Behavioural ecology of the lapwing Vanellus vanellus L. In upper Teesdale

David M.B. Parish

How to cite:

Parish, David M.B. (1996) Behavioural ecology of the lapwing Vanellus vanellus L. In upper Teesdale. Doctoral thesis, Durham University.

BEHAVIOURAL ECOLOGY OF THE LAPWING *Vanellus vanellus* L. IN UPPER TEESDALE

By

David M.B. Parish B.Sc. (U.C.N.W., Bangor)

A thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham. 1996.

Behavioural ecology of the Lapwing *Vanellus vanellus* L. in Upper Teesdale

David M.B. Parish

ABSTRACT

From 1993-95, the behavioural ecology of the Lapwing *Vanellus vanellus* L. was studied in Upper Teesdale, Co. Durham, with the aim of describing the behavioural mechanisms underlying some population characteristics.

Significant effects of age and individuals were found in many aspects of Lapwing breeding biology. Older Lapwings returned to the breeding grounds before yearlings, with adult males returning earliest of all. First breeding attempts occurred at one-year-old for most females, but at two-years-old for most males. Males two-years-old and over showed a remarkable degree of consistency in breeding status (breeding or non-breeding) in consecutive years, even where this meant persistent non-breeding. The age of first breeding, and consistency of breeding status among males, indicates intense intermale competition for limited breeding habitat, with some males, perhaps of low quality, apparently permanently prevented from breeding.

However, few differences in annual breeding success were found among females of different ages. With the exception of egg size in first clutches, where yearling females laid eggs around 5% smaller than adults, yearling and adult females were similarly fecund. Laying dates and egg volumes in first clutches exhibited high indices of repeatability between years, probably reflecting a high degree of heritability of these traits.

High frequencies of polygyny were recorded, despite the traditional view of strict monogamy for this species. The mating success of male Lapwings increased between one and three years-of-age. The distinct parental roles of the sexes facilitated the occurrence of polygyny by reducing activity-budget costs of polygynous associations for both sexes. Polyterritoriality, polyandry and double-brooding were also recorded and discussed.

I declare that this thesis is original and entirely my own work, except where otherwise stated. No part of it has been submitted previously for a degree at any other university.

ACKNOWLEDGEMENTS

I am indebted to Pat Thompson, for advice and helpful suggestions throughout my study, for encouragement when it was most needed and for his patient assistance and company in the field. I am grateful to John Coulson for his supervision and particularly for his constructive criticism of the thesis, and also to Peter Evans for supervision during the latter stages of the study.

Many thanks to Raby Estates for providing access to land and to the farmers of Upper Teesdale for their co-operation, in particular Mr Howard Bainbridge who kindly stored equipment over the winter months. Special thanks also to Lindsay Waddle and the underkeepers in Upper Teesdale (Andy and Gary) for their sterling efforts at controlling predators on my sites, and for many informative conversations.

I thank the attendants of the 10th International Waterfowl Ecology Symposium and Wader Study Group Conference for useful comments on a presentation of my work, and likewise to Steve and Simon.

I am grateful to the following friends for much assistance in the field: Andy Hoodless, Michelle Metcalfe, Ian Mitchell, Matt Parsons, Sarah Pattinson and Robin Ward. Special thanks to Mark and Glen for their companionship, wit and for teaching me to play pool! Eric Henderson provided much technical assistance for which I am most grateful. Many thanks to Keith Hamer, Phil Hulme and Ian MacPhee for help with statistical problems, and to Professors Bowler and Evans at Durham University for kindly providing departmental facilities. This work was funded by a studentship from the Natural Environment Research Council.

Special thanks to all my family for their support and encouragement in recent years, but especially to Rose, Keith and my Grandparents. Finally, I thank Michelle, for providing immeasurable support, both practical and emotional, and for making all those boring visits to Teesdale to keep me company!

TABLE OF CONTENTS

1. ARRIVAL DATES ON THE BREEDING GROUNDS AND THEIR IMPLICATIONS

2. THE SOCIAL MATING SYSTEM OF THE LAPWING

3. THE BREEDING BIOLOGY OF THE LAPWING, WITH PARTICULAR REFERENCE TO THE INFLUENCE OF AGE

The following papers, based on data from Chapter 2, have been accepted for publication:

1) Parish, D.M.B., Thompson, P.S. & Coulson, J.C. 1997. Mating systems in the Lapwing *Vanellus vanellus* L. Ibis 139: (in press).

2) Parish, D.M.B., Thompson, P.S. & Coulson, J.C. 1997. Attempted double-brooding in the Lapwing *Vanellus vanellus* L. Bird Study (in press).

GENERAL INTRODUCTION

Recent changes in agricultural practices, in terms of crop types, distribution within Britain and management, have had drastic effects on many species of birds typically associated with farmland habitats (O'Connor & Shrubb 1986). The effects resulting from agricultural changes have been varied, and can be found in a number of diverse groups. The Corncrake *Crex crex*, for example, was once a relatively common bird of agricultural grassland, with a breeding distribution that stretched across much of Britain and Ireland (Gibbons *et al.* 1993; Evans 1995). In the last 150 years, however, numbers of Corncrakes in this region have been in accelerating decline, with a decrease in numbers in Britain of around 80% between 1968-72 and 1991. This has been associated with a dramatic restriction in range so that today the species in the U.K. is limited to breeding in parts of northwest Scotland and in Ireland (Gibbons *et al.* 1993; Evans 1995). These changes in numbers and distribution stem from the species' dependence on long grass as a breeding habitat (e.g. hay and silage crops): no changes in mortality on the wintering grounds (SE Africa) have been detected (Gibbons *et al.* 1993). The mechanisation of the process by which farmed-grass is harvested, the widespread use of inorganic fertilisers and the introduction of faster growing species of grass, have increased the annual mortality of clutches, young and adults in many breeding areas by advancing the date of mowing, and destroyed suitable habitat altogether in others (Gibbons *et al.* 1993; Evans 1995).

Likewise, the Skylark *Alauda arvensis* commonly breeds on farmland, with its preferred nesting habitat being young (<5 years) ley grass (Gibbons *et al.* 1993). A decline in the acreage devoted to this crop during the last 10-20 years, associated with an increase in the area sown with autumn cereals, has reduced the availability of suitable nesting habitat (autumn cereals having grown too high in spring to permit nesting) (Gibbons *et al.* 1993). This, together with a loss of winter stubbles (again associated with the increased area of autumn-sown cereals), which provide a good feeding habitat during the winter, has resulted in a 54% decline in numbers detected by the British Trust for Ornithology's Common Bird Census (CBC) over the last 25 years.

