutches of 4, both on 7 June. Table 2 below shows the Daily Survival Rates of Individual Eggs from nests where not all eggs were lost:

Table 2. Daily Egg Survival Rates.

	Eggs lost	Egg-Days	Daily Survival Rate (b)	SE	95% conf. intervals
Lapwing	3	1206	0.998	0.001	0.003
Ringed Plover	2	575	0.997	0.003	0.005
Skylark	-	93	1	-	-
Redshank	-	296	1	-	-

Using these rates and known average incubation periods (I) the following probabilities were calculated for each species:

p_1 = The probability of a nest surviving incubation, (a^I)

p_2 = The probability of an individual egg surviving in nest where clutches are not totally lost, (b^I)

The probabilities, for each species, of an egg in any nest surviving incubation $(p^1 * p^2)$ were then calculated:

Table 3. Probabilities of Egg Survival through Incubation.

	Incubation Period	p_1	p_2	$p_1 * p_2$
Lapwing	28 days	0.499	0.933	0.465
Ringed Plover	24 days	0.559	0.920	0.514
Skylark	11 days	0.559	1	0.559
Redshank	25 days	0.567	1	0.567

Seasonal trends in the survival and mortality rates of Lapwing and Ringed Plover nests were also studied, these being summarized in Tables 4 & 5 below where nest survival rates are given for periods of typically 2 or 4 weeks.

Table 4. Seasonal Lapwing Nest Survival Rates.

Date	23/4-30/4	30/4-14/5	14/5-28/5	28/5-11/6	11/6-26/6
Predations	4	5	2	1	0
Nest-Days	79.5	147.5	65	28.5	18
Surv. Rate	0.950	0.966	0.969	0.965	1
SE	0.025	0.015	0.021	0.035	-
95% Conf. intervals	0.048	0.029	0.042	0.068	-

Table 5. Seasonal Ringed Plover Nest Survival Rates.

Date	23/4-30/4	30/4-28/5	28/5-26/6	26/6-31/7
Predations	0	3	0	1
Nest-Days	8	75.5	61	22.5
Surv. Rate	1	0.960	1	0.956
SE	-	0.023	-	0.043
95% conf. intervals	-	0.044	-	0.085

Site differences of predated and unpredated clutches were also investigated, these being summarized in Table 6 below:

Table 6. Successful and Unsuccessful Lapwing Nest Characteristics.

	Mean Veg. Height (cm)	SE	Mean Tuft Height (cm)	SE	Mean Veg. Cover (%)	SE	n
Successful	3.4	0.8	8.3	6.2	71	9	18
Unsuccessful	3.7	1.0	6.3	1.4	78	8	13
t	0.184		0.816		0.515		
df	25		21		29		

The t-tests for each variable show that there is no significant difference between the mean vegetation height, tuft height, and vegetation cover at successful and unsuccessful nests.

Hatching.

Hatching Rates (p_3) for eggs of each of the species, together with the subsequent probabilities of individual eggs surviving the incubation period and hatching ($p_1*p_2*p_3$), are given below:

Table 7. Hatching Rates and Overall Egg Survival Rates until after hatching.

	No. of Eggs Present At Hatching	No. of Eggs Successfully Hatching	Hatching Rate (p_3)	$p_1*p_2*p_3$
Lapwing	55	5	0.909	0.423
Ringed Plover	27	3	0.889	0.457
Skylark	14	1	0.929	0.618
Redshank	18	0	1	0.567

Fig.2. Nest Sites.

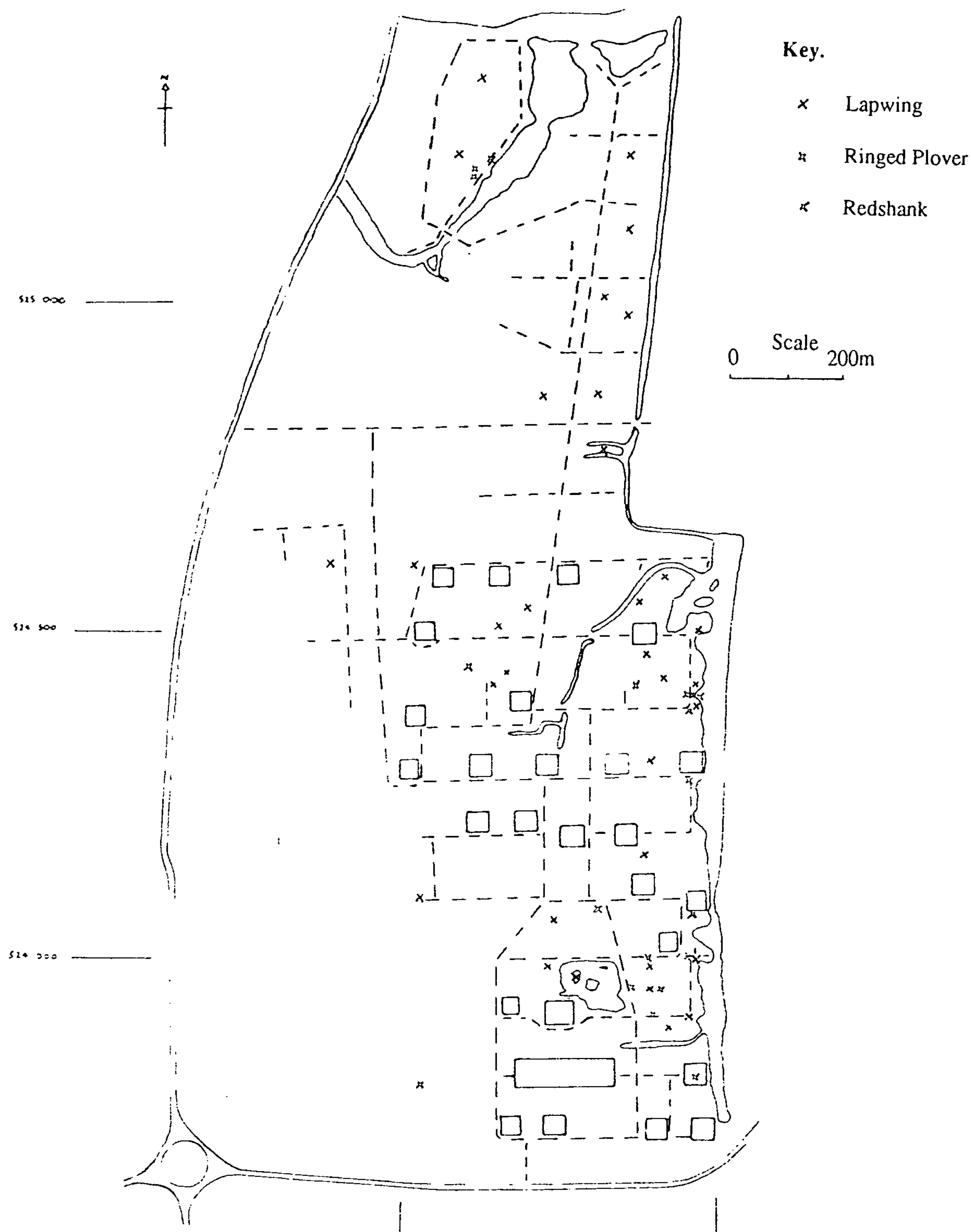


Fig.3. Skylark Territories.

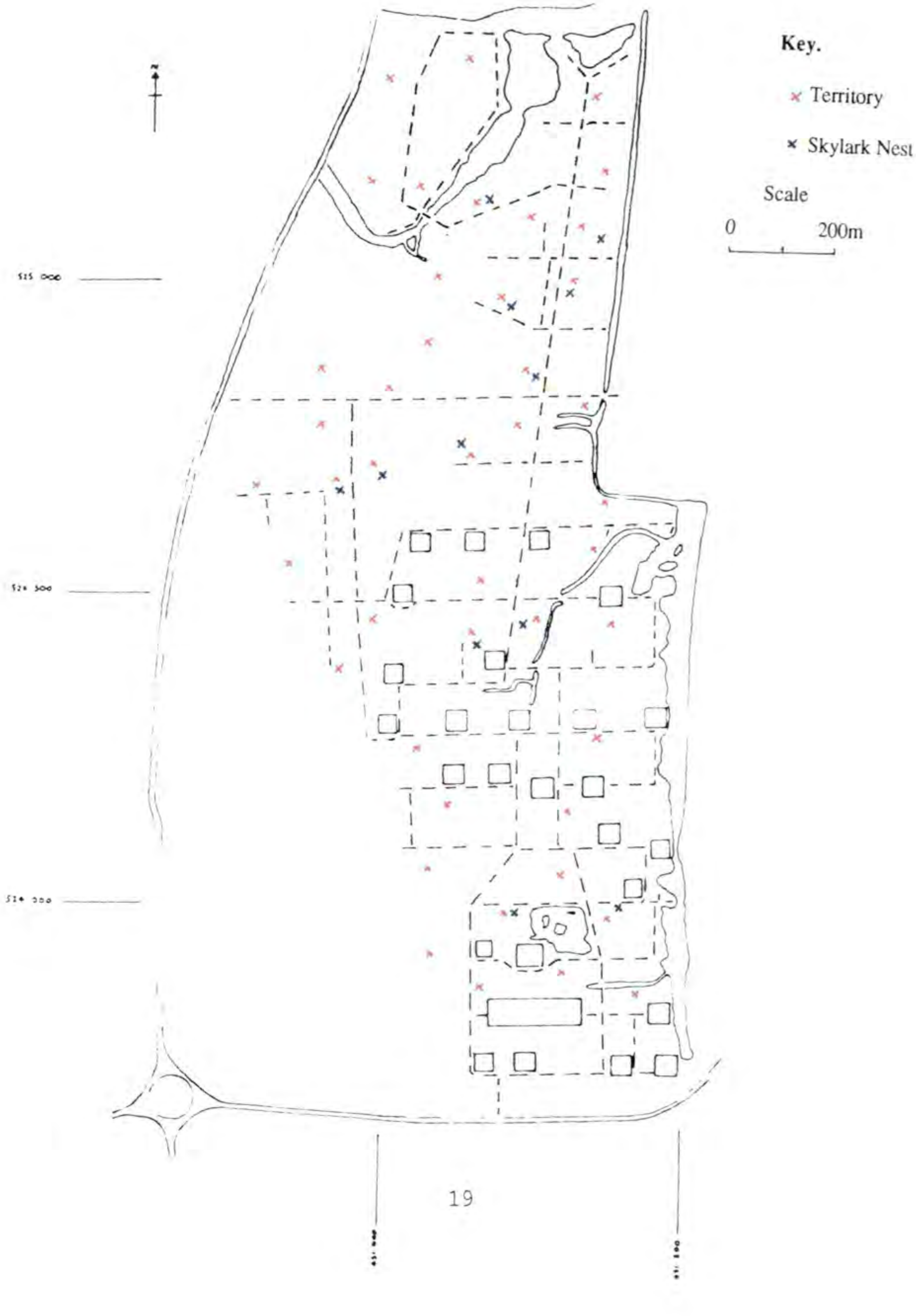


Fig.4. Nest Site Characteristics.

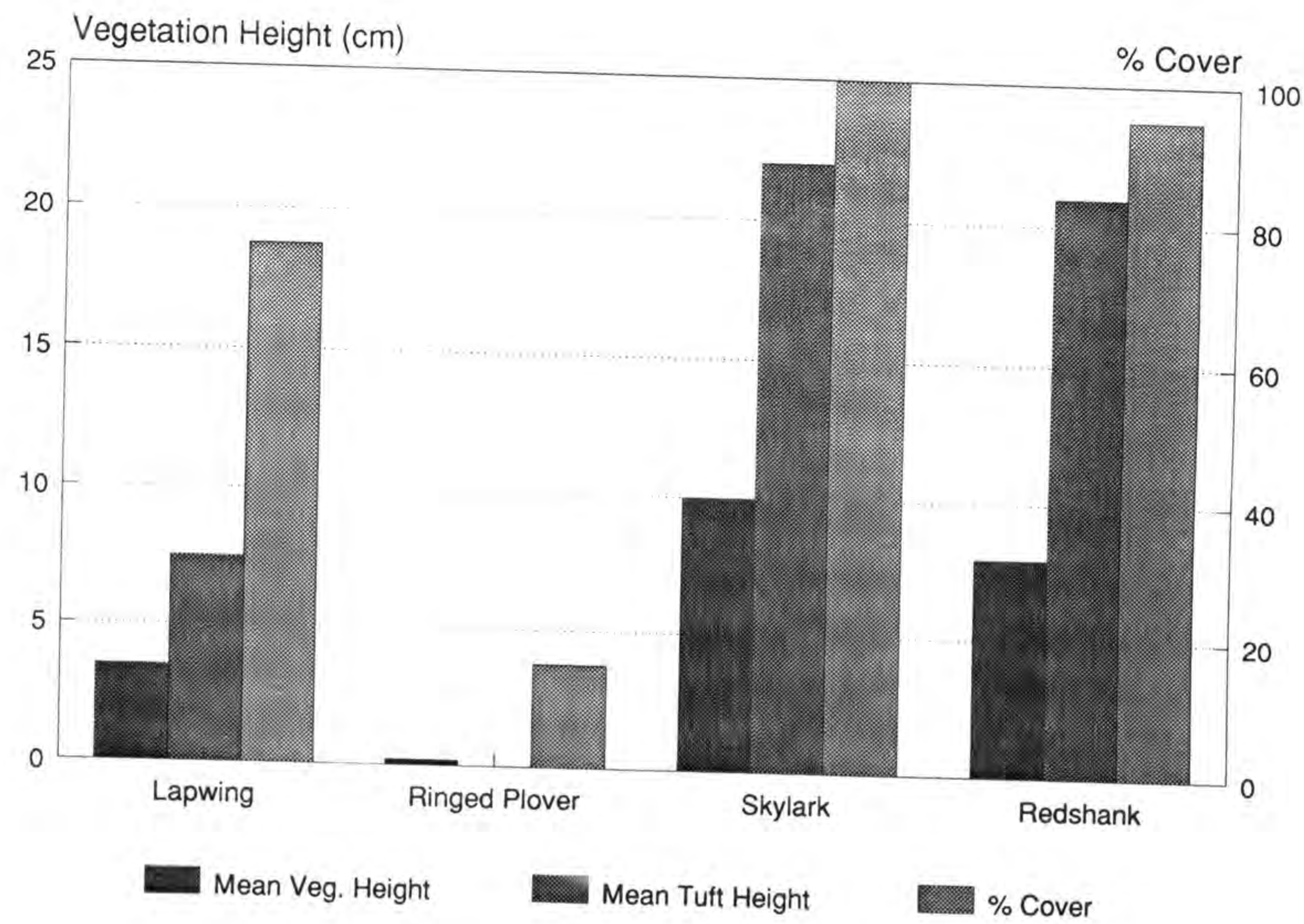


Fig.5. Lapwing Nesting Season.

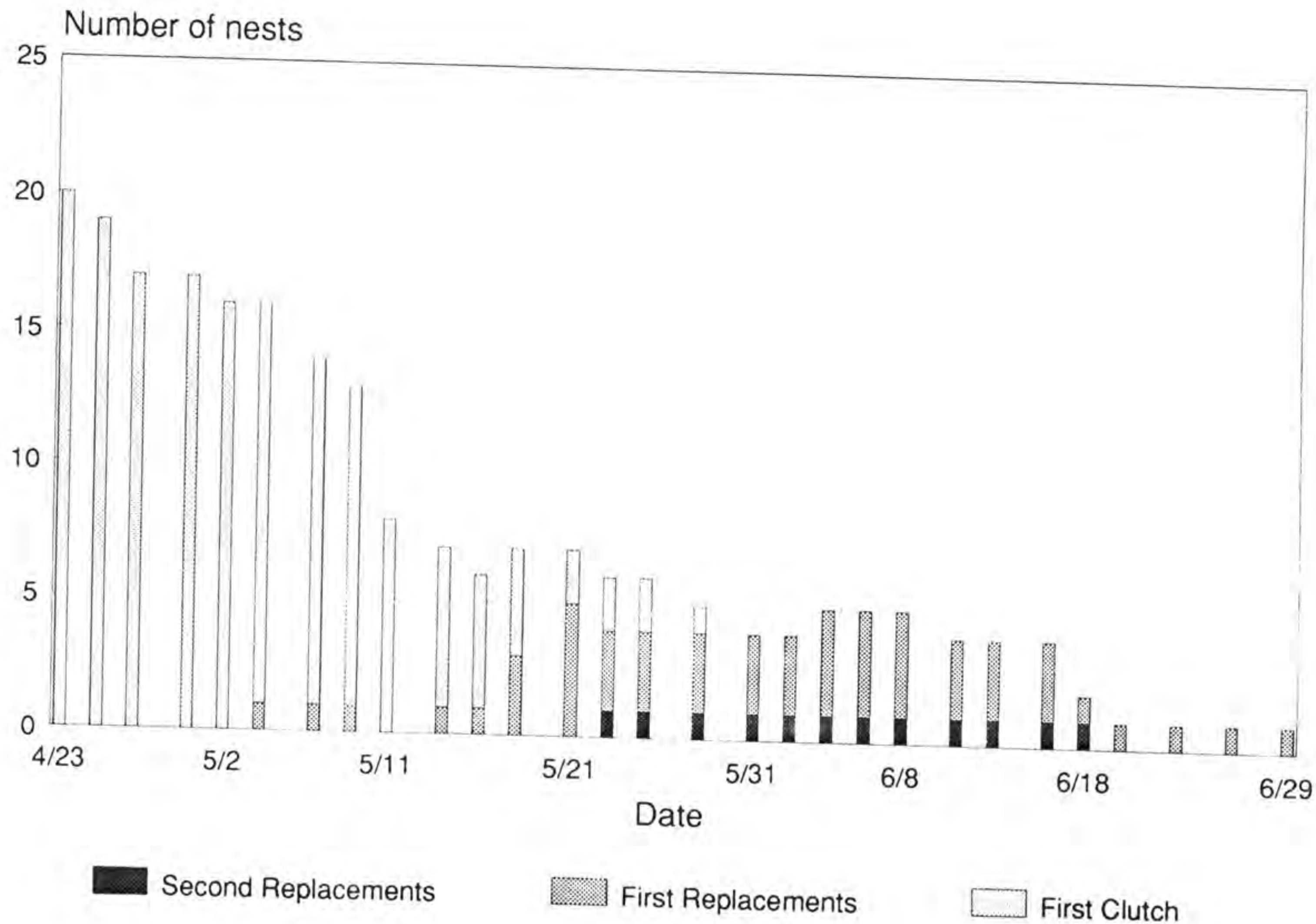


Fig.6. Ringed Plover Nesting Season.