A more complicated picture of decline and recovery has occurred in the Barn Owl *Tyto alba*. This Owl, perhaps more than any other raptor, breeds almost exclusively on farmland (Shawyer 1987). The current number of breeding pairs estimated for Britain is around 4400, a decline of about 60% on an estimate made in 1934, but a slight increase on figures for 1968-72 (Gibbons *et al.* 1993). The overall decline in numbers has been attributed to a suite of potential contributing factors, including climate change, road developments and urbanisation (Shawyer 1987), but high on this list are a number of agricultural causes. The dependence of Barn Owls on dwindling tussocky grassland and "grassland edge" habitats for foraging, and the extensive use of organochlorine pesticides in the 1960's and 70's, were probably major causes of their decline (Shawyer 1987; Newton *et al.* 1991). The important influence of the latter has been emphasised in the recent increase in numbers of this species, which may be associated with the cessation of use of these chemicals (Newton *et al.* 1991; Gibbons *et al.* 1993).

The preceding examples are for birds dependent on farmland primarily during the breeding season, although both the Skylark and Barn Owl also rely on this habitat to a large degree during the winter. Other species have suffered serious declines in number due primarily to changing agricultural practices which exert their influence during the winter. For example, the Corn Bunting *Miliaria calandra* and Reed Bunting *Emberiza schoeniclus*, largely seed-eating birds, depend heavily on farmland habitats for food during the winter. The loss of large areas of winter stubble and fallow ground (rich in weed seeds and spilled grain) has taken place over the last 20-25 years as farmers switched to autumn-sown cereals. This has probably led to the decline in number of these birds over the same period (Gibbons *et al.* 1993; Evans *et al.* 1995): numbers detected by the CBC fell by around 60%, although in the case of the Corn Bunting at least, this may have been further exacerbated by changes to their agricultural breeding habitat (Gibbons *et al.* 1993).

The Lapwing is also heavily dependent on agricultural habitats, with 96% of British breeders found on farmland, the preferred nesting habitat being spring-tilled fields followed by rough grazing (Shrubb & Lack 1991). The Lapwing has an extensive breeding distribution, stretching east across Europe from Ireland to Russia and south from Scotland to Spain (Cramp & Simmons 1983). Within this range, Britain has one of the highest numbers of breeding Lapwing of any country (Cramp & Simmons 1983), with recent estimates in the region of 225 000 pairs (Shrubb & Lack 1991; Gibbons *et al.*

1993). Long-term data from the CBC, however, revealed that breeding Lapwings declined by 62% between 1969-94.

The recent decline in Lapwing numbers is thought to be due to their reduced productivity in farmland habitats (Galbraith 1988a; Baines 1988, 1989; Shrubb 1990; Shrubb & Lack 1991) caused by concurrent changes in agricultural practices, rather than by a decline in survival rates (Peach *et al.* 1994). For example, the area of farmland devoted to spring tillage and permanent grass has decreased by around 9% and 15% respectively since 1960, with an associated increase in the area of autumn tillage (23%) (Shrubb & Lack 1991). The latter is largely unsuitable for breeding Lapwings as the vegetation is already too high in spring to permit nesting. There is also a trend towards fewer mixed farms, where a variety of crops are grown within a relatively small area. Such farms are thought to provide excellent breeding habitat as they combine good nesting and chick-rearing areas (spring tillage and pasture, respectively) (Galbraith 1988a; Shrubb 1990; Shrubb & Lack 1991; Gibbons *et al.* 1993). Associated with the changes in agricultural habitats has been an increase in the proportion of Lapwing nests found on upland grass (Shrubb 1990). The success of nests laid on tillage is generally higher than for those laid on grasslands, with nests on upland grass having a lower success rate than those on lowland grass (Shrubb 1990). Further, in detailed studies, Galbraith (1988a) and Baines (1988, 1989) found that the agricultural improvement of grassland resulted in decreased productivity of breeding Lapwings. Recent studies have also demonstrated high frequencies of philopatry and site-fidelity, inflating further the effect of reduced productivity on breeding populations by limiting immigration (Thompson *et al.* 1994). Northern England and the Pennines support some of the highest densities of breeding Lapwings in Britain (Gibbons *et al.* 1993). However, Shrubb (1994) recently stated that all farmed grassland was an unsatisfactory nesting habitat for Lapwings due to the reduced productivity of those nesting in it, and Gibbons *et al.* (1993) suggested that, because of its poor productivity, the large populations of Lapwings in northern England nesting on farmed grasslands, were supported by immigrants from more productive areas. Although Lapwings nesting on improved grassland may indeed rear fewer young than those on, for example, spring tillage, such remarks are contrary to evidence from grassland areas which clearly produce sufficient chicks to maintain the local population (Galbraith 1988a; Baines 1989; Chapter 3) and which support high densities of breeding Lapwings (Thompson *et al.* 1994).

Lapwing ecology

Compared with many waders, the Lapwing *Vanellus vanellus* has been extensively and intensively studied (Cramp & Simmons 1983; Galbraith 1987, 1988a,b,c,d, 1989a,b; Baines 1988, 1989, 1990; Shrubb 1990; Beintema 1991; Shrubb & Lack 1991; Berg *et al.* 1992; Berg 1993; Blomqvist & Johansson 1994, 1995; Byrkjedal *et al.* 1996). Lapwings are migratory inasmuch as they leave their breeding grounds at the end of the season and move to separate areas to spend the winter, returning to their breeding grounds in the following spring (Cramp & Simmons 1983). Most aspects of

Lapwing breeding biology are discussed later in the thesis; to give a complete picture of the annual cycle, here I give a brief overview of their winter habits.

Lapwings feed almost exclusively on surface and sub-surface invertebrates (mainly insects, molluscs and earthworms) (Cramp & Simmons 1983). Prey are located primarily using visual cues, restricting Lapwings mostly to day-time foraging, although much foraging has been reported on brightly moonlit nights during the winter (Milsom 1984). The dependence of the Lapwing on these prey items is probably one of the main causes of their migratory habit, although the importance of other factors should not be ignored. For example, individuals will probably reduce travel costs by migrating before their moult has begun rather than during, and so benefit by departing early from the breeding grounds. Food availability on the breeding grounds is likely to decrease in many areas as increasing summer temperatures dry the ground, making probing more difficult and forcing many prey into deeper soil. Also, the increasing height of vegetation at this time impedes the search for prey (Klomp 1954; Lister 1964). The importance of food availability (and other seasonally fluctuating resources) in relation to migration and its origins has been discussed at length elsewhere (Baker 1978; Gauthreaux 1982; Sinclair 1983; Gwinner 1990a, and refs. therein). Conditions on the breeding grounds may remain inhospitable until after the winter, when snow and frost have receded and temperatures rise again, providing improved feeding conditions. On occasion, where individual birds have arrived at the breeding grounds early, or where winter conditions were prolonged, weight loss and increased mortality have been reported as a consequence of poor feeding and maintenance conditions (Morrison 1975; Møller 1994).

Lapwings leave their breeding areas in continental Europe from late May onwards and journey to moulting and wintering grounds (Imboden 1974; Cramp & Simmons 1983). This is somewhat earlier than the major movements of breeding Lapwings leaving Britain and again has been linked to weather-induced food shortages on the continent (Cramp & Simmons 1983). Being sensitive to inclement weather, the primary wintering areas for Lapwings are coastal and low-lying regions where conditions are more favourable for efficient feeding. Together, Britain and Ireland provide winter refuge for well over one million Lapwings (Lack 1986), most of which arrive from Scandinavia and parts of northern and central Europe (Imboden 1974). In turn, many British Lapwings move to Ireland (especially those breeding in northern England), and to France and the Iberian peninsula (Imboden 1974), although around a quarter of British Lapwings move less than 60km (Cramp & Simmons 1983; see Chapter 1), and remain in this country. However, the movements of British Lapwings have been assessed from recoveries of ringed birds (Imboden 1974), and as such are subject to biases caused by the legal shooting of Lapwings on the continent, which may have over-emphasised the proportion of individuals migrating to these areas. The heavy use of farmland by Lapwings is maintained during the winter, with many birds feeding on invertebrates on both arable and grass fields (Barnard & Thompson 1985; Milsom *et al.* 1985; Lack 1986; Gregory 1987; Shrubb 1988; Village & Westwood 1994). They are not sedentary, however, as they often move around in response to cold weather (Lack 1963; Milsom *et al.* 1985; Lack 1986; Shrubb 1988; Kirby & Lack 1993). Further, Lack (1963) referred to the Lapwing as a “weather migrant” and, using radar equipment, recorded frequent movements in both directions across the North Sea in response to harsh weather during winter. Lapwings are highly gregarious during the non-breeding season, forming flocks which can number several thousands of individuals (Cramp & Simmons 1983). The main advantages gained from forming such large groups seem to be improved foraging efficiency and protection from predators (Barnard & Thompson 1985). Departure from the wintering grounds begins during mid-January for those Lapwings wintering in the Mediteranean area, but reaches a peak during early March in temperate regions (Cramp & Simmons 1983; see Chapter 1).

Against the background of declining numbers of the Lapwing, and in particular the findings of Thompson *et al.* (1994) which showed strong site-fidelity and philopatry in this species, my study aimed to investigate the mechanisms underlying group trends and patterns, using the large number of uniquely-ringed individuals in Upper Teesdale (see General Methods). The thesis is presented as discrete but related chapters, broadly following the breeding chronology of the Lapwing. Chapter 1 describes the pattern of arrival on the breeding grounds, particularly in relation to age and sex, and discusses the influence of arrival dates on breeding parameters during the subsequent season. Chapter 2 documents the social mating system of the Lapwing and discusses the factors associated with the occurrence of polygyny. Chapter 3 summarises the breeding biology of the Lapwing with particular attention given to the influence of age. Finally, Chapter 4 uses activity-budget data to describe the roles of the sexes during reproduction and hence determine the mode of reproductive investment of male and female Lapwings. The relevant subject matter is reviewed in detail in each chapter.

STUDY AREA AND GENERAL METHODS

Study site

This study was conducted in northern England, in Upper Teesdale (grid ref. NY8531), part of the Pennine mountain range within County Durham, from February to July of 1993-95. The study site was a 412ha. area of upland, marginal farmland, ranging between 350-480m a.s.l. The site consisted of pasture (grazed) and meadow (cropped) grassland, surrounded mainly by game moorland, and has been designated as an Environmentally Sensitive Area. Gamekeepers removed most mammalian predators and corvids on the study site.

The study site was divided into two unequal areas: six fields totalling 44 ha. were termed the intensive site, the remainder forming the extensive site. Most of the data from the extensive site were collected by P.S. Thompson. Visits to the intensive site were more frequent than to the extensive site (visits every 2-4 days and 4-7 days respectively). In 1995, an extra three fields were included in the intensive site, increasing the area to 63ha., and observations on the extensive site were reduced.

Fields were classified according to the management regime as agriculturally improved (through drainage, reseeding or with the application of inorganic fertilisers) or unimproved (Baines 1989). Improved fields are vegetatively more homogenous (i.e. fewer species of grass and little or no rush *Juncus* spp. cover) and appear more uniform and generally greener to the observer than unimproved fields. Unimproved fields usually support a greater variety of grass species with a greater proportion of rush cover and are often browner in appearance.

Lapwings in Upper Teesdale

Lapwings in this area have been studied since 1985 (Baines 1989, 1990; Thompson *et al.* 1994), and numbers have remained relatively stable, with between 80-88 pairs per km^2 (Thompson *et al.* 1994). Chicks were marked every year from 1990, using British Trust for Ornithology (B.T.O.) rings and plastic coloured rings. After hatching, chicks were fitted with a single coloured ring and a B.T.O. ring. This allowed the identification of chicks on recapture later in the season, when they were fitted with additional coloured rings. The full compliment of rings formed a unique combination, such that individuals could be recognised when seen in the field, without the need for recapture. However, if a chick was not re-captured later the same season, the single coloured and B.T.O. ring would indicate the year of hatching, and aid in the recording of social interactions between individuals. A total of 1265 chicks were uniquely colour-ringed in this way between 1990-95 (mean±S.D.= 253±45 per year).

Adult Lapwings were also marked between 1990-93, albeit in smaller numbers. They were captured at night during the pre-laying period (February-April), using a bright lamp which dazzled the birds, and thereby immobilised them, allowing them to be captured with a long-handled net. A unique combination of B.T.O. and coloured rings were fitted to each individual to allow individual recognition in the field. A total of 154 adults were marked in this way (mean±S.D.=39±25 per year). Such intense ringing effort, and the high site-fidelity and philopatry of Teesdale Lapwings (Thompson *et al.* 1994), meant that large numbers of uniquely ringed individuals were present each year, and 268, 284 and 146 were recorded during surveys in 1993, 1994 and 1995 respectively (numbers were lower in 1995 as fieldwork was restricted mainly to the intensive site). This represented approximately 40% of the Lapwings present on the entire site.

Throughout this thesis "adult" is used to refer to Lapwings in at least their second year after hatching; a "yearling" is in its first year after hatching. The two classes cannot be distinguished in the field, or hand, from external characteristics, so a bird caught at night as described above could be either a yearling or an adult.

Sex determination

The sex of individuals was determined where possible using plumage and behaviour. Female Lapwings are generally duller in appearance, with a slight mottling to the nape and wing coverts. They also have a much shorter crest than the males, and usually less black colouration on the breast and around the face (which may appear yellowish-brown). By contrast, the males have a bolder plumage. They have longer crests, a larger, more complete, black breast patch and the face is characteristically black and white (no brown).