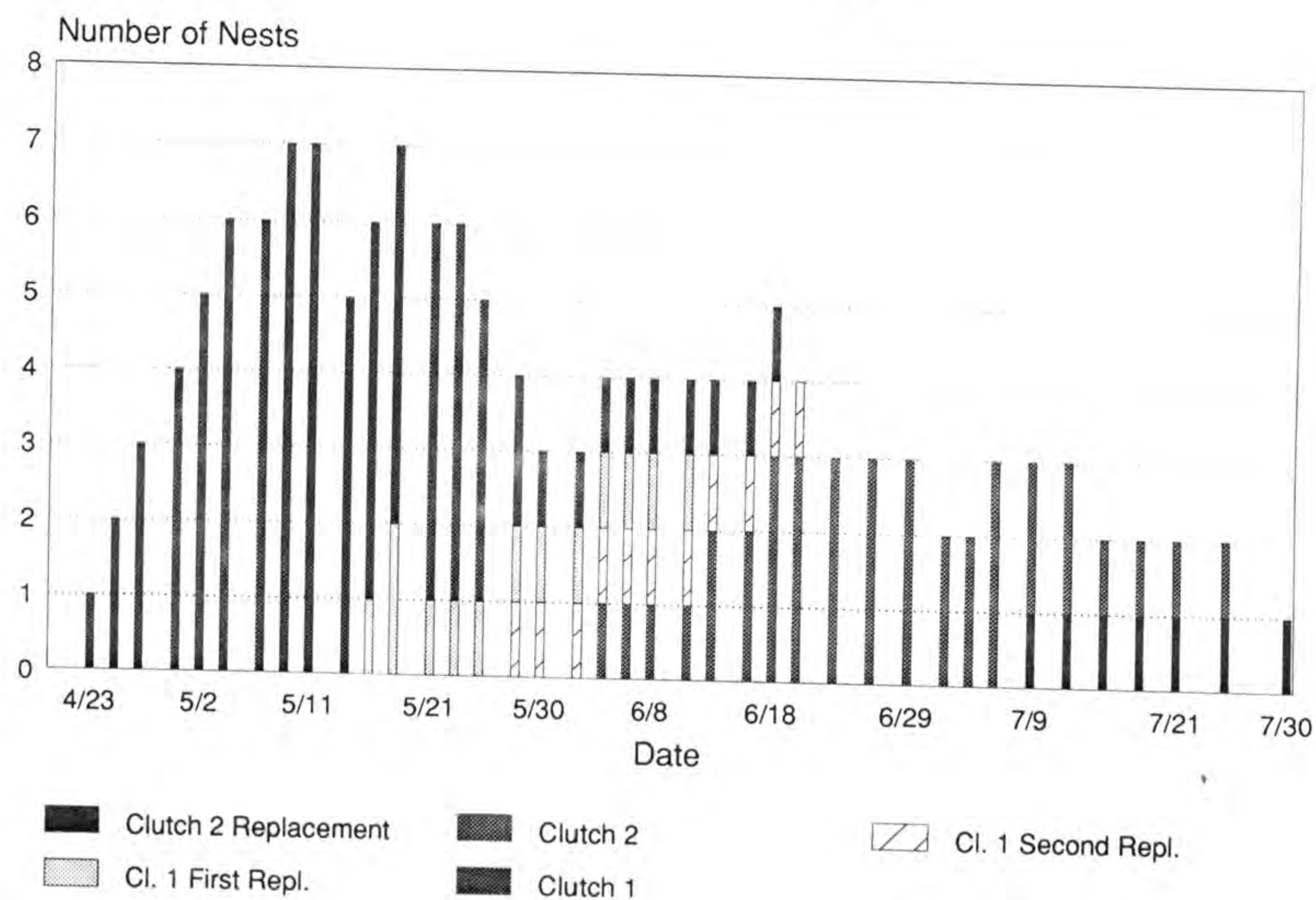
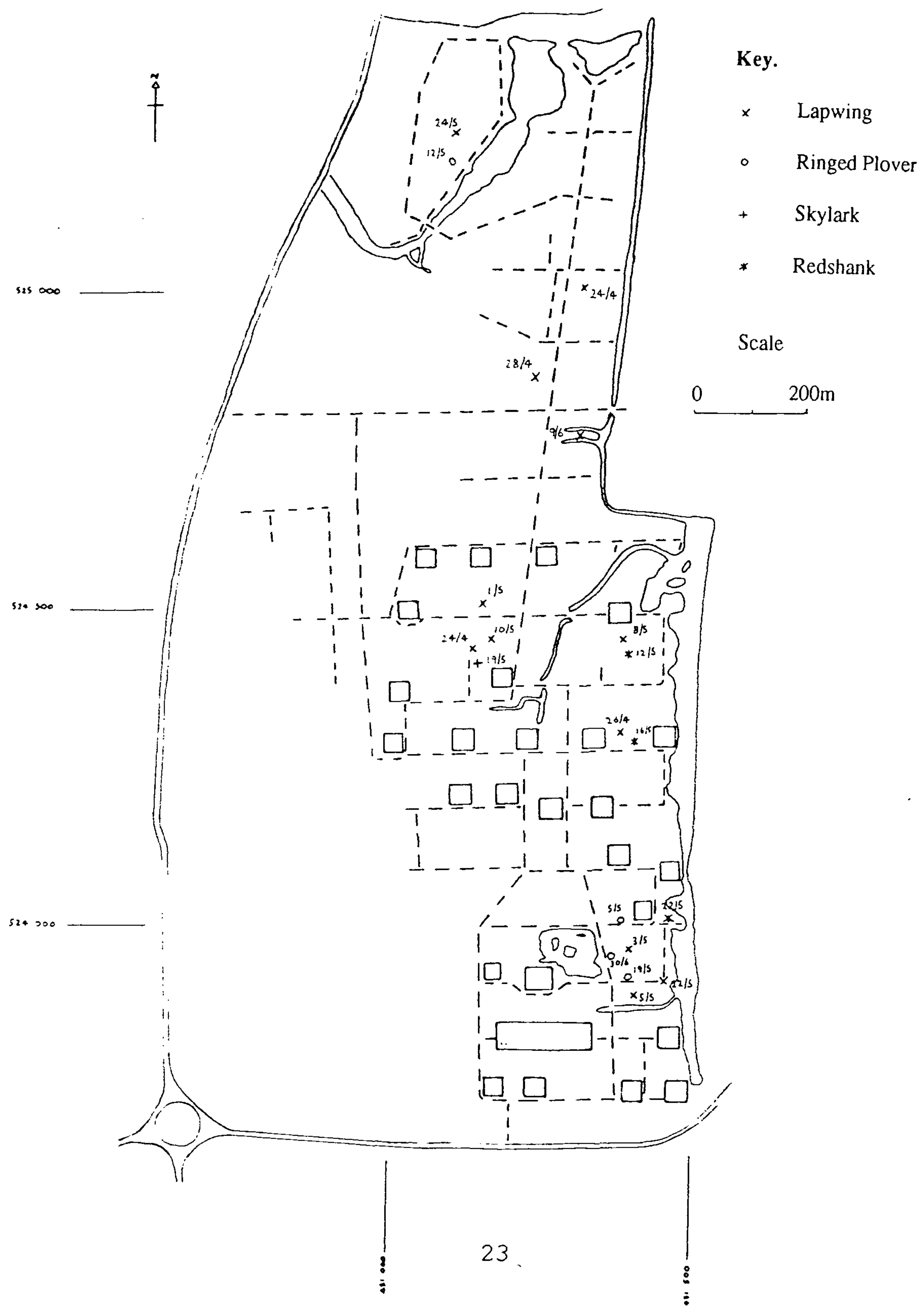


Fig.7. Predated Nests.



3.2. Growth and the Food of the Chicks.

Weights and Growth Curves.

The weights taken for individuals of each species are recorded in Appendices 3 - 6. Figs. 8 - 11 summarize these results graphically with plots showing each weight recorded against chick age and growth curves, (for all but the Redshank), drawn through the mean weights for each age. Growth starts slowly in all the species, a number of individuals losing weight in the first day or two, but after two days weight gain begins and thereafter it increases rapidly. As the birds near fledging, growth starts to diminish and weights reach an asymptote shortly after this.

Regression equations for the Lapwing and Ringed Plover were calculated for birds of 3 days or more, growth being minimal before this. These equations give a good representation of the essentially linear stage of growth in the middle part of the curve, (see Figs. 12 & 14). For the Skylark, the regression equation was calculated omitting the top part of the curve where the growth rate was beginning to diminish (Fig.15). The 3 final equations used are shown below.

For Lapwings: Weight (g) = 5.12 + 3.57 Age (Days) $r^2 = 0.883$

For Ringed Plovers: Weight (g) = 6.06 + 1.52 Age (Days) $r^2 = 0.912$

For Skylarks: Weight (g) = 2.3 + 2.93 Age (Days) $r^2 = 0.913$

Data was also available for this year for Lapwings breeding in Teesdale, Co. Durham. The following regression equation, (see Fig.13), for birds of 3 days or more, is based on these data:

Weight (g) = 6.1 + 4.42 Age (Days) $r^2 = 0.695$

The growth here was significantly higher than that seen for Lapwing chicks at Teesside, ($F = 4.33$; $df = 1,61$).

Table 8 below summarizes these growth rates:

Table 8. Growth Rates calculated by regression.

	Growth Rate (g/day)	SE	Growth Rate as a % of adult weight
Lapwing - Teesside	3.57	0.03	1.59
Lapwing - Teesdale	4.42	0.12	1.96
Ringed Plover	1.5	0.02	2.62
Skylark	2.93	0.03	7.71

Figure 16 expresses the mean weights of the species with age as a percentage of their final asymptotal weights. The fast rate of growth of Skylark chicks is particularly clear from this, (as it is from the above table), whilst it can be seen that Lapwings, due to their longer fledging period, grew relatively much more slowly. Lapwings and Ringed Plovers both fledge at between 60% and 70% of their final asymptotal weight.

Tables 9 & 10 below give average growth rates at different ages for the Lapwing and Ringed Plover, these being based on the growth rates of individual birds.

Table 9. Mean Growth Rates of Lapwing chicks with Age.

Age (Days)	Average Growth Rate (g/day)	SE	t	df
0 - 5	0.48	0.25		
			2.81*	50
5 - 10	1.74	0.37		
			3.87*	21
10 - 15	4.23	0.49		
			0.22	7
15 - 20	4.00	1.00		

Table 10. Mean Growth Rates of Ringed Plover Chicks with Age.

Age (Days)	Average Growth Rate (g/day)	SE	t	df
0 -5	0.63	0.21		
			4.36*	17
5 - 10	2.17	0.19		
10 - 15	2.00	-		
15 - 20	1.35	0.46		

* - significant at the 5% level.

The rates for the Lapwing show that growth does not become significantly linear until day 10, this being in conflict with the earlier use of a linear regression for birds of 3 days or more. It is however probably still safe to use the regression as the above growth rates are biased in the first few days by chicks that did not grow and subsequently died soon after.

The values from the tables and particularly those for the Ringed Plover, do however help to show the sigmoidal nature of the growth curves.

Food.

Eleven pitfall traps were set in eight different sites to look at the available food for the birds, the Meadow/Bare Ground sites (1c,1d,2a,2b,3a,3b) running from 27 April to 1 July. The 3 Channel sites (C1,C2,C3) ran from 25 May, whilst traps in one of the fenced off Compound areas and on the Plateau ran from 6 June. The totals of all the invertebrates caught are given in Appendix 7. The following graphs (Figs. 17 - 31) help show the important details from these results, whilst Figures 32 - 42, in Appendix 8, show the relative proportions of different invertebrate types caught at the traps through the season.

Beetles (*Coleoptera*) and Spiders and Harvestmen (*Arachnida*) were both most numerous in the two Meadow Sites (2a, 2b, 3a & 3b) and rose sigmoidally in numbers during spring (see Figs. 17 - 24). The numbers of *Arachnida* peaked in early June, (with 140 individuals or more caught at each of the meadow sites), this being mainly due to an increase in the numbers of *Lycosidae*. The numbers of *Coleoptera* caught peaked in early July - these becoming the most numerous invertebrate at this time. There seemed to be no significant difference between the patterns seen at each of the Meadow Sites. The numbers of *Coleoptera* caught increased with the average grass length at the different sites of the pitfall traps; (grass length increasing as spring progressed).

No. of *Coleoptera* = -6.00 + 3.53 Grass Length (cm) SE = 0.05; $r^2 = 71.9$

Froghoppers and Leafhoppers (*Aphrophoridae and Cicadellidae*) and Mites (*Acarina*) also increased at the Meadow Sites through spring and at a similar rate to the Beetles. The numbers of *Diptera* did not however change significantly at any of the sites.

Site 1, by one of the briny pools, changed physically through the study due to the dumping of sludge and the subsequent evaporation of the water there, as a result there were some significant changes in the numbers of invertebrates caught. *Arachnida* numbers (Fig.26) decreased to near zero at the end of June at both pitfalls, whilst *Diptera* and their larvae increased (Fig.25) - probably as a result of the increasing amount of brine.

The three Channel Sites showed slight seasonal trends in the numbers of *Arachnida* caught, these peaking, as in the Meadow Sites, in early June (Fig.29). There was a noticeable increase in *Diptera* numbers in late June at these sites (Fig.30), 70% of the invertebrates caught at this time being *Diptera*. The numbers of the Sandhopper *Talitrus saltator* showed a slight decrease in numbers through June and July at two of the three sites, (Fig.30), the other site, (C3), showing no notable change.

The Plateau and Compound Sites though seemingly similar in vegetational characteristics - both being stony with sparse grass and ruderal vegetation - had different patterns in the changes of their invertebrate life. At the Plateau Site *Diptera* and *Acarina* numbers increased significantly through late June and early July whilst at the Compound Site *Diptera*, *Acarina*, *Coleoptera* and *Arachnida* all decreased.

Faecal samples from chicks were also obtained for analysis the results of which are summarized in Table 11 below.

Table 11. Composition of Droppings from Lapwing, Ringed Plover and Skylark chicks.

	Lapwing a	Lapwing b	Lapwing c	Ringed Plover	Skylark
Age (days)	1	9	22	15	5
Date	16/5	26/6	9/7	15/7	29/6
*Coleoptera**	3	14	10	25	9
*Diptera**		1	1	50	20
*Arachnida**		1	7	1	5
*Talitrus**		2	3	3	
Unknown*	25	30	30	25	50

* Figures represent the number of fragments found.

It is difficult to directly compare the number of fragments found for chicks of different species and ages because they may break down their prey to different degrees and because some types of prey will be better preserved than others. The Chi-square test used on some of the data takes into account the relative differences in the total quantities of fragments found, so overcoming the species' differences and thus just showing prey preferences. The test was calculated for data from the droppings from the 22 day old Lapwing chick, the Ringed Plover chick and the Skylark chick, these being of relatively similar development and the samples being taken from similar dates. The values for *Talitrus* and *Coleoptera* had to be combined to ensure statistical validity in the test. The Chi-square value calculated was 59.08, this being extremely significant, ($df = 6$, $p < 0.001$).

Table 11 shows that *Coleoptera* were probably taken in numbers by both the Lapwing and Ringed Plover, whilst the Lapwing also took a number of *Arachnida*. The Ringed Plover chick, unlike the Lapwing, also took a large number of *Diptera*. The change of the Lapwings' diet with age could not be analysed by a Chi-square test, but it is clear from the table that Lapwings took a number of *Coleoptera* even from an early age.

Skylarks were also observed feeding their young, the summary of four 50 minute watches being shown below:

Table 12. Prey items fed by Skylark parents to chicks in the nest.

6 Green Caterpillars

3 Worms

1 Moth

20 Brown larvae - probably caterpillars.

3 Spiders

8 Unidentified.

This suggests that Skylarks have a preference for more fleshy prey such as larvae, the faecal analysis also showing that they take *Diptera*.

It is important to note that the diets seen are the result of the availability of the prey as well as feeding preferences.

The use of the areas of the pitfall trap sites by feeding waders, or by Skylark adults looking for prey for their young, was also noted. Their occurrence is summarized in Table 13 below, figures representing, for the given periods, the total number of days that individual families were observed feeding in the area of the site.

Table 13. Use of Pitfall Sites by Young Waders.

Site	Species	Date 27/4 - 25/5	Date 25/5 - 23/6	Date 23/6 - 21/7	Number of families
C1	Lapwing	6			1
	Ringed Plover		27	21	2*
	Redshank		1		1
C2	Lapwing	7	6	1	3
	Ringed Plover	2	21		1
	Redshank		1		1
C3	Lapwing	13	14	18	3
	Ringed Plover		26	32	3*
	Redshank			16	1

* - includes pairs' first and second broods.