Copulation position and the characteristic song flight provided a good means of separating the sexes. The latter is only performed by the male (Dabelsteen 1978; Chapter 4).

During the three years of study, only 1%, 1% and 4% of individuals seen more than once, remained of unknown sex by the end of the season (3/268, 3/284 and 6/147 individuals in 1993, 1994 and 1995 respectively).

Census protocol

Regular counts and observations of ringed Lapwings were carried out from field boundaries, from inside a car at the roadside, from behind dry-stone walls, and from inside one of three purpose-built hides (intensive site only). In some cases the birds were unavoidably disturbed whilst getting to an observation point. When this happened, behavioural observations were suspended until the birds returned to their territories and continued their normal behaviour (e.g. incubation, feeding). Recording of marked individuals continued however, as this was often a good time to identify ringed birds, as they exposed rings on their legs whilst walking around.

Breeding status

The breeding status (i.e. breeding or not breeding) of ringed individuals was determined each season from behavioural cues; birds seen paired (i.e. consistently accompanying a particular individual of the opposite sex), copulating, incubating eggs or attending chicks were classified as breeders. Only two known extra-pair copulations (i.e. copulations between individuals not in a long-term pair bond) have been recorded between uniquely marked individuals during the three years of study; one in 1994 and one in 1995. It was therefore assumed that Lapwings seen copulating were in a relatively long-term pair bond. Non-breeders were individuals for whom no such information was recorded, often despite frequent observation. This definition does not exclude the possibility that non-breeders were simply transients on the study site and moved on to breed elsewhere, or that they did make a breeding attempt but were not seen doing so. The frequency of the former aspect was not known, but the latter was rare: breeding attempts were rarely so brief as to increase the chance of being overlooked (pers. obs.), especially given the intensity of observations. However, a few breeders were seen for the first time late in the season with chicks (i.e. they must have been present for some time previously), having presumably moved from areas which were hard to observe, to areas that were more visible. This behaviour was recorded on the intensive site in 1994 only, when 2 of 71 (3%) breeders appeared with chicks. It is likely that this was a more frequent occurrence on the extensive study site due to a lower frequency of visits, the less accessible nature of parts of the extensive site, and the fact that unobserved areas (e.g. moorland, rough pasture and marginal farmland) adjoined many of the fields in this area (about 47 of the 90 fields that comprised the total study site adjoined unobserved areas (=52%); only the three additional intensively studied fields in 1995 were among them. Lapwings were not counted regularly in such adjoining fields but have been seen on occasion, breeding only in small numbers). This suggests that it is possible for a few birds classified as non-breeders to have bred in such places without being seen, although the frequency of such occurrences was low. Moreover, such drawbacks are assumed to apply to birds of different ages and sex equally such that the data are comparable.

Statistical analysis

Throughout this thesis, inferential analyses are preceded by detailed descriptive exploration in order to identify initial trends and patterns, and to determine the normality of the data. The following descriptive statistics were summarised for each sample: measures of central tendency (mean, median and mode), measures of dispersion (sample standard deviation and variance about the mean) and measures of the nature of the frequency distribution (i.e. skewness: the degree of asymmetry about the mean of a distribution, and kurtosis: the degree of “peakedness” of the distribution). The significance of the scores for skewness and kurtosis was tested after Sokal and Rohlf (1995). In addition, the frequency distribution was plotted and examined by eye for normality. If any of the aforementioned descriptive statistics suggested some form of non-normality (e.g. mean, median and mode widely dispersed, significant skewness score), a further test was applied. Using the “explore” facility of the SPSS for Windows statistical package (Norusis 1993), the Kolmogorov-Smirnov one-sample test was used. If normality of the data was confirmed (or not suspected) a final check was conducted, when appropriate, before moving to inferential statistics: the homoscedasticity of sample variances was confirmed using Levene’s test (Norusis 1993). A summary of the full procedure is provided for examples in Chapter 1, but to save space is not repeated elsewhere. The normality of data samples was uncertain on a number of occasions in all sections of this thesis. Where this was confirmed, an attempt was made to normalise the data via transformation according to Sokal and Rohlf (1995). Transformed data were analysed as described above to check again for normality. Where data were resistant to transformation (i.e. remained non-normal after the appropriate transformation), further inferential analyses were carried out using non-parametric tests, as these make no assumptions regarding sample distributions and normality and so have a greater power-efficiency under such conditions (Siegel & Castellan 1988). In the case of two-sample comparisons, the Mann-Whitney U test was used (for unrelated samples) or the Wilcoxon signed-ranks test (for related samples) (Siegel & Castellan 1988). For comparisons involving more than two samples, the Kruskal-Wallis one-way-ANOVA was employed (Siegel & Castellan 1988). As these tests compare sample *medians* (and/or mean ranks) rather than *means* (Siegel & Castellan 1988), data relating to such comparisons were summarised as medians, with inter-quartile ranges providing a measure of dispersion.

Means were presented ±1 standard error and two-tailed tests were used throughout the thesis, unless stated otherwise. Corrections for ties were made where appropriate and a minimum significance level of $P<0.05$ has been employed. G-tests were used to analyse frequencies, with William's correction for tests of homogeneity and 2x2 contingency tables (Fowler & Cohen 1990). Data handling and most analyses were conducted using SPSS for Windows (Norusis 1993).

1. Arrival dates on the breeding grounds and their implications.

1.1 INTRODUCTION

The date on which an individual arrives at the breeding grounds depends on two major components of the spring movement: the date of departure from the wintering grounds and the time taken to reach the destination, which in turn will depend on how far the birds have to travel. For migrating birds, the decision to leave the wintering grounds is an important one which must be timed correctly: too early and the bird may leave before sufficient metabolic reserves have been accumulated to make the journey, or it may arrive in a harsh environment where survival is threatened and breeding impossible; too late and valuable time will be lost from the breeding season. However, for those species making shorter journeys to their breeding grounds, like many Teesdale-breeding Lapwings (Table 1.1.1), the consequences of an ill-timed departure are likely to be less severe, as they will rarely be so far from suitable foraging sites in amenable areas to be at risk.

The presence of circannual, endogenous rhythms in migratory birds has been known for many years (see Gwinner 1990b for a review). Such rhythms are thought to prepare individuals for migration, through the storage of dietary fats at the appropriate time(s) of year for example (Ramenofsky 1990; Wingfield *et al.* 1990), as well as performing other migratory functions (Gwinner 1990b). This results in individuals becoming responsive to external stimuli which finally lead to migratory movements (Wingfield *et al.* 1990). For example, various weather conditions can provide such stimuli (Richardson 1978; 1990).