This shows that Ringed Plovers used the areas around all of the channel sites for raising their young, and that Lapwings favoured the areas around site C3. Two Ringed Plover pairs also used two of the compounds for bringing up their broods, whilst some older Lapwing chicks used the plateau area. Skylarks were observed finding food for their young in the areas around sites 2a/2b and 3a/3b from early May until mid June, the areas being used by adults throughout the study period.

Brooding.

The brooding of Lapwing and Ringed Plover chicks was studied to investigate how weather affected the amount of time that the chicks had available for feeding at a given age. The data gathered is shown in Appendices 9 & 10. Figures 43 & 44 show how the percentage of time brooded falls with the age of the chick and also that chicks were rarely brooded in the sun.

Regression analysis showed for the Lapwing the relative importance of age, sunlight, temperature and time of day in explaining the relative length of brooding bouts. The first equation below shows the effects of age and sunlight on the percentage of time brooded. As little brooding took place in sunlight, a second equation was also calculated to investigate how the percentage of time that chicks were brooded during cloudy periods varied with age.

Log (% Time Brooded + 1) = 1.92 - 1.34 Sunlight - 0.093 Age (Days)

SE (for Sunlight) = 0.031 SE (for Age) = 0.003 $r^2 = 0.756$

Log (% Time Brooded + 1) = 1.948 - 0.099 Age (Days)

SE = 0.004 $r^2 = 0.576$

Brooding was seen on occasion to be less at higher temperatures and also in the middle of the day, though stepwise regression showed that these factors were insignificant. No analysis was calculated for the Ringed Plover due to lack of data.

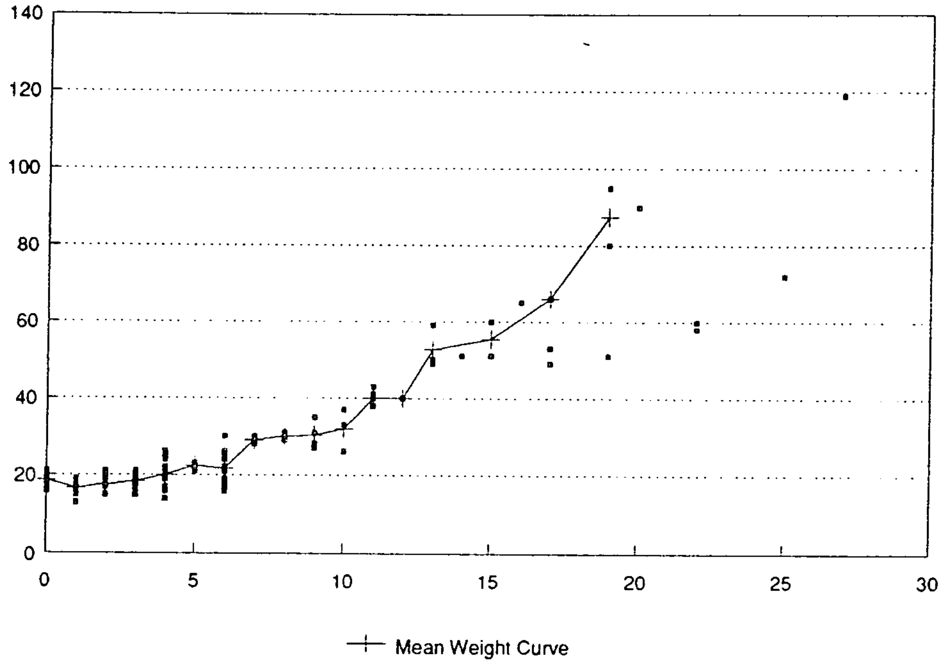
Though the effect of temperature on the brooding of Lapwing chicks was insignificant, there was clearly less brooding in warm weather. The increasing thermoregulatory ability with age is reflected in the fact that the highest temperatures that chicks were brooded at decreased with age:

Log Temp. Threshold = 1.30 - 0.016 Age (Days) SE = 0.001; $r^2 = 0.684$

At any particular age the threshold represents the temperature at which 100 per cent of the chicks' time is available for feeding.

Weight may also affect the amount of brooding needed and three Lapwing broods, which were on average underweight, were seen to have more brooding than expected.

Fig.8. Lapwing Mean Weight Curve.



Curve excludes underweight individuals.

Fig.9. Ringed Plover Mean Growth Curve.

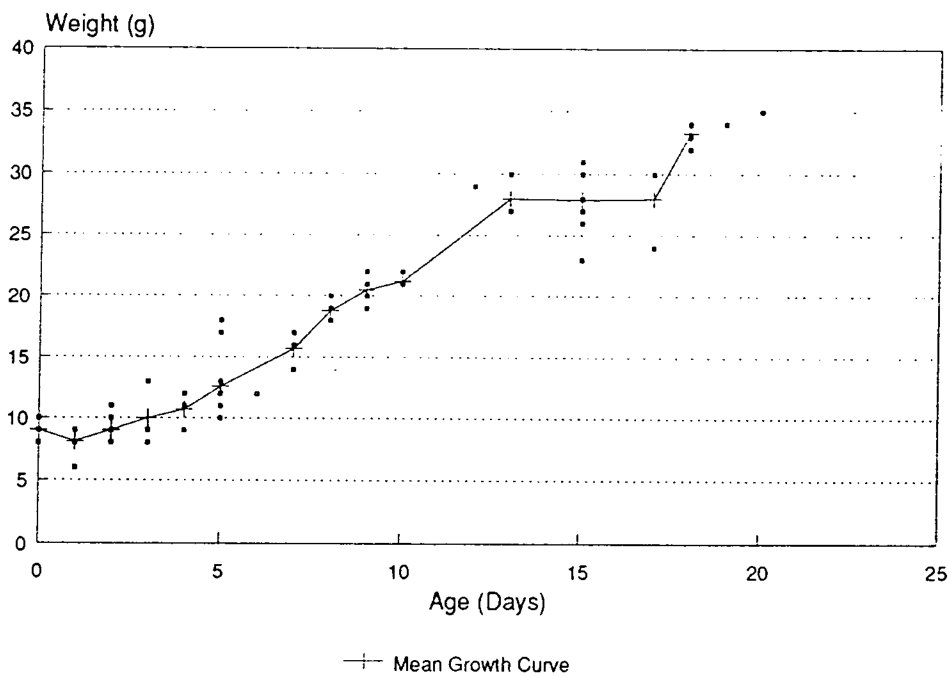


Fig.10 Redshank Growth Curve.

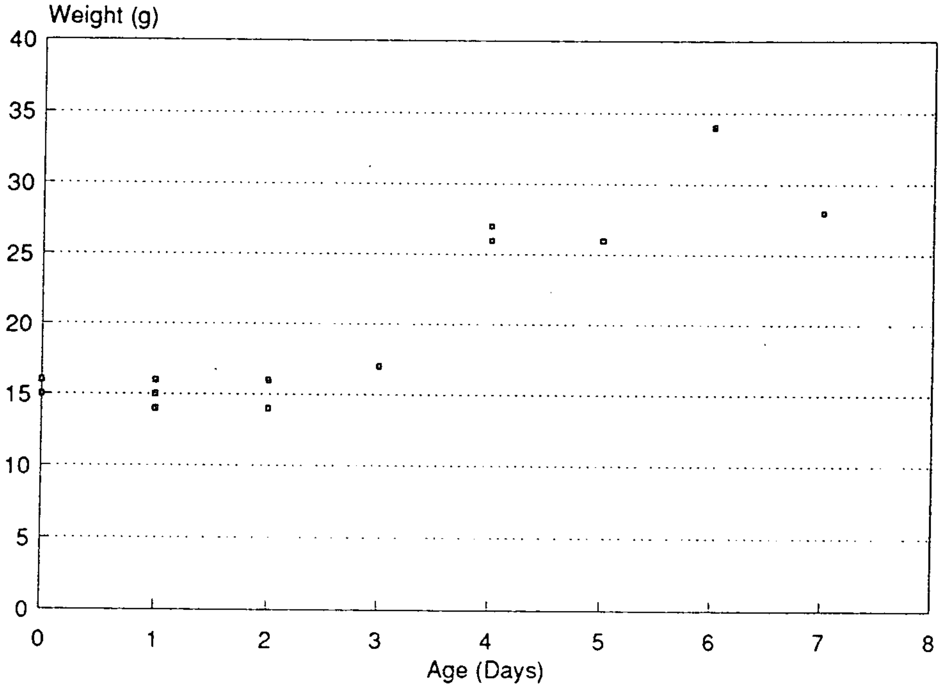


Fig.11. Skylark Mean Growth Curve.

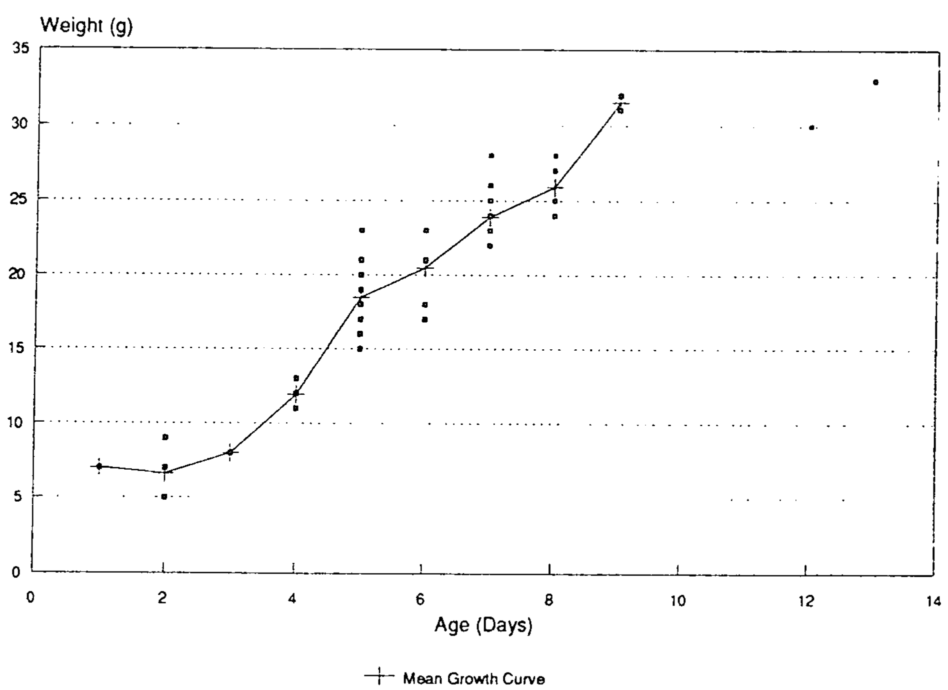


Fig.12. Lapwing Growth Curve
- as used for regression.

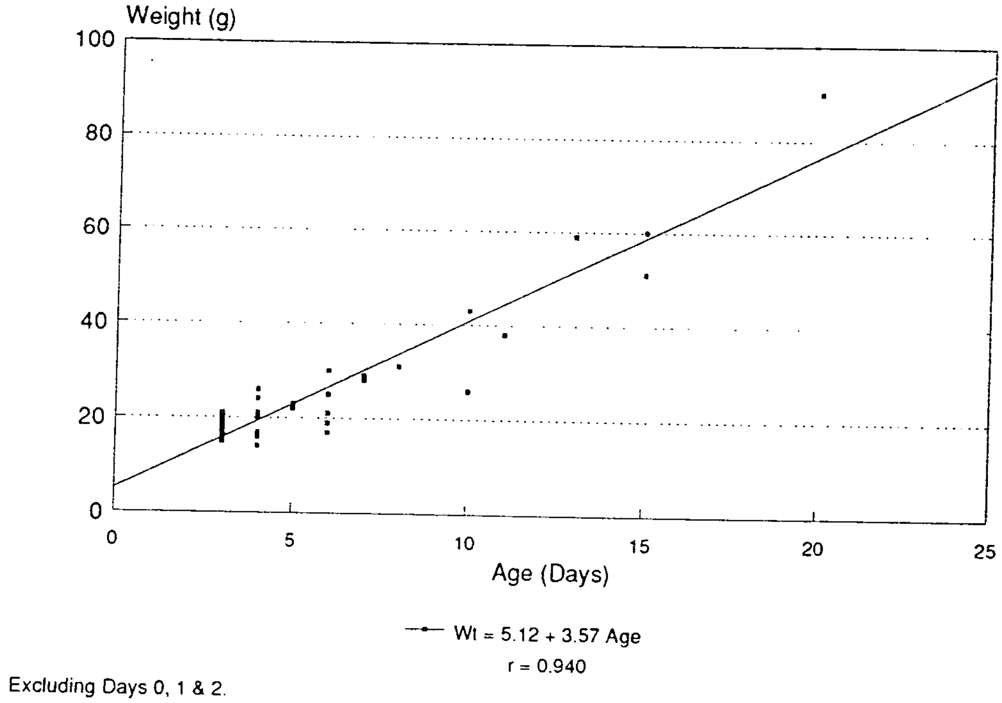


Fig.13. Lapwing Growth in Teesdale.

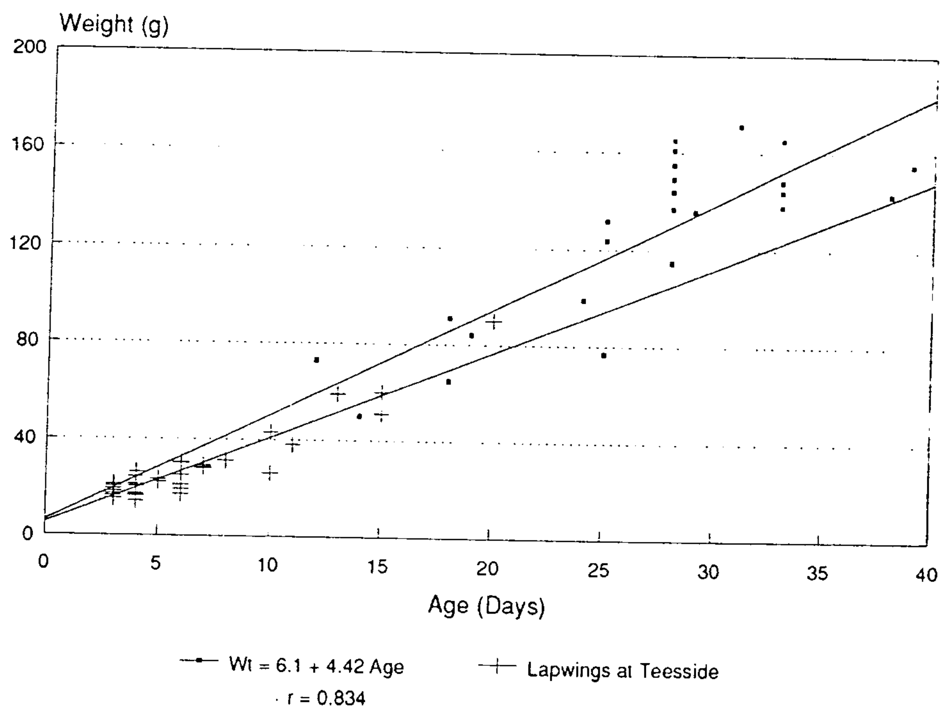
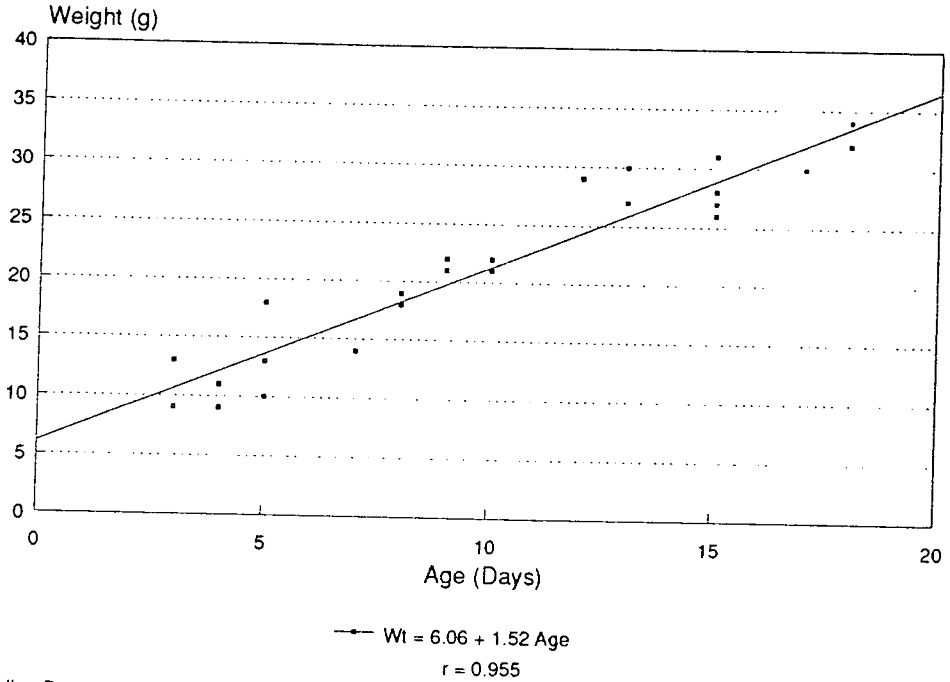


Fig.14. Ringed Plover Growth Curve

- as used for regression.



Excluding Days 0, 1 & 2.

Fig.15. Skylark Growth Curve

- as used for regression.