As well as influencing the date of departure of migratory birds from the wintering grounds and the progress made during the movement (Richardson 1978; 1990), weather conditions on the breeding grounds also affect the date on which birds arrive in such areas. For example, snow cover often has an adverse effect on the arrival of waders breeding in Arctic regions, as territorial establishment cannot get underway until the snow clears (Holmes 1966; Nettleship 1973; Green *et al.* 1977). Indeed, Holmes (1966) suggested that Dunlin *Calidris alpina* may follow the receding snow-line back to their breeding grounds in Alaska. In Arctic regions, particularly if the birds have travelled a long distance, they may return to the general area at a relatively constant date each year, with only the final movement to the breeding grounds affected by snow-cover (Nettleship 1973; Green *et al.* 1977).

Very often there are differences in arrival dates within a population of migratory birds. This arises from differences in behaviour between the sexes, breeders and non-breeders, age-groups and individuals (Hinde 1951; Preston 1966; Myers 1981; Evans and Davidson 1990; Møller 1994).

The date of arrival on the breeding grounds has been shown to influence the timing of breeding in some birds, e.g. the Kittiwake *Rissa tridactyla* (Coulson & White 1958), so it is possible that the timing of return could affect an individuals reproductive success.

Throughout most of its range the Lapwing is a migratory species, moving in the summer and autumn from open habitats where it breeds, usually to coastal environments, where it spends the winter before making the return journey. British coasts and lowlands are a major overwintering site for many continental Lapwings avoiding harsh weather. In turn, some British breeders move to Ireland, France and the Iberian peninsula (Imboden 1974), although estimates from ring-recoveries suggest that 23% move less than 60km and remain in this country (Cramp & Simmons 1983; Table 1.1.1). The reliability of this estimate is questionable, however, as the sample may have been biased by excessive recoveries from shot birds on the continent. The movement back to the breeding grounds has been recorded as early as mid-January, with flocks beginning to break up around a month later (Cramp & Simmons 1983).

Table 1.1.1. Sightings and ring-recoveries between 1 October and 31 January 1992-95, of adult and juvenile Lapwings ringed in Upper Teesdale.

Number of sightings/recoveries	Distance between ringing and sighting/recovery site (km)	Place name
1	57	North Yorkshire
1	60	Teesmouth
1	72	Morecombe Bay
6	80	Solway Firth
1	85	North Yorkshire
1	160	Humberside
1	1159	Gironde, France

Biases in the above data prevent the inference of the frequency with which sites at different distances are used (e.g. data from the Solway Firth region were provided by field ornithologists studying individually-ringed Barnacle Geese *Branta leucopsis*, greatly increasing the likelihood of discovering ringed Lapwings in the area). However, it does indicate that some individuals move relatively short distances in winter, whilst others move much further (possibly the result of annual variation).

The purpose of this section is to investigate inter- and intra-year variability in arrival dates in the Lapwing, and to determine if the date of arrival influences an individuals breeding behaviour.

1.2 METHODS

This study was conducted in 1993 and 1994. For a description of the study area, and details regarding the marking and identification of individuals and of census methods, see General Methods.

To determine when Lapwings arrived on the breeding grounds a census of uniquely-ringed individuals was carried out in all fields throughout the season. The date of arrival on the breeding grounds was taken as the date on which an individual was first seen on the study site. This definition relies on the assumption that ringed Lapwings were conspicuous after arrival and not likely to be overlooked. This was investigated in 1993 by examining subsequent sightings of individually-ringed Lapwings. The median period between the first and second sighting for all birds was four days (n=195). This suggests that once a bird had arrived it would soon be seen, although the ease of detection by field workers varied between fields of different sizes and vegetation height.

Exploratory analyses revealed that the arrival dates did not conform to a normal distribution (Fowler and Cohen 1990). Two examples are shown here: first all data for each year are summarised, then a single sub-set within each year, namely yearling females (Table 1.2.1, Figures 1.2.1 and 1.2.2).

Figures 1.2.1 and 1.2.2 show that the data are highly skewed and do not show the characteristic bell-shape of a normal distribution, although this is less extreme for first-year females. If the data were normally distributed, Table 1.2.1 would show the mean, median and mode to be of similar values; the proportion of the data falling within ±1 standard deviation (S.D.) would be around 68%; and the measures of skewness and kurtosis would have a magnitude of less than one (and be insignificant). All of the examples in Table 1.2.1 do not fulfil at least two of these criteria, and this is representative of all sub-sets of the data used in this section.

Table 1.2.1. Summary statistics for arrival dates (where 1=1 Jan) for all Lapwings and a sub-set of the data, yearling females. Figures in parentheses are the proportion (%) of the data that fall within ±1 Standard Deviation (S.D.) of the mean.

	All birds		Yearling females	
	1993	1994	1993	1994
Mean	87.4	79.6	99.9	91.5
Median	77	71	85	88
Mode	69	63	85	92
S.D.	24.9 (84)	21.7 (88)	27.5 (70)	20.6 (69)
Variance	621	471	754	423
Skewness	1.8***	2.2***	0.7	1.2**
Kurtosis	2.8***	5.8***	-0.8	1.6*

Significance of skewness and kurtosis scores (Sokal and Rohlf 1995): *$P<0.05$; **$P<0.01$; **$P<0.001$.

Further, the tests for normality all showed significant deviations from a normal distribution: all Lapwings, 1993: Kolmogorov-Smirnov test, $P<0.001$; 1994: $P<0.001$; yearling females, 1993: Shapiro-Wilks test, $P<0.05$; 1994: $P<0.01$.

Figure 1.2.1. Frequency distribution for data on Lapwing arrival dates (grouped into five-day periods): all birds, 1993 and 1994.

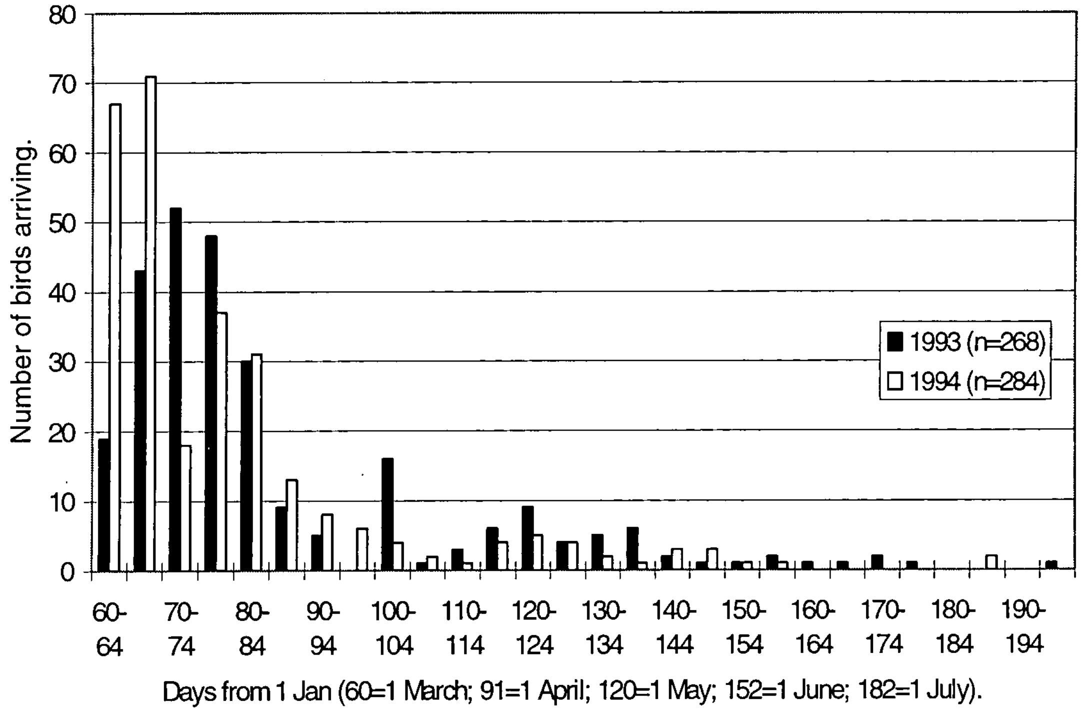
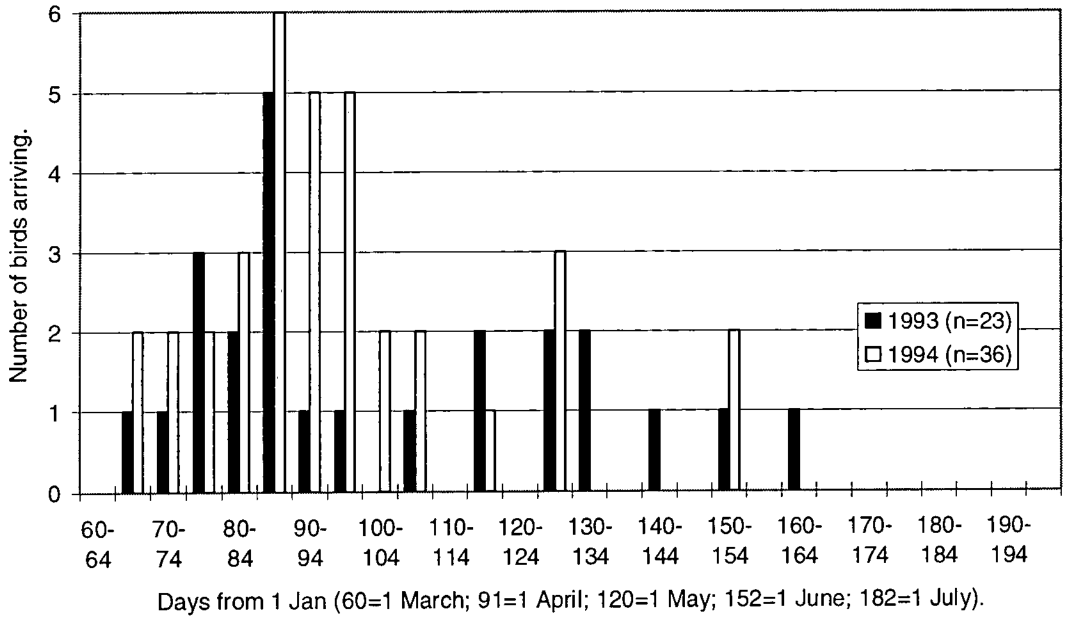


Figure 1.2.2. Frequency distribution for data on Lapwing arrival dates (grouped into five-day periods): yearling females, 1993 and 1994.



Thus, non-parametric statistics are used in the first part of the results, and summaries of the data are presented as medians with inter-quartile ranges (I.R.). Raw data (dates) have been converted to days of the year, where 1=1 January. Other manipulations of the data are described in the relevant sections of the results.

1.3 RESULTS

Differences in arrival dates between years

Data for arrival dates are summarised in Table 1.3.1. Lapwings arrived on average 6 days later in 1993 than in 1994 (all ringed individuals, median arrival date 1993=77, I.R.=73-92, n=268; median arrival date 1994=71, I.R.=66-83, n=284; Mann-Whitney U test (M.W.T.): Z=5.4, $P<0.0001$). Table 1.3.1 suggests this difference in date of arrival is due to the delayed arrival in 1993 of those groups that arrived earliest in 1994. Adult males were, on average, 10 days later in 1993 than 1994 (median arrival date 1993=77, I.R.=71-86, n=103; median arrival date 1994=67, I.R.=63-79, n=108) and adult females were 4 days later (median arrival date 1993=75, I.R.=69-85, n=99; median arrival date 1994=71, I.R.=67-81, n=95). Both differences are statistically significant (males, Z=6.1, $P<0.0001$; females Z=2.5, $P<0.02$). There are no significant differences in arrival dates for yearlings between the two years.

The proportion of birds arriving during different periods throughout the season were compared for the two years. This indicates whether the late arrival of adults in 1993 was spread throughout the year or occurred at one particular time (Table 1.3.2).

Table 1.3.1. Median date of arrival, with inter-quartile range (I.R.) and sample size (n), for Lapwings of each age group (years) and sex in 1993 and 1994 (1=1 January; 60=1 March; 91=1 April). “All”=all age groups combined, plus those individuals ringed as adults who cannot be categorised as adults or yearlings (see General methods). M=Male; F=Female.

		Arrival dates for birds aged:														
		One			Two			Three			Four			All		
		Median	I.R.	n	Median	I.R.	n	Median	I.R.	n	Median	I.R.	n	Median	I.R.	n
1993	M	78	73-106	29	75	72-88	38	80	69-86	27		-		77	73-87	138
	F	87	78-123	24	75	69-85	32	77	69-99	37		-		78	69-93	127
1994	M	79	70-88	43	68	63-85	27	66	63-79	33	65	63-80	22	70	64-83	151
	F	89	80-100	35	72	66-79	20	71	68-79	22	75	68-84	26	79	68-87	130

Table 1.3.2. The number of ringed Lapwings arriving on the study site during different periods of the season (% of total in parentheses), 1993 and 1994. Period 1 includes all birds arriving on-or-before 15 March; 2=16-31 March; 3=1-15 April; 4=16-30 April; period 5=all birds arriving after 30 April.