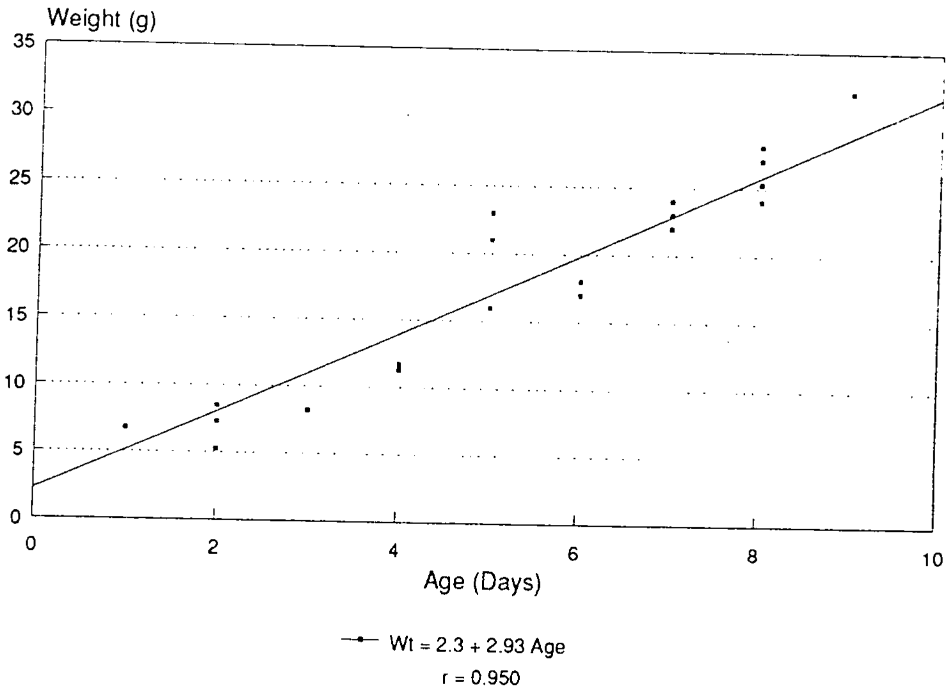


Fig.16. Growth in relation to Adult Weight.

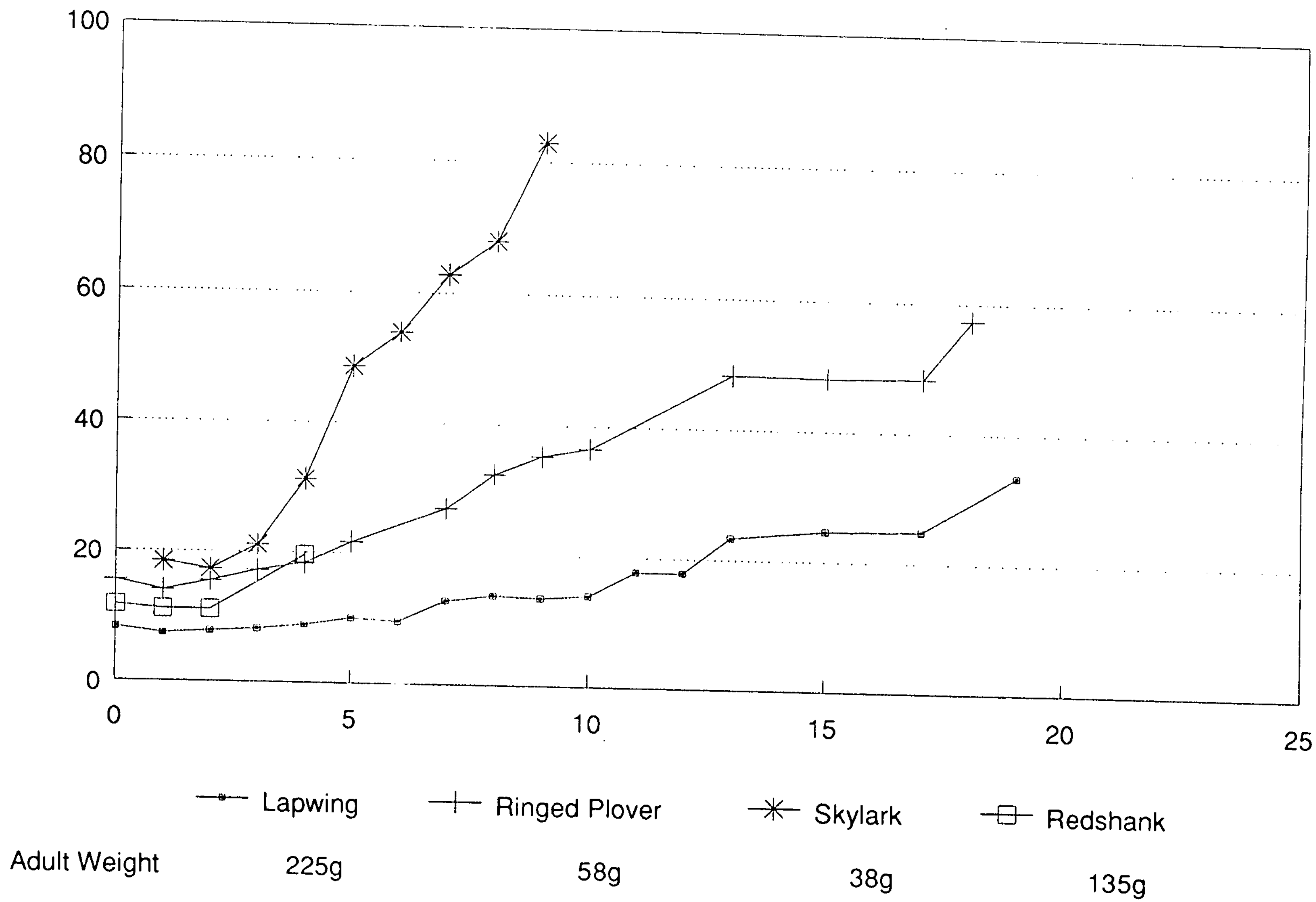


Fig.17. Numbers of Coleoptera - Site 2a.

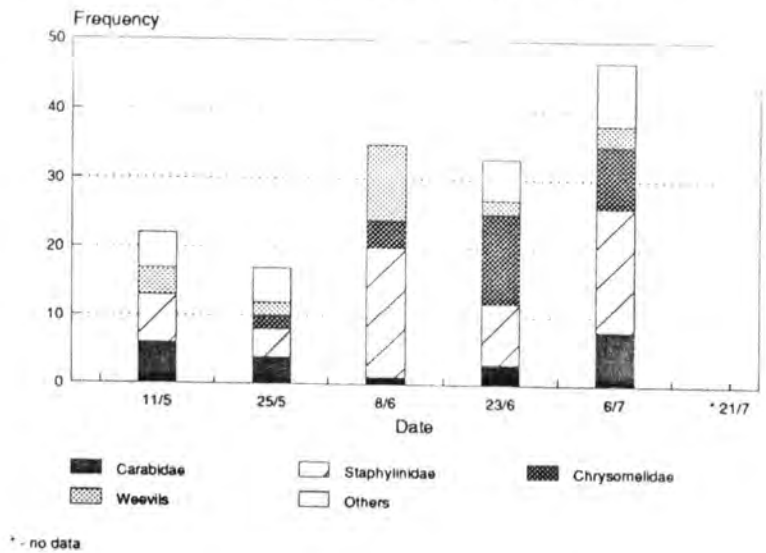


Fig.18. Numbers of Coleoptera - Site 2b.

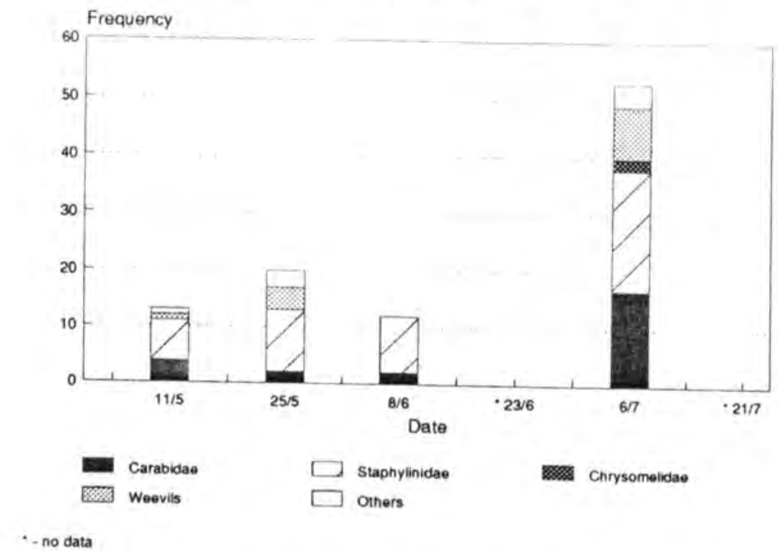


Fig.19. Numbers of Coleoptera - Site 3a.

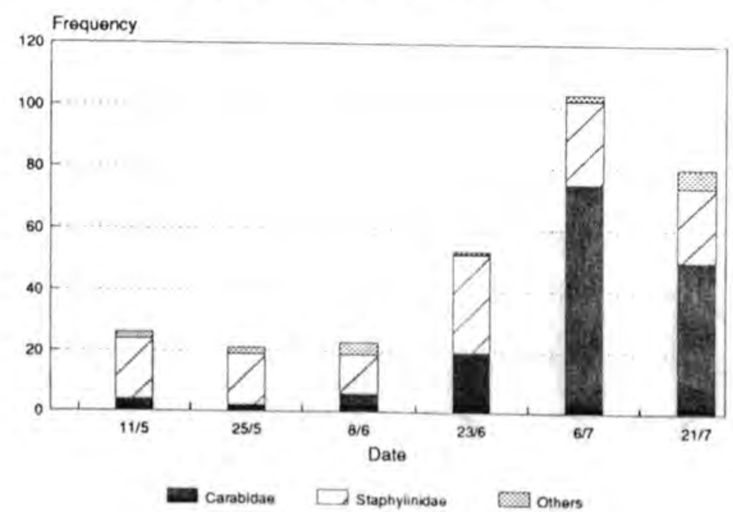


Fig.20. Numbers of Coleoptera - Site 3b.

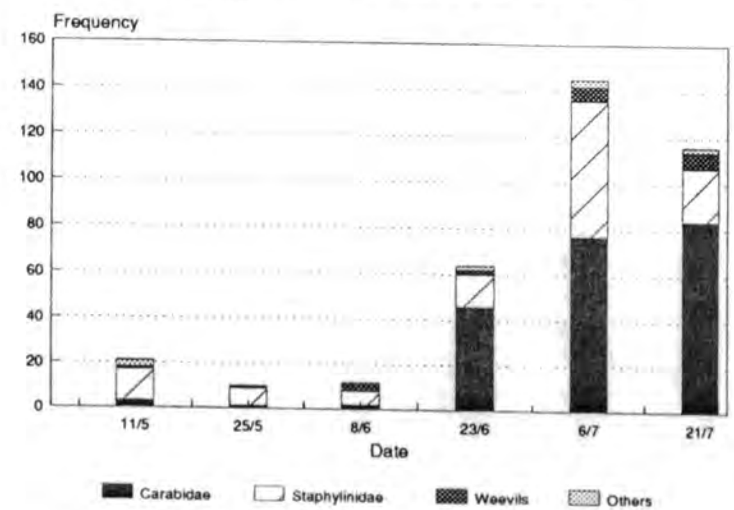
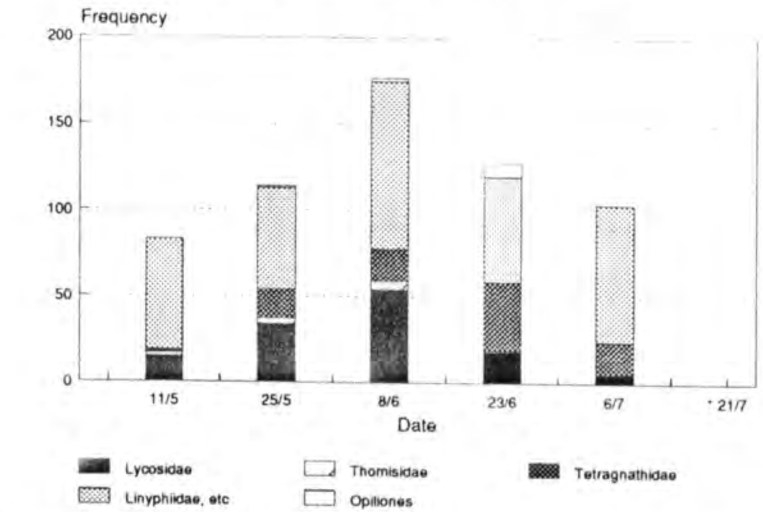
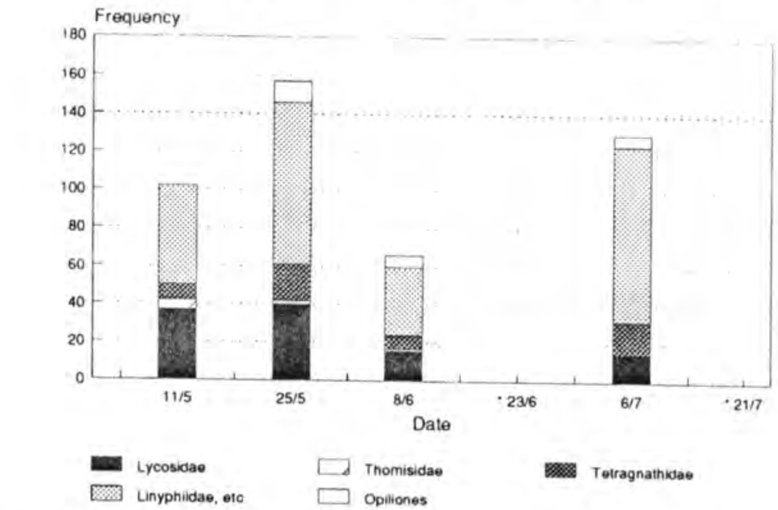


Fig.21 Numbers of Arachnida - Site 2a.



* - no data

Fig.22. Numbers of Arachnida - Site 2b.



* - no data

Fig.23. Numbers of Arachnida - Site 3a.

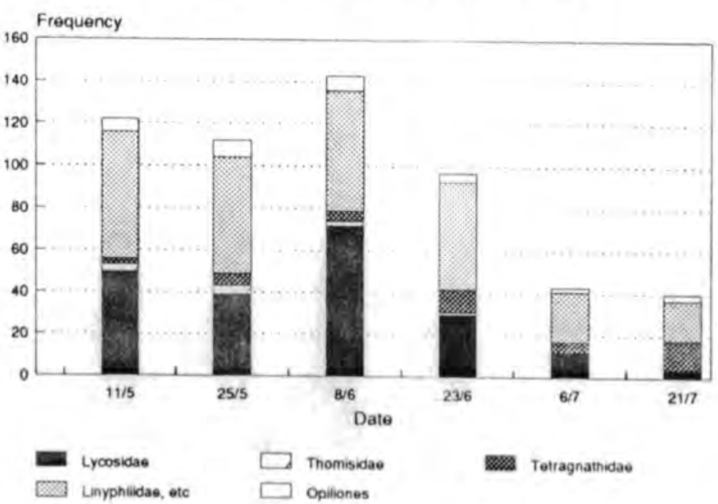


Fig.24. Numbers of Arachnida - Site 3b.

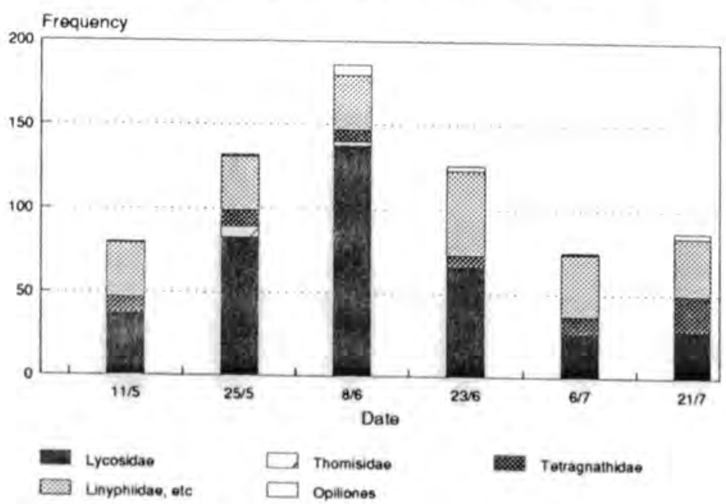


Fig.25. Numbers of Diptera - Sites 1d and 1c.

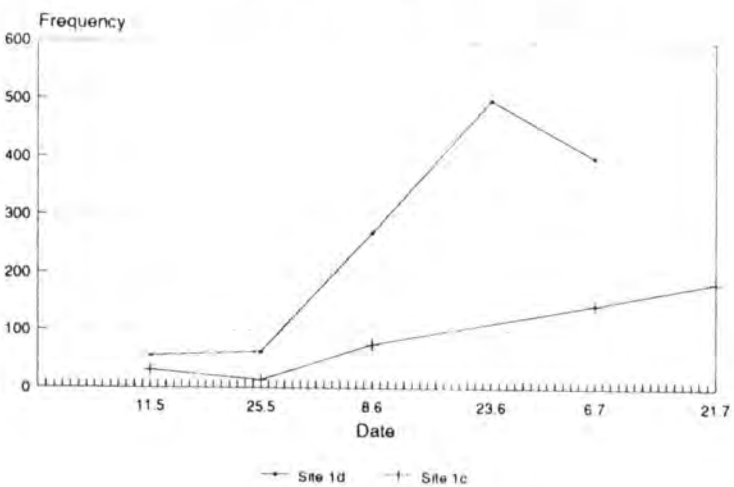


Fig.26. Numbers of Arachnida - Sites 1d and 1c.

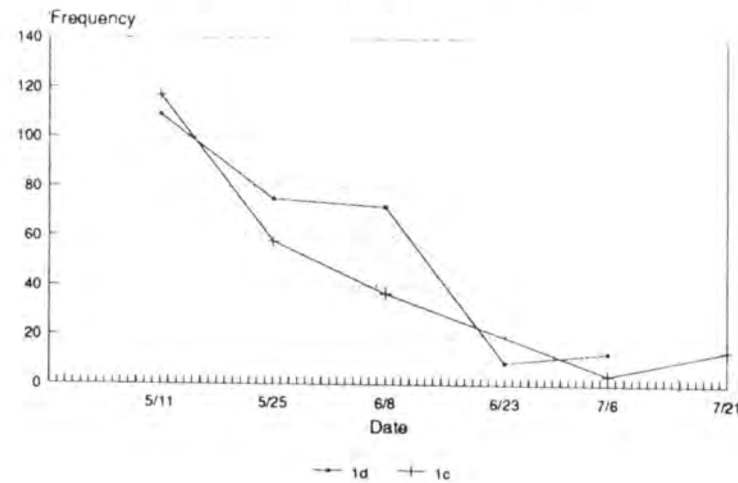


Fig.27. Invertebrate Numbers at the Plateau Site.

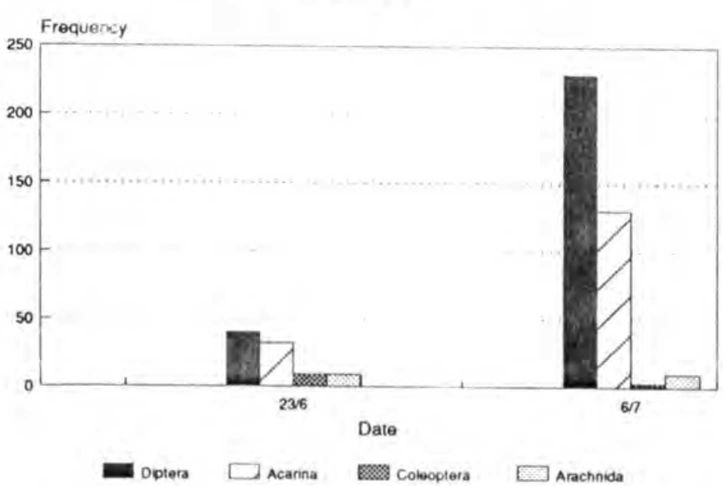


Fig.28. Invertebrate Numbers at the Compound Site.

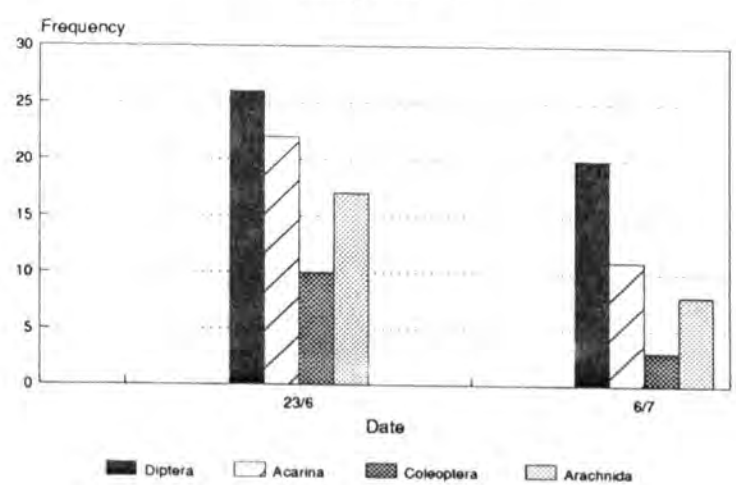


Fig.29. Arachnida Numbers at the Channel Sites.

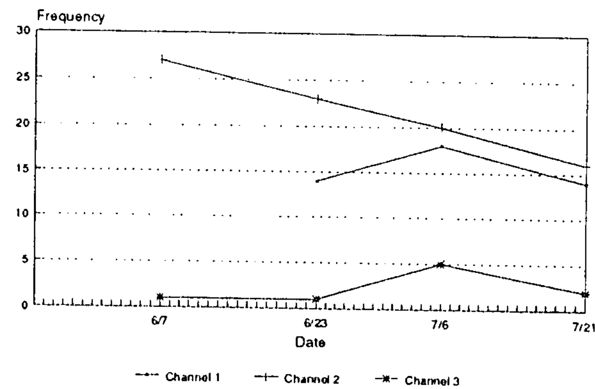


Fig.30. Diptera Numbers at the Channel Sites.

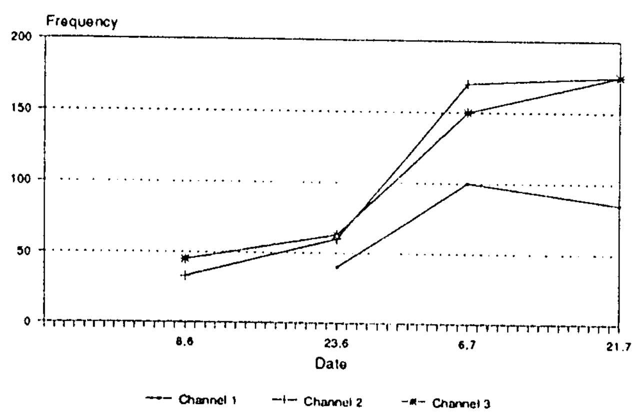


Fig.31. Numbers of Talitrus at the Channel Sites.

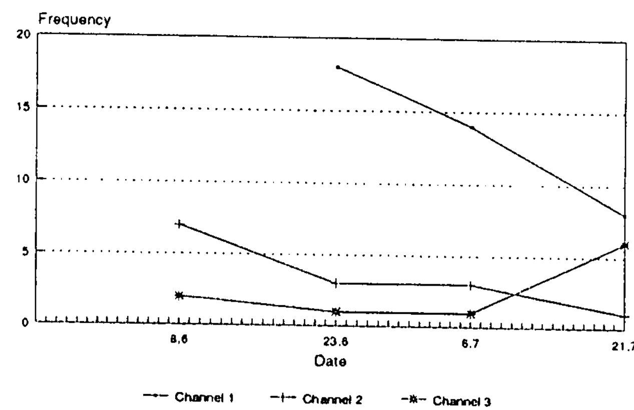


Fig.43. Lapwing Brooding with Age.

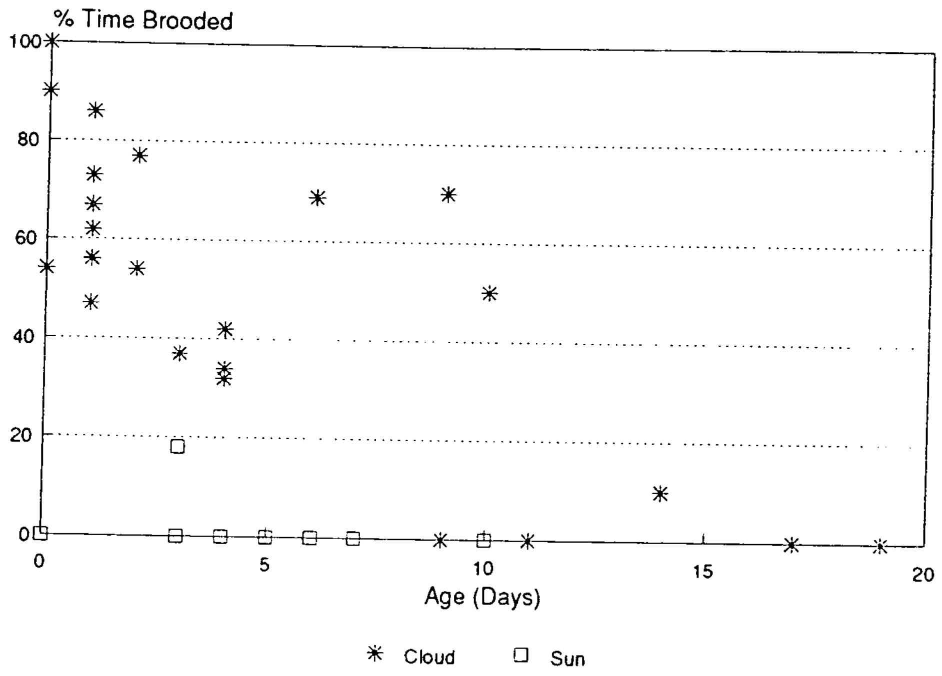
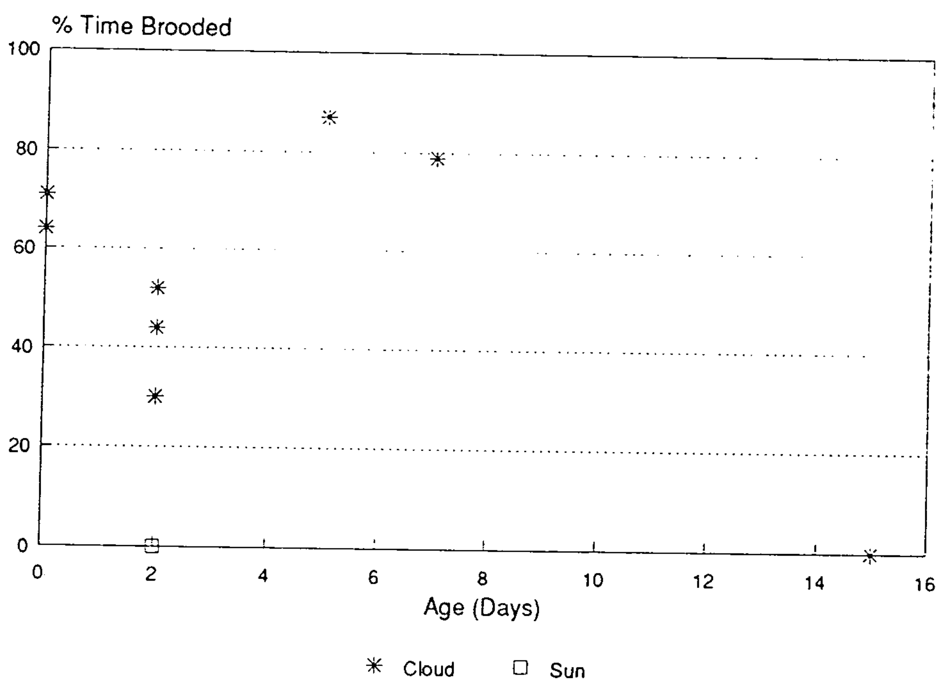


Fig.44. Ringed Plover Brooding with Age.



3.3. Survival and Mortality of Chicks.

Survival rates of chicks were calculated for Lapwings, Ringed Plovers and Skylarks, there being insufficient data on the Redshank. The rates calculated for the Skylark only look at the period whilst the chicks were in the nest, the birds typically leaving before fledging at 9 days of age. There was insufficient data to see if their mortality changed once out of the nest.

Causes of chick losses were largely unknown, the only dead chicks seen being a Ringed Plover that was crippled at birth, a brood of Skylarks that was trampled by cattle and a Partridge chick that drowned. Chicks that disappeared were presumed to have died, the possible causes including predation, starvation or loss of energy, drowning or trampling.

Lapwing and Ringed Plover survival is summarized in Figure 45. Of the Lapwing broods whose full histories were known no chicks survived, as the graph shows. It is however known that 1 or possibly 3 chicks fledged from the total of 64 hatched, (a fledging rate of 1.6 - 4.7%). Most chicks died by the age of 7 or 8 days, a few lasting to 2 or 3 weeks of age - still well below the fledging age of 30 - 40 days. Table 14 below shows that there was a significant difference between the growth rates of Lapwing chicks surviving to 8 days of age and those not. Those that did survive typically grew at a faster rate.

Table 14. Growth Rates of Chicks surviving to 8 days and those not.

	Chicks Surviving to 8 days	Chicks not Surviving to 8 days.	t	df
Growth Rate 0 - 5 days	1.61	0.28	2.23*	34
Growth Rate 5 - 8 days	2.08	0.90	1.75	5

* - Significant at the 5% level.

Overall productivity for the Lapwing, based on the data used above, was zero.

Ringed Plovers showed much better survival, 12 or 13 of the 22 chicks whose full family histories were known fledging, (a fledging rate of at least 54.5%). Mortality was quite evenly spread through the fledging period though there was an increase in chicks lost as fledging approached. Overall productivity for Ringed Plover pairs, whose full breeding histories were known, was at least 1.71 chicks per pair, (i.e. 12 or 13 chicks from 31 eggs laid).

The table below shows Mayfield survival rates for the individual chicks of the two waders, rates for Skylarks being based on nest survival.

Table 15. Wader Chick Survival Rates, (in chicks/day).

	Chicks Lost	Chick -Days	Daily Survival Rate	SE	95% confidence limits
Lapwing	38	272	0.860	0.021	0.041
Ringed Plover	8	436.5	0.982	0.006	0.013

Differences in daily survival rates of Lapwing chicks through the spring were also compared. The rates of survival of individual chicks born previous to 20 May and for those born afterwards, (these including many young from replacement broods), are shown below in Table 16 together with the t-test used to compare them. The rates are shown to be statistically different the chicks born later surviving, on average, a little longer.

Table 16. Seasonal Lapwing Chick Survival Rates.

	Chicks born before 20/5	Chicks born after 20/5
Daily Survival (Chicks/day)	0.819	0.906
SE	0.032	0.026
t	2.111	
df	36	

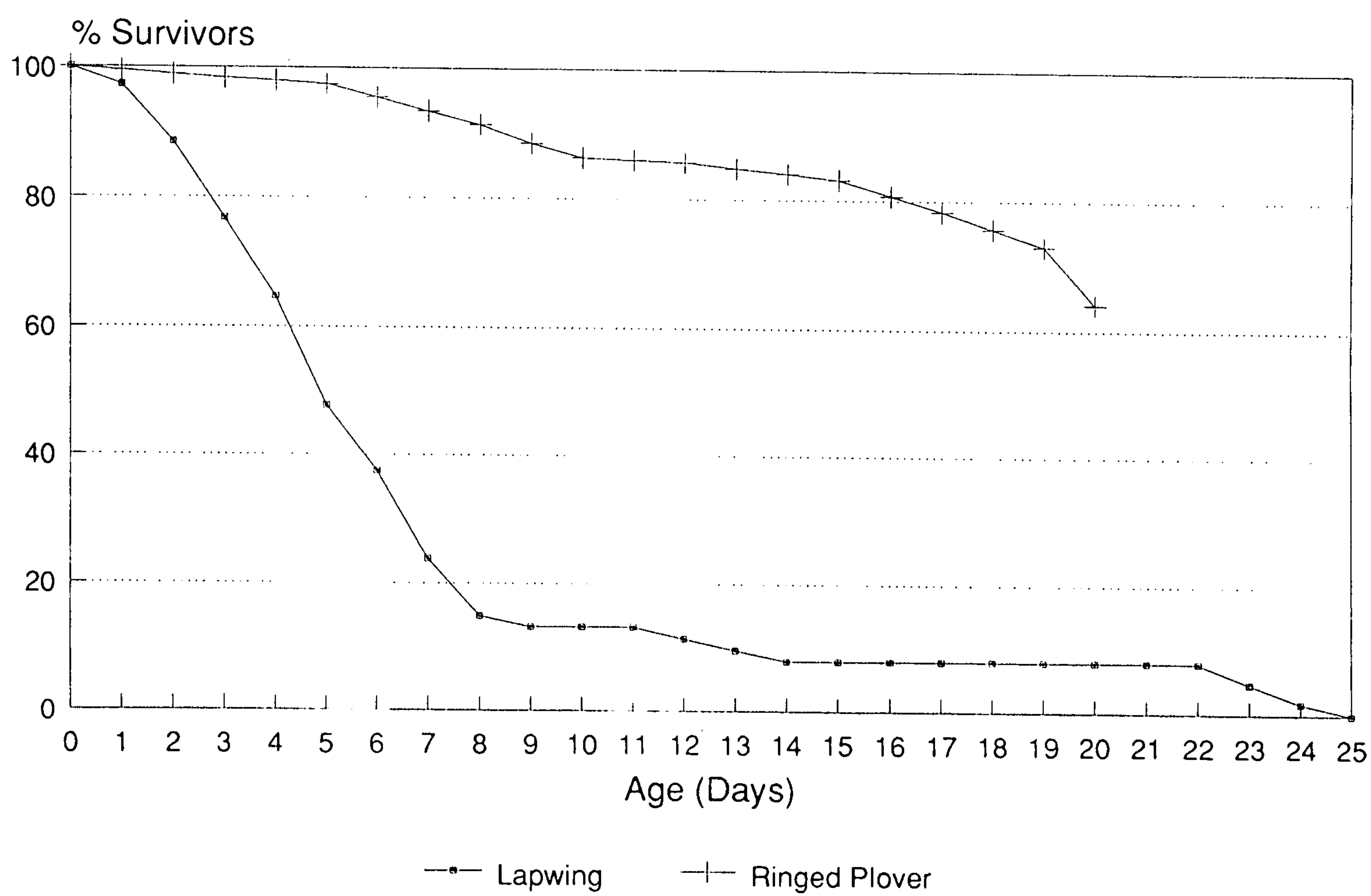
Using known fledging periods, (35 days for the Lapwing and 22 days for the Ringed Plover, Nethersole-Thompson & Nethersole-Thompson, 1986), the probabilities of individual Lapwing and Ringed Plover chicks surviving until fledging were calculated. Lapwings had a probability of surviving until fledging of 0.005 and Ringed Plovers a probability of 0.666. The method used assumes a constant loss rate over time. For the

Ringed Plover, whose losses do not change much through time, this does not matter much, but it does mean that the figure calculated for the Lapwing may not be too accurate - losses for this species being concentrated in the first 10 days.

Skylark broods had a 0.7915 probability of survival for the period of 9 days that they were in the nest, no individual chicks being lost in this time. Using the calculations for egg survival in Skylark nests, an overall probability of 0.4773 was calculated for an egg surviving to give a chick that successfully left the nest. Of the known nests, 13 chicks fledged from 18 eggs laid. Productivity was not calculated due to lack of data on the number of nesting attempts made by each pair.