		Number of Lapwings arriving during period					
		1	2	3	4	5	Total
1993	Adult	94 (46%)	64 (32%)	16 (8%)	7 (3%)	22 (11%)	203
	Yearling	11 (20%)	22 (40%)	5 (9%)	3 (5%)	14 (25%)	55
	All	105 (41%)	86 (33%)	21 (8%)	10 (4%)	36 (14%)	258
1994	Adult	129 (63%)	54 (26%)	8 (4%)	5 (2%)	10 (5%)	206
	Yearling	20 (26%)	34 (44%)	10 (13%)	2 (3%)	12 (15%)	78
	All	149 (52%)	88 (31%)	18 (6%)	7 (2%)	22 (8%)	284

There was a significant difference in the proportion of Lapwings arriving at the study site during the different periods between years (All birds: $G_4=10.6$, $P<0.05$). Inspection of the figures in parentheses in Table 1.3.2, suggests that the primary cause of this result is a difference in the proportion of birds arriving before 16 March (period 1), with fewer ringed birds seen for the first time during this period in 1993. This difference occurs in adult birds only (adults $G_4=14.1$, $P<0.01$; yearlings $G_4=3.2$, n.s.).

There are at least two possibilities that could account for this difference in arrival between years: 1) harsh weather during the period from mid-February to mid-March in 1993 may have caused the adult birds to delay their return; 2) less observer effort in 1993 may have resulted in the late recording of adult birds that had been present for some time previously.

Weather - Lapwings move relatively short distances to their wintering grounds (Imboden 1974; Table 1.1.1) and are known to be mobile during the winter, moving between areas in response to weather conditions (Lack 1963; Milsom *et al.* 1985; Shrubb 1988; Kirby & Lack 1993). Thus, it is reasonable to assume that during the period preceding the breeding season, Lapwings returning to Upper Teesdale will not be far from the breeding grounds (e.g. northern England). For this reason, consideration is given here to the influence of the meteorological conditions in and around the breeding grounds on the arrival dates of Lapwings.

The influence of meteorological variables on the numbers of returning ringed Lapwings was investigated during March 1994. This was a period of regular and frequent visits by fieldworkers to the study site, thus discounting the influence of observer effort, and a large number of arrivals (n=237; Figure 1.3.1). There was clearly a great deal of variation in the daily number of arrivals on the study site during this period. There were six days on which more Lapwings arrived than average (mean=7.6 birds; median=4 birds). These were 4, 7, 9, 11, 20 and 24 March, days on which 140 (59%) of the 237 birds arrived. Therefore, these "peak" days were compared with those from the remainder of the month to identify consistencies in the weather that could then be used to try and explain the differences in arrival dates between years. The variables investigated were presence or absence of snow cover (present if greater than 50% of the ground was covered), the amount of sunshine in 24-hours, maximum and minimum temperatures (Tmax and Tmin) for each 24-hour period and average wind velocity and direction over 24-hours. Meteorological data were collected from the nearest weather station to the study site, Widdybank weather station (no. (DCNN) 7198). The closest part of the study site was about 1.75 km away, and the furthest about 5.25km (Table 1.3.3).

Figure 1.3.1. The daily number of ringed Lapwings (all ages, both sexes) arriving in Upper Teesdale during March 1994. The letter "S" indicates those days on which snow cover was recorded.

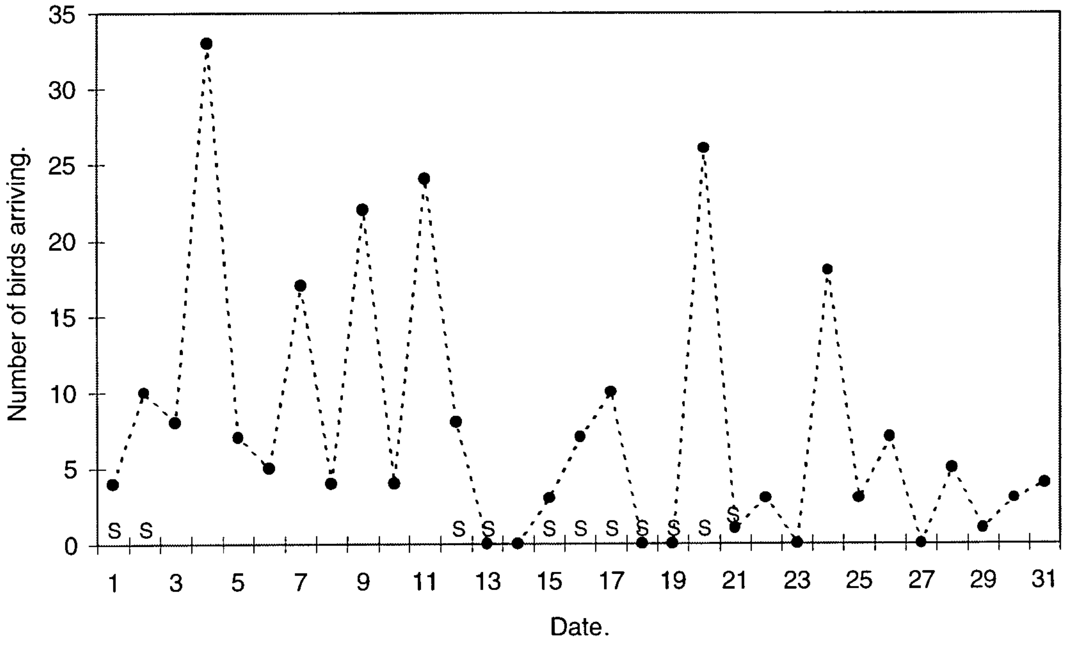


Table 1.3.3. Summary of meteorological data from Widdybank weather station, no. (DCNN) 7198, March 1994. Peak=peak days (when large numbers of ringed Lapwings arrived on the study site, n=6); other=remaining days in the sample period (n=25). Snow: proportion (%) of days when snow cover was recorded; Sun: hours of sunshine per day; Tmax and Tmin are average daily maximum and minimum temperatures (ºC); WindD: average daily wind direction in degrees; WindV: average daily wind velocity (km hr^{-1}). All means are ±1 S.E.

	Snow (%)	Sun (hrs)	Tmax (ºC)	Tmin (ºC)	WindD (º)	WindV (km hr^{-1})
Peak	17	2.2±1.5	4.9±1.0	0.9±0.5	267±8.0	38.9±5.9
Other	60	3.3±0.7	5.0±0.4	0.3±0.4	251±8.0	40.9±2.3

The proportion of days with snow cover in each category cannot be analysed in the normal way due to the lack of independence between days. However, the pattern illustrated in Table 1.3.3 suggests that the absence of snow on the ground is associated with the peak numbers of arriving Lapwings. This can also be seen in Figure 1.3.1, which shows that small numbers of Lapwings arrived in Upper Teesdale during periods of snow cover, with the exception of 20 March: snow cover on this day was receding, as the snow cover score declined from 4 (max.) on 18 March, to 2 on 19 and 20 March, and the depth of lying snow decreased from 3cm on 18 March to 1cm on 19 and 20 March. The remaining data in Table 1.3.3 were analysed using Mann-Whitney U tests. None of the comparisons indicated statistically significant differences between the two categories of days, a conclusion not altered by the use of one-tailed tests (based on the premiss that Lapwings are likely to return during moderate weather).