The survival rate of Redshank chicks was unknown due to a lack of data.

Fig.45. Lapwing and Ringed Plover Survival.



Lapwing n = 38; Ringed Plover n = 22

4. Discussion.

4.1. Populations, Densities and Use of Habitat.

Breeding densities of birds are influenced by two main factors: firstly the availability of food, (and particularly its availability to the breeding adults), and secondly the suitability of the habitat for nesting. Lapwing nesting densities may, for example, be affected by soil moisture, drainage and pH through their effect on the numbers and availability on the Lapwing's invertebrate food (O'Connor and Shrubb, 1986). In this study the fairly high density of Lapwings partially reflects the high availability of such prey on the ground surface in early spring.

Lapwings typically nest in short grass so that, when sitting, they can keep a good look-out for predators. The need for fairly short grass is a restriction however and high densities only really occurred in this study in the areas of saltmarsh where vegetation was short. Ettrup and Bak (1985) in their study of Danish Lapwings also noted that densities were high on saltmarsh and attributed this to food availability and the suitability of the areas for nest sites.

The high densities of Skylarks found in the study reflects both the high availability of food for the species through the season and the overall suitability of the area for nesting. The species occurred over nearly all of the site only avoiding areas where there was no grass for nesting in, breeding lasting until late July.

Ringed Plovers and Redshanks both had restricted nesting habitats on the site and so both occurred in much lower numbers and densities than either the Lapwing or Skylark. Pienkowski (1984b) reports on Ringed Plover territory sizes ranging from 0.06ha in Co. Dublin, Ireland (Mason, 1947 in Pienkowski, 1984b) to 20ha in Greenland, though only from 0.3ha to 10ha at his study site on a typical coastal habitat at Lindisfarne in Northumberland. The density of 0.5 pairs/ha found in this study seems to be similar to the density typically seen at Lindisfarne, though, as Pienkowski does not give a mean territory size, direct comparison is impossible. Despite this, the density does seem to indicate that the site is of fairly good quality at least for nest sites and for the feeding adults.

4.2. Nest Survival.

Losses of clutches were found to be mainly due to predation, only three of the nests failing due to any other reason. The nest survival and mortality rates calculated give therefore a quite accurate indication of the level of predation on the site, this being of subsequent use when looking at reasons for chick losses.

Table 1 shows that the basic daily clutch survival rates do not differ significantly between the species and that predations, (and other losses), are in general not particularly high for any of the species. Galbraith (1988a) in his study of Lapwings in Scotland gives daily survival rates ranging from 0.960 to 0.977, (the variation being due to differences in habitat and the time of the season), rates which are similar to the rate of 0.975 (± 0.0168) found for the Lapwing here. Pienkowski (1983b) gives a range of values of daily survival rates for Ringed Plover clutches from his and other studies, these varying from 0.8623 (± 0.0400), on part of Lindisfarne in Northumberland, to 0.9733 (± 0.0161) in a study in the Outer Hebrides. The mean survival rate here of 0.9760 (± 0.0232) is above all of these and although it is not significantly higher, it does nonetheless indicate that predation is quite low on the site.

Table 3 shows that eggs in Lapwing nests have, due to their longer incubation period, less chance of surviving to hatching than those of any of the other species. The eggs in Skylark and Redshank nests may have better overall chances of survival due to their protective covering of grass, though, in the case of the Skylark, the short incubation period is of undoubted importance.

The Effect of the Stage of Incubation and the Choice of Nest Site on the Probability Of Predation.

The Mayfield technique, although solving one problem by looking at losses as functions of time, creates two more by assuming a constant predation rate and thus overlooking the varying probability of predation due to differences in nest sites and the stage of incubation. Whilst the first factor may obviously affect the chances of predation, it is clear that the increasing protection given by parents to their eggs as incubation progresses may also cause variation. In this study few nests were observed from the start of incubation and so it is difficult to investigate such an effect. 3 of 4 Lapwing clutches observed from laying were predated - after 0, 10 and 22 days of incubation respectively - whilst of the 5 Ringed Plover clutches observed from laying 2 were predated - after 3 and 8 days of incubation respectively. It is difficult to draw conclusions from such a small data set, though there may, at least for the Ringed Plover, be a slightly higher rate of predation in the early stages of incubation.

Although the nest site characteristics of predated and successful Lapwing clutches were shown to be insignificantly different, there is an indication that tuft height is greater at successful nests. This would be understandable as vegetation around the nest would obviously help hide the eggs and afford them greater camouflage, (whilst still allowing the sitting bird a look-out for predators). Baines (1988) shows that a greater percentage of Lapwing pairs hatched chicks from their nests on unimproved, as opposed to improved pasture, the unimproved pasture having a significantly higher grass length.

Seasonal Trends in Nest Survival.

Seasonal variations in predation rates may occur due to vegetation development or due to a change in the numbers of predators through time, (through breeding or immigration). In this case no significant seasonal trend was seen for either the Lapwing and Ringed Plover, the predation rates of Lapwing clutches being particularly even through time.

4.3. The Growth Rates of the Chicks.

The calculated growth rate of the Lapwing chicks of 3.57g/day is, in comparison with some other studies, somewhat low. The study in Teesdale this year, for example, showed chicks growing at a rate that was 0.85g/day higher than that for the chicks in this study - this difference being significant. A study in the New Forest over 4 years by Jackson & Jackson (1980) gives the following growth rates for 5 day periods of the chicks lives:

Table 17. Pullus weight increases in g/day during the fledging period.

Age (Days)	0 - 5	6 - 10	11 - 15	16 - 20	21 - 25	26 - 30
Mean Growth	2.0	3.8	3.8	4.8	4.3	5.0

The rates found in the present study, (see Table 9), are for most periods below the above and are, in particular, much lower in the first 10 days. The lack of growth during this period may help explain the subsequent overall low growth rate throughout fledging.

Ettrup and Bak (1985), in their study in Denmark, also showed that the slowest part of the Lapwings development was in the first week, (with growth rates of 2.0 - 2.5g/day), and that the quickest was in the second to fifth weeks, (with growth averaging 4.9g/day). These values and particularly those in the first week, are though again much greater than those found in the present study.

Comparison with the Ringed Plover shows that this too had a growth rate that was lower than those found in other studies, the growth rate found here being, for chicks of 3 days or more, 1.52g/day (SE = 0.09435). Pienkowski (1984a) found a growth rate of 2.49g/day for birds in his study in Lindisfarne, (Weight (g) = 1.5 + 2.49 Age (Days); n = 35; $r^2 = 0.90$) and in Mestersvig, Greenland a rate of 1.92g/day (Weight = 7.6 + 1.92 Age (Days); n = 13; $r^2 = 0.95$) - both rates being greater than that found in this study. The difference between the rate found in Lindisfarne and that found here is especially significant as the two populations are, in terms of the birds distribution, in more or less the same region. Environmental conditions for the breeding birds at the two sites should as a result be not too dissimilar and the breeding success of the birds, and the growth rates of their chicks, should not vary greatly between them. The fact that the growth rates of the Ringed Plovers and those of the Lapwing were both so relatively low at the Brinefields seems to suggest that either the weather at the site this year, or the quality of the habitat, prevented adequate feeding.

Skylarks nested and fed primarily in the meadow areas and differed from the Lapwing and Ringed Plover in the quick and unrestricted growth of their chicks. The occurrence of such differences seems to suggest that the weather did not have a particularly large effect on growth rates this year. Instead, the quality of the habitat for feeding would seem to be the more important factor.

The effects on growth rates of the weather, and of habitat and food availability, are discussed in the following two sections.

Weather, Brooding and their Effects on Growth.

Young birds are generally born with little thermoregulatory ability and whilst this develops in their first days or weeks they are often dependent on parental brooding for warmth (O'Connor, 1984). Poor weather - i.e. high winds, rain or cold temperatures - causes heat energy losses and will increase the need for brooding - thus decreasing the time available for the chicks to feed. Growth rates will then suffer.

Figure 43 shows that the Lapwing chicks continue to be brooded for at least 10 days, one chick in this study still being brooded at 17 days - (this being due to rain). The chicks only reach thermal independence at 70%, (25 days), of their fledging age (Beintema and Visser, 1989b) and they are dependent on their parents warmth for much of this period. This does have advantages however as the chicks, due to their relatively low body temperatures, have reduced heat energy losses. The need to rapidly gain energy from feeding is reduced therefore and chicks can afford to grow quite slowly - as was seen in this study. Ringed Plovers and Redshanks reach thermal independence much more quickly (Redshanks at 40 - 50% of their fledging age (Beintema and Visser, 1989b) and Ringed Plovers at 10 - 12 days (Kespaik et al, 1970 in Pienkowski, 1984a)) and therefore have to grow more quickly to keep up their resultant high energy costs.

The effects of temperature and the time of day on brooding, (and therefore on feeding rates and growth), were both shown to be insignificant in this study. Some individual chicks did show noticeable daily changes in their brooding requirements, one Lapwing chick of 9 days being brooded for 70% of its time in cool damp conditions early one morning, but needing no brooding at 1300BST when the ground was dry and the temperature $4^{o}C$ higher. Wind and rain increased brooding, though the effects were not statistically analysed.

Beintema and Visser (1989b) in Holland have modelled similar temperature and age data and conclude by saying that Lapwings and Black-tailed Godwit (*Limosa limosa*) chicks need to forage for 25 - 30% of their time to maintain their weight, and for 50% of their time if growth is not to be hampered. Lapwing chicks most at risk are those in their first week or 10 days which needed some brooding even at quite high temperatures, (i.e. 16 - 22^{o}C). If weather conditions are poor, with rain, cold and wind, young chicks may quickly lose energy and being unable to regain it by feeding, die. In this study a number of chicks may have died in their first 3 or 4 days as a result of such weather induced energy and weight losses. Older underweight chicks may also suffer in such conditions and one chick of 15 days, which had previously been growing at 3.7g/day, lost 2g in 2 days due to persistent rain reducing its feeding opportunities. The three main discrepancies in the Brooding/Age graph are from broods that were on average underweight and that had above average brooding.

The weather during the study period was only poor for a short period at the end of June, (temperatures dropping to 13^{o}C and there being a number of heavy showers), and for most of the spring weather conditions were quite favourable, (see Appendix 11). For most chicks therefore, feeding and growth rates are unlikely to have been restricted by the need for increased brooding.

Food and Choice of Habitat and their influence on Growth Rates.

The food needed for growth to occur, and that available in the habitats of the site will obviously influence the growth rates of the birds. Young birds mainly feed on, or are fed upon, protein rich food, this giving the optimum, (though not necessarily the quickest), growth rates (O'Connor, 1984). Invertebrates are as a result common prey with *Arachnida*, *Diptera* and larvae of all sorts being eaten by the birds in this study. A variety of nutrients and thus foods is of course needed and this is especially the case in the early part of growth when tissue synthesis is high. Later on more energy rich food is taken so that the maintenance costs of thermal independence can be kept up (O'Connor, 1984). The food taken will obviously also change as chicks get older and become able to take larger and harder prey. Wader chicks, being nidifugous, feed themselves, taking any prey available to them and it is their parents' responsibility to lead them to areas where the food is most suitable for their growth. Water is also important to chicks, as without it they may dehydrate. Wader chicks are, as a result, often led away from drier areas to wetter pastures.

The food taken here, as revealed by faecal analysis and observations, (see Tables 11 & 12), is similar to that seen in other studies, (e.g. for Lapwings, Galbraith 1989); Lapwing chicks taking *Arachnida*, larvae, *Diptera* and especially when older *Coleoptera.* These foods are typical of meadow habitats but in this study the dry weather from early May, (see Appendix 11), may have forced many invertebrates deeper into the soil, (Barnard and Thompson 1985), whilst the lengthening grass made even some more numerous prey items difficult for the wader chicks to find. Dry conditions also meant that some chicks growing up in the meadows may have become dehydrated. The growth rates of chicks in the meadow areas may have suffered as a result and many chicks were moved to the channel and pool edges where water was available and where the more open vegetation meant that prey was more easily found. Here however, the available food was different and often poorer. Two of the three Channel sites studied for invertebrates, (C1 & C2), had relatively high conductivity, and thus salinity, levels and this probably restricted the numbers of most prey except *Diptera*, (see Figs. 29 - 31). Two Lapwing broods moved from these areas within a few days of birth, whilst 3 other broods died, (when on average underweight), within their first week. The other Channel site, (C3), had a lower conductivity level, better vegetation cover, (of *Phragmites* and *Salicornia*), and a greater range of food (see Appendices 7 & 8) and was thus favoured by two Lapwing broods. Due to the better conditions, these survived for a longer period than most. Even here the growth rates were often relatively small for the species (as compared to the study in Teesdale for example) and two chicks were moved later in life to the plateau area where food, due to the openness of the habitat, was more easily found. The chicks at this stage were able to hide more effectively from predators and the open habitat was not therefore too much of a problem.

The choice of habitats and movements are, therefore, largely controlled by the need for adequate and suitable food to maintain growth rates, whilst being balanced by the need, when the chicks are young, for some cover as protection from predators. Other studies (Baines 1989; Galbraith 1988a; O'Connor & Shrubb, 1986 and Redfern, 1982) all note that chicks are often moved from the relatively exposed nest site areas to areas of moister pasture. Food and water are more readily available in such areas, whilst the increased cover allows the chicks to feed efficiently and hide from predators. Picozzi and Catt (1987) show how the growth rates of Lapwings differed, (over 2 years), between habitats. Chicks on farmland grew at 4.27g/day, whilst those on moorland, a relatively poorer feeding habitat, grew at 3.25g/day.

Ringed Plover broods were generally more stationary, being brought up by the channel edges near their nests, (sometimes in the company of Lapwings). The food available for the chicks at these sites, (C1,C2,C3) - *Diptera*, *Talitrus* and thin intertidal living worms - are typical prey of Ringed Plovers at more normal shore habitats, (e.g. Lindisfarne - Pienkowski, 1983b). Only *Diptera* were numerous however, these being perhaps dominant; other prey often only made up 30% of the individuals caught at the pitfalls. The Ringed Plovers' relatively low growth rates probably reflect this lack of prey diversity. The use of the compound areas by two families may have helped give the chicks a more varied diet, whilst also allowing protection from predators such as foxes. In general, the channels and pools allowed adequate, if not optimum growth rates for the Ringed Plover chicks.

Skylarks bred in the meadows where the vegetation harboured often large numbers of *Arachnida* and *Coleoptera* and their larvae; (150 *Arachnida* or more were caught, for example, at the pitfalls in the meadows in early June). They were able to take advantage of this prey source much more easily than the wader chicks which had problems hunting in the long meadow grass. The Skylarks, therefore, often brought up their chicks in areas quite separate to those which the waders used. Young skylarks were fed largely on energy rich prey such as larvae and *Arachnida*, and the large sources of such food allowed them to grow quickly and successfully.

Redshank chicks were often born in meadow areas far from the pools and channels that provided them their best feeding opportunities. The families often, therefore, undertook journeys of a few 100ms over the first day or two. Chicks may have suffered a little in their growth due to this, whilst they may also have been a little restricted, as Lapwings were, by the food availability at their chosen channel habitats.

4.4. Survival and Productivity.

The survival of chicks is dependent on the level of predation at the site, the effects of weather conditions and food availability on growth rates and the problems of lack of water and dehydration. Productivity is a measure of this together with the rate of survival of pairs' nests and eggs.

The most notable feature of this study was the zero survival calculated for the Lapwing chicks and thus the zero productivity of the Lapwing pairs. Predation is not likely to be the major cause of this, as, because the predation levels of clutches of eggs were fairly low for all the species, the levels of chick predation would be expected to be fairly low too. Instead it seems probable that the low growth rates of the chicks, or perhaps dehydration, best explain their poor survival; the low growth rates here being largely due to poor food availability rather than poor weather. Survival to 8 days of age was shown to be positively correlated to the rate of growth of chicks in the first 5 days, (see Table 14). Starvation will obviously cause mortality, but low growth rates can often also cause problems. Galbraith (1988b) shows how the size of Lapwing chicks often still increases at a fast rate even when weight increases are low, zero or negative, this causing a weakening in the chicks' body condition.

Dehydration may, as stated, also be important in explaining the high level of mortality seen in this study. There was little available water for the chicks on the site this year, partially because of the dry weather, but also because of the high salinity of much of the water. The poor feeding efficiency of the chicks when young and the problems caused by poor thermoregulatory ability, (i.e. loss of energy and the need for brooding), would have increased the likelihood of mortality during the occasional day or two of poor weather.

Beintema and Visser (1989a) note that the first 10% of Lapwing chicks born each year are unlikely to survive as the poor weather of early spring restricts the chicks feeding opportunities and thus decreases their growth rates. In this study chicks born after 20

May were shown to survive longer than those born before, this despite the relatively good weather in early May this year. Klomp (1971), in his study in Holland, saw that later ringed chicks survived slightly better to 1 September than those ringed earlier in the season. Beintema and Visser give a mean date of 8 May as the earliest safe hatching date for Dutch Lapwings, (this being based on a number of years' data).

If the overall productivity is typical for the site, the continuation of breeding there is, of course, dependent upon immigration each year. Galbraith (1988a) has suggested that each female in a hypothetical population would, taking into account subsequent mortality, have to fledge, on average, 0.8 young per year to maintain the population size.

That Ringed Plovers survive at a much higher rate to fledging is perhaps due to their more reliable food source, (which provides an adequate if not good growth rate), the earlier development of their thermoregulatory ability, (which allows them to better avoid the problems of bad weather), and their shorter fledging period. Even if underweight, the ability to fly fast improves a chick's chances of survival; new sources of food will be available and the ability to escape from predators is improved.

Skylark chicks survived well in the nest, the daily survival rate of 0.9744 nests/day being similar to the 0.9631 nests/day survival rate of nests containing eggs. This indicates that not only were the loss levels of clutches of eggs and broods of young similar, but also that the chicks were growing well. There must easily have been adequate food for the chicks in the meadows - as the pitfall results suggested.

Differences in growth rates, and perhaps survival and productivity, may therefore be attributed to the differences in the food available to the birds in their chosen foraging habitats. Overall the site is probably poor for Lapwings and perhaps also for Redshanks. The meadow areas dry out easily, restricting food availability and possibly causing dehydration, whilst the pools are often too saline to provide enough food and good water. Ringed Plovers faired better, the pools providing more suitable and available food. The meadow areas of the site, though not so suitable for Lapwings, do provide a good nesting and feeding habitat for Skylarks.

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Appendix 1. Plant Species.

Meadows.

Ruderals:

Achillea millefolium
Cirsium arvense
Cirsium vulgare
Epilobium angustifolium
Hieracium murorum
Lotus corniculatus
Melilotus officinalis
Plantago lanceolata
Ranunculus acris
Reseda luteola
Rumex acetosa
Rumex acetosella
Senecio jacobaea
Senecio vulgaris
Taraxacum Sect. vulgaria
Trifolium pratense
Trifolium repens
Tripleurospermum inodorum
Urtica dioica

Grasses:

Deschampsia flexuosa
Elymus sp.
Festuca rubra
Holcus lanatus
Juncus articulatus

(*Ammophila arenaria* - in Plateau area).

Pools and Channels.

Salt-water/brine:

Aster tripolium
Centaurium pulchellum
Salicornia europaea
Spergularia media

Freshwater:

Ranunculus aquatilis

Appendix 2. Nests - Histories and Sites.

Lapwing.

No.	Dates Observed	No. of Eggs	No. of Nest-days	Outcome	Mean Veg. Height (cm)	Mean Tuft Height (cm)	Average Cover (%)
1a	23/4-4/5	4	12	P	3	3	80
R1b	16/5-21/5	4	4	P	2	8	90
2a	25/4-2/5	4	10	P	5	10	90
R2b	11/5	2					
	12/5	3	1				
	13/5-21/5	4	10	P	2	5	40
3	27/4-18/5	4	22	H(4)	1	5	15
4	30/4-25/5	3	26	H(2)	0	0	0
5	23/4-11/5	4	19	H(4)	1	1	80
6	4/5-18/5	4	15				
	21/5-28/5	2	8	H(1)	4	8	95
7	23/4-14/5	4	22	H(4)	4	10	70
8	23/4-9/5	4	17	H(4)	2	8	100
9	23/4-25/4	?		P	?	?	100
10a	23/4-7/5	4	15	P	1	1	40
R10b	21/5	3	1				
	22/5-17/6	4	27	H(4)	3	12	100
11	27/4-9/5	4	13	H(4)	1	1	30
12a	23/4	?		P	?	?	100
R12b	4/5	3	1				
	5/5-9/5	4	5	P	4	10	100
R12c	18/6	3	1	H(1)	15	20	100
13	25/4-30/4	4	6	P	6	10	60
14	23/4	4	1	H(4)	5	15	95
15	30/4-5/5	4	6	H(3)	2	2	90
16	25/4-9/5	4	15	H(4)	6	10	90
17	25/4-27/4	?		P	?	?	100
18	23/4-25/4	4	3	H(4)	2	2	90
19	23/4-25/4	?		P	5	5	100
20	23/4	?		P	?	?	100
21	25/4-16/5	4	22	H(4)	1	1	5
22	10/5-12/5	3	3	H(3)	6	15	95
R23	18/5	3	1				
	19/5-23/5	4	5				
	24/5-8/6	3	16	P	0	0	10
R25	23/5	1		P	10	10	100
R27	16/6	4		H(3)	3	10	95
R28	20/6-30/6	4	11	H(4)	0.5	0.5	95

Outcome: P - Predated Clutch
H(x) - x Eggs Hatched

R - Replacement Clutch

Appendix 3. Lapwing Weights.

Brood No.	Date Born	No.	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
			Age (Days)																							
1	23/4	17								28																
		20																								
2	25/4	21						23																		
		23						23																		
		24						22																		
3	6/5	26		16																						
		27		16																						
		28		17																						
4	9/5	29	19	18	19			23																		
		30	19																							
		31	20	19	19																					
		32	18	18	18																					
5	10/5	33	18				14		17																	
		34	19				17		19																	
		35	19				17		18																	
		36	18				17		19																	
6	10/5	37	20	18																						
		38	21	19																						
		39	19	17																						
		40	19	18																						
7	10/5	41		18																						
		42		17							31															
		43		19																						
8	13/5	44		16		19																				
		45		17		20																				
		46		16																						
9	12/5	47			19		25		30			35				59						95				
		48			15		19		21																	
		49			18		24		26																	
		50			17		22		25			31		38		50			65			80				
10	15/5	1		17																						
		2		16		15																				
		3		16																						
		4		16																						
11	18/5	5	20																							
		6	21																							
		15				19																				
		16						21		30			37	40		49		60			66					
12	19/5	8			20																					
		9			21																					
		10			18																					
13	17/5	11					20																			
		12					21		24																	
		13					21		25		29			38												
		14					20																			
		17							25					43												
14	25/5	18	18			19					30		33													
		19	19			18																				
15	29/5	20	18		18																					
16	16/6	28	18		15		16																			
		29	18		15																					
		30	17		15		17						26													
17	15/6	31		13		16																				
18	17/6	33		15		16			16																	
		34		15		20			22			27			40			51		49		51			58	
		35		15		18			17																	
		36		15		19						28			40										60	
19	19/6	37		16																						
20	9/6	38												41			51						90			
21	23/6	39	18			20																				
		40	17			21																				
		41	16			17																				

Ringed Plover.

No.	Dates Observed	No. of Eggs	No. of Nest-days	Outcome	Mean Veg. Height (cm)	Average Cover (%)
1	2/5-23/5	4	22	H(4)	0	0
*12a	29/6	4	1	P	0	0
*R12b	12/7-30/7	2	20	H(2)	0	5
2a	25/4	2				
	27/4	3	2			
	30/4-4/5	4	6	P	0	0
R 2b	14/5	1				
	16/5	3	2			
	18/5	4	1	P	0	15
R 8	23/5	1				
	25/5	2	2			
	28/5-4/6	4	10			
	6/6-20/6	3	14	H(3)	0	0
3	25/4	3	2			
	27/5-21/5	4	27	H(2)	0	15
4a	9/5-11/5	4	3	P	1	60
R 4b	28/5-6/6	4	11			
	8/6	3	3	H(3)	1	60
5	9/5-11/5	3	4	H(3)	0	0
6				?	0	0
7	21/5-28/5	4	8	H(3)	0	20
9	25/5	3	2			
	28/5-18/6	4	23	H(4)	0	30

* - Second Clutch

Skylark.

No.	Dates Observed	No. of Eggs	No. of Nest-days	Outcome	Mean Veg. Height (cm)	Mean Tuft Height (cm)
1	2/5-5/5	3	4	H(2)	4	12
	5/5-14/5	Y		O(2)		
2	4/5-7/5	4	4	H(4)	8	10
	7/5-14/5	Y		O(4)		
3	4/5-7/5	Y		O(3)	5	15
4	7/5-11/5	Y		O(3)	8	25
5	7/5	B				
	18/5	4	1	P	4	15
6	18/5-27/5	4	10	H(4)	12	25
	27/5-29/5	Y		T		
7	18/5	Y		O(3)	12	20
9	6/6-8/6	Y		O(4)	15	25
10	13/6	Y		O(1)	15	30
12	20/6-26/6	3	7	H(3)	6	20
	27/6-4/7	Y		O(3)		
14	29/6-2/7	Y		O(3)	25	45

B -Building
Y -Young
T - Trodden on
O(x) - x Young left nest

Redshank.

No.	Dates Observed	No. of Eggs	No. of Nest-days	Outcome	Mean Veg. Height (cm)	Mean Tuft Height (cm)	Average Cover (%)
1	4/5-11/5	4	8	D	10	25	100
2	9/5-11/5	4	3	P	2	10	75
3	9/5-21/5	4	13	H(4)	5	20	100
4a		?		T	8	25	95
R 4b	16/5-4/6	4	20	H(4)	8	12	100
5	16/5	Tr			10	20	100
		?		P	?	?	?
6	30/4-23/5	2	24	H(2)	10	15	100
7	4/6-11/6	4	8	H(4)	12	30	100
8	20/6-29/6	4	10	H(4)	10	25	100
-		Tr			10	25	100

D - Deserted
Tr - Trial Scrape

Appendix 7. Invertebrates caught at Pitfall Sites.

Site 1d

	Date 11/5	25/5	8/6	23/6	6/7	21/7
Arachnida:						
Lycosidae	30	39	28	1	2	
Thomisidae	3					
Tetragnithidae	10	15	9	2	2	
Linyphiidae, etc	66	75	35	6	9	
Acarina					13	
Coleoptera:						
Carabidae		2	1			
Chrysomelidae	3					
Staphylinidae	2		2			
Coccinellidae			1		1	
Nitidulidae				4		
Unidentified	6	1				
Larvae	6				1	
Diptera	56	63	270	500	400	
Homoptera:						
Cicadellidae					16	
Hymenoptera:						
Formicidae			1			
Collembola	2000$^+$	500		2		

Site 1c

	Date 11/5	25/5	8/6	23/6	6/7	21/7
Arachnida:						
Lycosidae	33	23	15		1	
Thomisidae	4	2	1			
Tetragnithidae	16	2	2			
Linyphiidae, etc	64	31	19		3	14
Acarina						9
Coleoptera:						
Carabidae	8	5	3			2
Chrysomelidae	5					1
Staphylinidae	1					
Coccinellidae	2					1
Nitidulidae					1	1
Weevil	1					
Unidentified	3					
Larvae	6				1	
Diptera	31	14	76			185
Larvae		3	2			
Lepidoptera:						
Noctuidae		1				
Homoptera:						
Aphrophoridae		1				
Lygaeidae			1			
Cicadellidae					1	
Chilopoda	1					
Collembola	2000$^+$	500				

Site 2a

	Date 11/5	25/5	8/6	23/6	6/7	21/7
Arachnida:						
Lycosidae	15	34	54	18	5	
Thomisidae	2	3	5	1		
Tetragnithidae	2	17	19	40	19	
Linyphiidae, etc	64	59	97	61	80	
Opiliones		1	2	8		
Acarina				28	74	
Coleoptera:						
Carabidae	6	4	1	3	8	
Chrysomelidae		2	4	13	9	
Staphylinidae	7	4	19	9	18	
Colydriidae		1				
Nitidulidae		2			5	
Throscidae				2		
Weevil	4	2	11	2	3	
Larvae	1		1	8	29	
Unidentified	5			4	17	
Diptera	29	18	24	45	70	
Larvae	1					
Lepidoptera:						
Noctuidae			4			
Larvae		2	1	1		
Neuroptera:						
Chrysopidae				1		
Homoptera:						
Cicadellidae	3	3	14	22	32	
Aphrophoridae	1		2			
Lygaeidae			3	1	1	
Hymenoptera:						
Formicidae			1			
Collembola	115	50		6	40	
Talitrus s.					1	
Oligochaetes:						
Lumbricidae			1		1	

Site 3a

	Date 11/5	25/5	8/6	23/6	6/7	21/7
Arachnida:						
Lycosidae	50	39	72	30	12	4
Thomisidae	3	4	2	1		
Tetragnithidae	3	6	5	11	5	14
Linyphiidae, etc	60	55	57	51	24	19
Clubionidae	1					
Opiliones	6	8	7	4	2	3
Acarina		1	1	2	13	10
Coleoptera:						
Carabidae	4	2	6	20	75	50
Chrysomelidae		1				1
Coccinellidae	2					
Staphylinidae	20	17	13	32	27	24
Nitidulidae				1		4
Unidentified					1	
Weevils		1	4		1	1
Larvae	2	5	3	8	30	30
Diptera	19	23	22	34	25	21
Homoptera:						
Cicadellidae		2	1	5	10	3
Aphrophoridae	5	1				
Collembola		3		6	14	23
Formicidae			2	1	1	
Oligochaetes:						
Lumbricidae	1	4		1		1

Site 2b

	Date 11/5	25/5	8/6	23/6	6/7	21/7
Arachnida:						
Lycosidae	37	40	16		15	
Thomisidae	5	2	1			
Tetragnithidae	8	19	7		17	
Linyphiidae, etc	52	85	36		92	
Opiliones		11	6		6	
Acarina					85	
Coleoptera:						
Carabidae	4	2	2		17	
Staphylinidae	7	11	10		21	
Chrysomelidae					2	
Nitidulidae		1			4	
Weevil	1	4			9	
Unidentified	1					
Larvae	1	1				
Diptera	24	34	8		75	
Lepidoptera:						
Larvae	2					
Homoptera:						
Cicadellidae	1	1	16		31	
Lygaeidae					2	
Apoidea		1			3	
Collembola		10	65		10	
Oligochaetes:						
Lumbricidae		1	2		1	

	Site C1			Site C2			
	Date			Date			
	23/6	6/7	21/7	8/6	23/6	6/7	21/7
Arachnida:							
Lycosidae	4	3		17	15	3	2
Thomisidae				1			2
Tetragnithidae	1	1				1	
Linyphiidae	9	14	14	9	7	16	12
Opiliones					1		
Acarina	6	4	2			1	
Coleoptera:							
Carabidae	3	8	4	2			2
Staphylinidae	2	4		1	1		1
Nitidulidae			2				
Dytisicidae				1			
Larvae		1					
Diptera	40	100	85	33	60	170	175
Larvae		1		9	7	1	2
Homoptera:							
Aphrophoridae					5		
Cicadellidae	6						
Lygaeidae	2		1	11		12	8
Miridae					8		
Collembola		500		20			
Apoidea						1	
Isopoda		1					
Talitrus s.	18	14	8	7	3	3	1
Formicidae							1
Oligochaetes:							
Lumbricidae		1					

	Site C3			
	Date			
	8/6	23/6	6/7	21/7
Arachnida:				
Lycosidae			1	2
Linyphiidae, etc	1	1	4	
Coleoptera:				
Staphylinidae			1	
Nitidulidae	7			2
Diptera	45	63	150	175
Larvae	1	1	3	
Homoptera:				
Lygaeidae		1	13	10
Aphrophoridae		1		
Cicadellidae			1	
Collembola	100	50	110	300
Talitrus s.	2	1	2	6
Lepidoptera:				
Noctuidae				1
Apoidea		1	1	

	Site 3b					
	Date					
	11/5	25/5	8/6	23/6	6/7	21/7
Arachnida:						
Lycosidae	37	83	138	66	66	28
Thomisidae	1	6	2			
Tetragnithidae	9	10	7	7	2	22
Linyphiidae, etc	32	39	33	50	37	34
Opiliones	1	1	6	3	1	3
Acarina	1		3	17	22	2
Coleoptera:						
Carabidae	3	1	2	46	77	84
Chrysomelidae						
Staphylinidae	14	8	6	14	59	23
Coccinellidae				1		
Nitidulidae	3			1	3	2
Weevils	1	1	3	2	6	7
Larvae	2	3	4	5	29	10
Diptera	20	5	9	13	40	40
Larvae	1	2	1			
Lepidoptera:						
Noctuidae						
Larvae	1		1		1	1
Homoptera:						
Aphrophoridae	1					
Cicadellidae	9			6	24	3
Miridae				1		
Collembola	10			4	10	20
Isopoda		1	1		1	
Chilopoda			1	1		
Oligochaetes:						
Lumbricidae		3	1		1	1

	Plateau Site		Compound Site	
	Date		Date	
	23/6	6/7	23/6	6/7
Arachnida:				
Lycosidae	5	4	5	1
Thomisidae			1	
Tetragnithidae			3	1
Linyphiidae, etc	3	2	4	4
Opiliones	1	4	4	2
Acarina	32	130	22	11
Coleoptera:				
Carabidae	7	2	1	
Chrysomelidae	1		4	2
Staphylinidae	1	1	3	1
Unidentified			2	
Diptera	40	230	26	20
Homoptera:				
Cicadellidae		4	6	1
Acrididae	1			
Formicidae	3	5	3	2
Chilopoda			1	

Fig.32. Relative Proportions of Invertebrates caught at Site 1d.

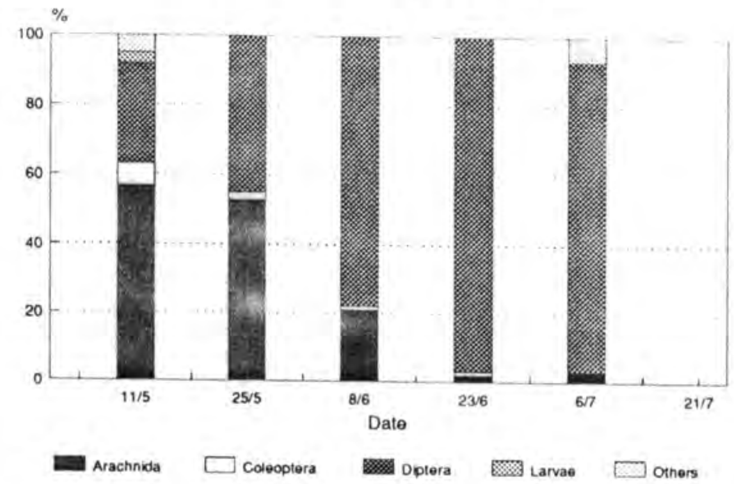


Fig.33. Relative Proportions of Invertebrates caught at Site 1c.

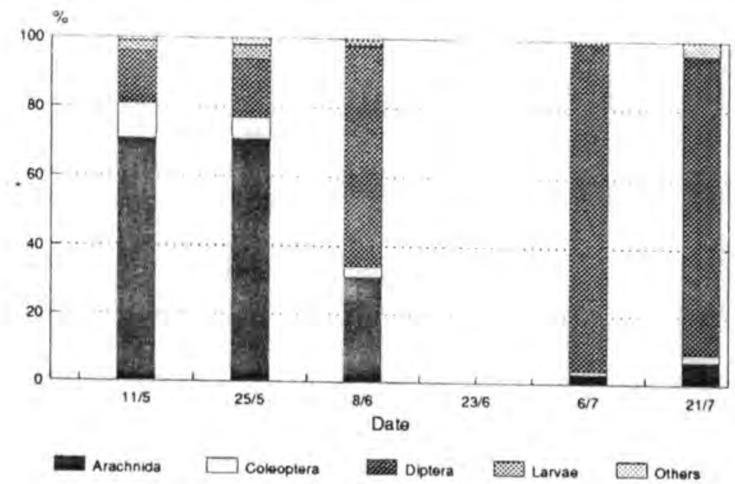


Fig.34. Relative Proportions of Invertebrates caught at Site 2a.

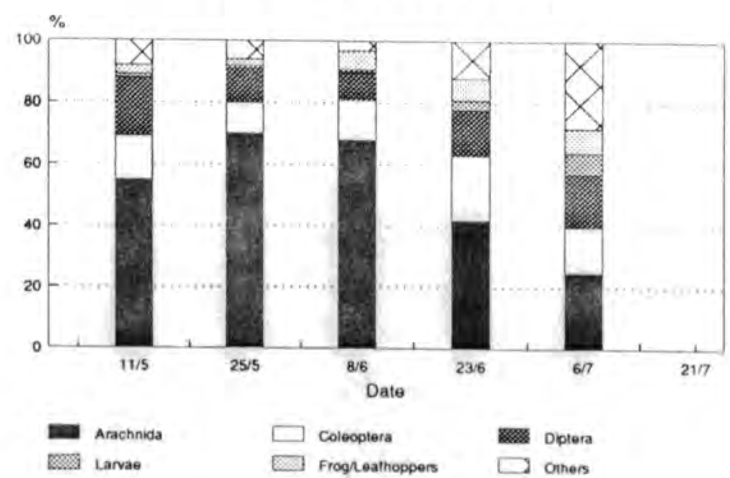


Fig.35. Relative Proportions of Invertebrates caught at Site 2b.

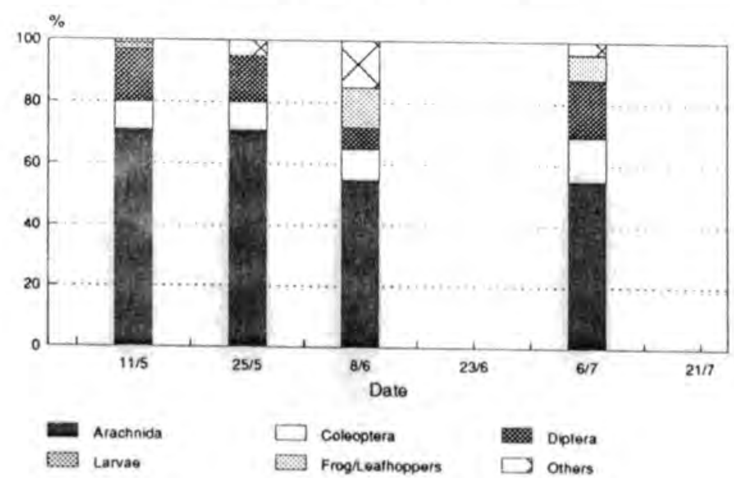


Fig.36. Relative Proportions of Invertebrates caught at Site 3a.

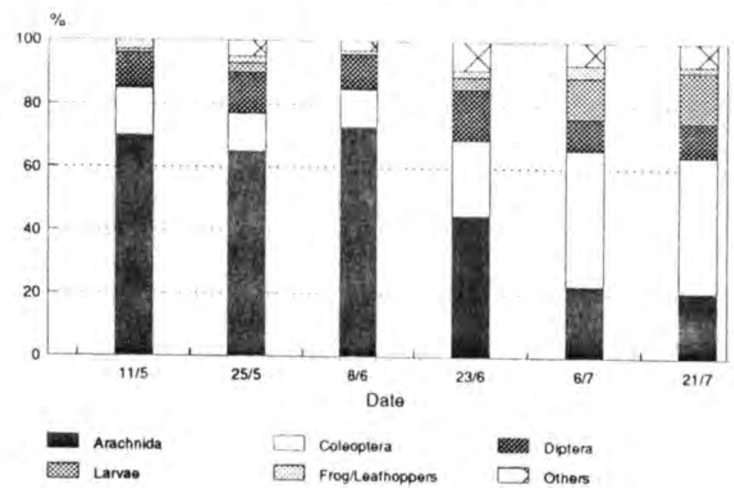


Fig.37. Relative Proportions of Invertebrates caught at Site 3b.

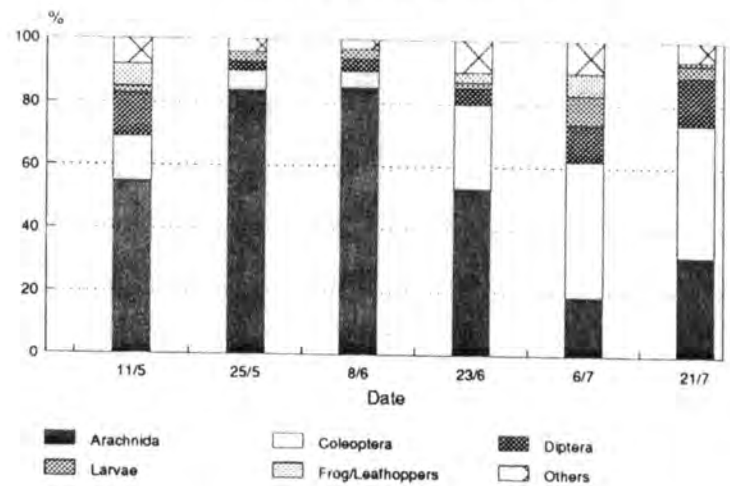


Fig.38. Relative Proportions of Invertebrates caught at Site C1.

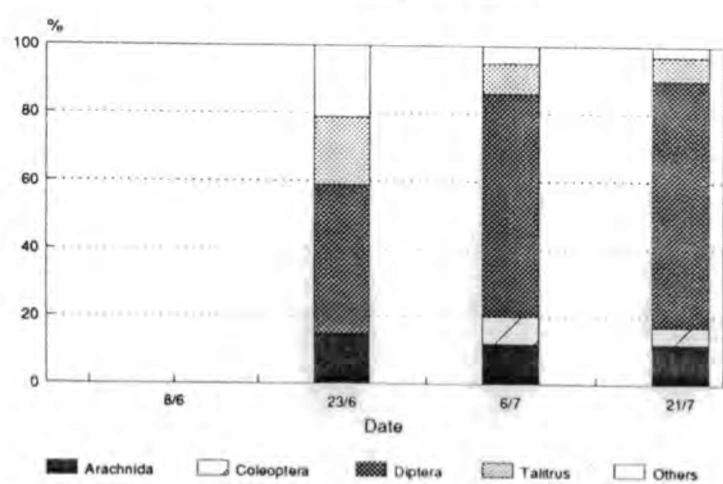


Fig.39. Relative Proportions of Invertebrates caught at Site C2.

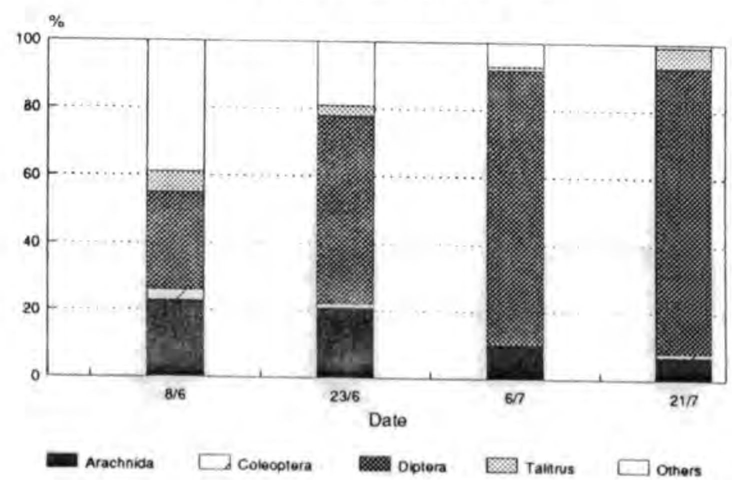


Fig.40. Relative Proportions of Invertebrates caught at Site C3.

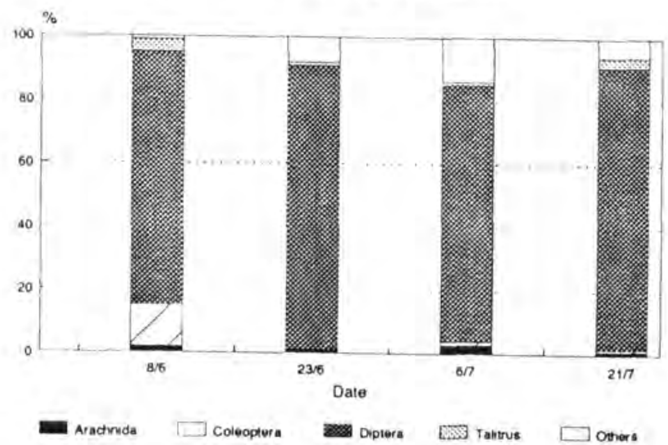


Fig.41. Relative Proportions of Invertebrates caught at the Plateau Site.

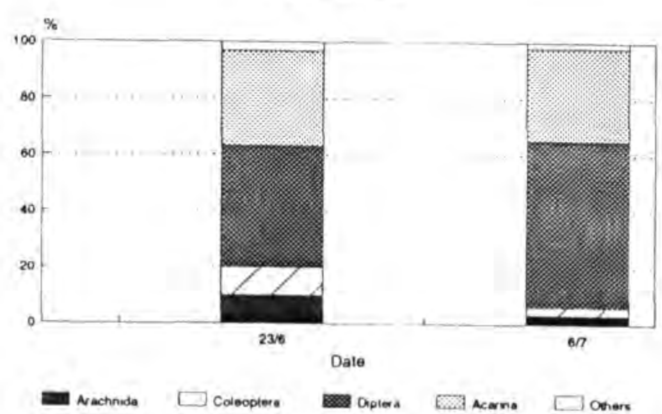
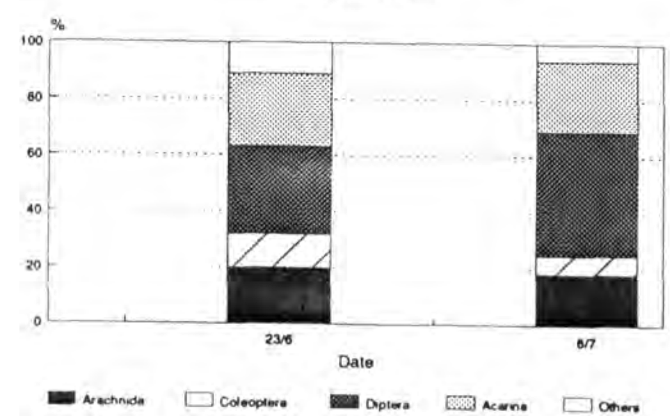


Fig.42. Relative Proportions of Invertebrates caught at the Compound Site.



Appendix 9. Lapwing Brooding.

Date	No. in brood	% Time Brooded	Age (Days)	Sunlight	Time (BST)	Temperature at 5cm (^{O}C)	Mean Brood Weight (g)
27/4	4	42	4	No	1410-1500	9	?
7/5	3	47	1	No	1315-1405	14.5	16.7
11/5	3	77	2	No	1345-1435	9	18.7
11/5	4	86	1	No	1504-1554	9	18.0
16/5	4	69	6	No	1750-1840	13	18.3
23/5	2	32	4	No	1435-1525	18.5	26.0
29/5	1	0	11	No	1113-1203	18	40.0
29/5	1	54	0	No	1250-1340	18	18.0
2/6	1	34	4	No	0820-0910	14.5	?
4/6	1	50	10	No	1216-1306	15.5	33.0
8/6	1	10	14	No	1220-1310	12.5	?
11/6	1	0	17	No	1212-1302	15.5	53.0
16/6	1	56	1	No	1657-1747	21	13.0
16/6	3	90	0	No	1800-1850	20	17.7
18/6	4	62	1	No	0825-0915	20	15.0
18/6	4	73	1	No	1236-1326	16.5	15.0
18/6	4	67	1	No	1716-1806	17	15.0
18/6	3	54	2	No	1140-1230	16.5	15.0
20/6	4	37	3	No	1229-1319	20	18.3
26/6	2	70	9	No	0651-0741	13	27.5
26/6	2	0	9	No	1230-1320	17	27.5
6/7	2	0	19	No	1210-1300	19	51.0
14/5	4	0	4	Yes	1610-1700	17	16.3
25/5	1	0	7	Yes	1100-1150	12.5	30.0
25/5	2	0	0	Yes	1720-1820	9.5	18.5
28/5	1	0	10	Yes	1110-1200	23	37.0
28/7	2	0	3	Yes	1202-1252	23	18.5
20/6	4	0	3	Yes	0755-0845	16	18.3
20/6	4	18	3	Yes	1840-1930	18	18.3
23/6	4	0	6	Yes	0740-0830	13.5	18.3
23/6	4	0	6	Yes	1245-1335	20	18.3

Appendix 10. Ringed Plover Brooding.

Date	No. in brood	% Time Brooded	Age (Days)	Sunlight	Time (BST)	Temperature at 5cm (^{O}C)	Mean Brood Weight (g)
25/5	2	0	2	Yes	1531-1621	12.5	11.0
29/5	3	64	0	No	1630-1720	17.5	8.7
29/5	4	44	2	No	1727-1817	17.5	8.0
31/5	4	30	2	No	1325-1415	23.5	9.7
11/6	3	71	0	No	1330-1420	15.5	9.0
13/6	3	52	2	No	1320-1410	14.0	8.0
16/6	3	87	5	No	1319-1409	20.0	12.0
18/6	3	79	7	No	1352-1442	16.5	15.7
26/6	1^{+}	0	15	No	1407-1457	17.0	?

Appendix 11. Weather Data.

Data taken on the site at 1200BST, or from newspapers for a Newcastle weather station at 1200BST

Date	Cloud (Octas)	Temperature at 1m (^{O}C)	Temperature at 5cm (^{O}C)	Wind	Rain
23/4	8	7		Light NE	
24/4		12			
25/4	1	14		Breeze NE	
26/4		12			a.m.
27/4	7	9	9.5	Light NE	
28/4					
29/4		16			
30/4	0	19	19	Light NE	
1/5					
2/5	0	12	13	Breeze NE	
3/5	0	11			
4/5	2	19	20.5	Breeze NE	
5/5		15			
6/5					
7/5	6	14	15	Breeze NE	a.m.
8/5		11			Yes
9/5	5	13	15	Breeze NE	
10/5	4	12.5	13.5	-	Yes
11/5	8	9	9	Light S	Yes
12/5		12			
13/5		12			
14/5	1	15	18.5	Breeze NE	
15/5		12			Storms
16/5	2	17	19	Light SW	p.m.
17/5		12			
18/5	8	10	11	Breeze NE	
19/5		10			Yes
20/5		11			
21/5	2	13	13.5	Breeze NE	
22/5		15			
23/5	6	15.5	17	Light W	
24/5		14			
25/5	2	12.5	14	Light NE	
26/5		17			
27/5		16			
28/5	0	22	23	Breeze NE	
29/5	8	17.5	18	Light SW	
30/5					
31/5	5	22.5	23	Medium S	
1/6					a.m.
2/6	6	16	17	Light NE	
3/6		15			
4/6	8	16	15.5	Light W	
5/6		15			Yes
6/6	8	16.5	17.5	Light SE	p.m.
7/6		13			Yes
8/6	7	11.5	12	Light NE	Yes
9/6		12			a.m.
10/6		12			
11/6	8	13.5	15.5	Light NE	
12/6	8	11			
13/6	8	13	14	Breeze NE	
14/6		14			
15/6		16			
16/6	3	19	20.5	Light NE	

Date	Cloud (Octas)	Temperature at 1m (^{O}C)	Temperature at 5cm (^{O}C)	Wind	Rain
17/6		19			
18/6	8	16	16.5	Medium S	Heavy
19/6		17			a.m.
20/6	5	19	20	Light S	Heavy
21/6					p.m
22/6		13			Yes
23/6	7	18	20	Light W	
24/6					
25/6		17			
26/6	8	16	16	Breeze NE	a.m.
27/6		19			p.m.
28/6		16			
29/6	2	21	23	Breeze S	
30/6					Yes
1/7		18			Light
2/7	8	16			Light
3/7		16			
4/7	8	10	10	Light SE	Yes
5/7		15			
6/7	6	18	19	Light NW	
7/7		15			Yes
8/7		17			
9/7	3	17	18	Med./Strong W	
10/7		17			
11/7		17			
12/7	7	23	24	Breeze NE	
13/7		16			
14/7		18			
15/7	2	22	25	-	p.m.
16/7		21			
17/7		21			
18/7	0	24	25	-	
19/7		26			
20/7		26			
21/7	8	20	24	Light NE	
22/7		17			
23/7		15			
24/7		19			
25/7	0	20	21	Breeze NE	
26/7		17			
27/7		18			light
28/7		19			
29/7		21			
30/7	7	21	23	Light SW	p.m.
31/7		21			