Does the influence of snow cover in Upper Teesdale on the arrival date of Lapwings help to explain the differences in arrival dates between years? The short-fall in the number of arriving Lapwings in 1993, occurred up to mid-March (period 1, Table 1.3.2). Snow cover during the latter two weeks of February 1993, occurred only on the last three days of the month. In the next two weeks (1-15 March), snow cover was recorded on nine days (1-8 and 10 March). However, every day of the last two weeks in February 1994 was characterised by snow covering the ground, but only four days of snow cover occurred in the next two week period (1-2 and 12-13 March). It seems unlikely that any birds arriving in Upper Teesdale during the snow-free period of late February 1993 would have been willing to endure the 12 days of snow that followed so early in the season, and would probably have left the area and thus avoided detection by fieldworkers. Conversely, in 1994, birds delayed from arriving by snow in late February would probably have returned early in March, and thereby been detected during counts. Therefore, it is conceivable that the late snow in Upper Teesdale in 1993 could have delayed the arrival of adult Lapwings in that year.

However, Lapwings would not be able to sample conditions on the study site until they have arrived, and are likely to respond to conditions encountered *en route*, or during stop-overs on low-lying ground. Data from the Durham University observatory were utilised, which lies about 45km east of Upper Teesdale, to investigate the influence of conditions encountered by the Lapwings at lower altitudes before returning to Upper Teesdale. This assumes that Lapwings breeding in Upper Teesdale return in spring in significant numbers via the north-east of England. Ringing recoveries and resightings of Teesdale colour-ringed Lapwings (Table 1.1.1), indicate that some individuals overwinter along the north-east coast of England, and so presumably return to Teesdale via an easterly route.

Table 1.3.4 summarises the data from the Durham Observatory for "peak" and "other" days (as in Table 1.3.3), for the two-day period prior to "peak" days, and, for comparison, the two-day period prior to six randomly chosen days, during March 1994. T-tests and Mann-Whitney U tests were employed according to the normality of the data. None of the comparisons revealed significant differences, although the minimum temperature (Tmin) recorded in Durham during the two-day period preceding the arrival of large numbers of Lapwings in Teesdale, was notably higher than that during the period prior to randomly selected days (Table 1.3.4: one-tailed test: $t_{22}=1.77$, $P<0.05$). That is, the arrival of Lapwings in Upper Teesdale may be preceded by a period of high minimum temperatures (greater than about 4°C), experienced *en route* or in neighbouring lowlands.

Table 1.3.4. Summary of meteorological data from Durham University Observatory, March 1994. Arrival=the day on which individuals arrived on the study site; Prior=the two-day period prior to arrival. Thus, Peak (arrival)=the day on which large numbers of Lapwings arrived; Peak (prior)=the two-day period prior to peak arrival days. Other (arrival)=all non-peak days in March 1994; Other (prior)=the two-day period prior to randomly selected, non-peak days. Sample sizes are: peak arrival=6 days; other arrival= 25 days; peak prior=12 days; other prior=12 days. Data are means±1 standard error. Note: wind velocity is in knots. No snow cover was recorded for this period at Durham.

	Sunshine		Tmax		Tmin		WindV		WindD	
	(hrs 24hrs $^{-1}$)		(°C)		(°C)		(knots)		(°)	
	Arrival	Prior	Arrival	Prior	Arrival	Prior	Arrival	Prior	Arrival	Prior
Peak	2.5	4.6	9.7	10.6	3.8	3.9	9.7	10.9	253	260
	±1.0	±1.1	±0.8	±0.7	±0.8	±0.7	±1.3	±1.4	±20.0	±9.0
Other	5.1	3.7	10.1	9.3	2.8	2.4	12.0	12.8	244	244
	±0.7	±1.0	±0.5	±0.6	±0.5	±0.5	±1.5	±2.5	±13.0	±16.0

Does this help to explain the differences in the number of Lapwings arriving in Upper Teesdale during late-February/early-March, between years? This period during 1993, when few individuals were arriving in Teesdale, was cold, with daily minimum temperatures at the Durham observatory averaging 1.3±0.8 °C for the last two weeks of February, and 1.1±0.6 °C for the first two weeks of March. If Lapwings were responding to temperature, this suggests they would not have started arriving in numbers during 1993, until the latter half of March, concurring with the arrival dates recorded, and the pattern predicted from snow cover. In 1994, the average minimum temperature for 15-28 February, recorded at the Durham observatory, was -3.5±0.8 °C, and that for 1-15 March was 3.7±0.5 °C. So in 1994, Lapwings were likely to have been deterred from returning by the cold weather in late February, but then encouraged to return by the absence of low temperatures in early March. Once again, this concurs with the data on arrival dates, and with the predictions from snow cover.

It seems reasonable to conclude that the daily minimum temperatures experienced by Lapwings away from the breeding grounds did influence their progress on the final stage of their return, and thus their date of arrival on the breeding grounds. Once in the vicinity of Upper Teesdale, the degree of snow cover on the ground probably also influenced their progress. Both of these factors go some way to explaining the discrepancy in arrival dates between the two years.

Observer effort - The number of visits to the study site are used as a measure of observer effort. The same two observers were present in each year. There was a clear difference in effort between years for observer A with 31% fewer visits in 1993 than 1994 (G_1=7.1, P<0.01) and just 18% of the visits in 1993 occurring before 1 May, compared to 43% in 1994 (G_4=12.8, P<0.02) (Table 1.3.5). There was no difference between years in the total effort of observer B (G_1=0.1, n.s.), nor in the distribution of that effort (G_4=5.1, n.s.).

Table 1.3.5. The number of visits to the study site (observer effort) for observers A and B, 1993 & 94. Period 1=up to 15 March; 2=16 to 31 March; 3=1 to 15 April; 4=16 to 30 April; 5=after 30 April.

		Number of visits during period					
Year	Observer	1	2	3	4	5	Total
1993	A	4	2	1	1	37	45
	B	4	12	6	11	39	72
	Total	8	14	7	12	76	117
1994	A	5	9	9	9	42	74
	B	10	6	8	10	41	75
	Total	15	15	17	19	83	149

To investigate the effect of the observed pattern of effort on arrival dates, adjusted arrival dates for all Lapwings in 1994 were calculated as if the pattern and number of visits in 1993 had been repeated in 1994. This was done by assuming that the same number of birds would have been seen, but where individuals had been recorded on a day when the study site was not visited in 1993, they were given the date of the next visit to the study site. Also, as observer A was responsible for recording the arrival date of the majority of individual Lapwings, the above calculation was made twice: first with visits by both observers in 1993 included, and then with those of observer B excluded (to prevent masking of any effects by visits which only covered a small proportion of the study site) (Table 1.3.6). Indeed, when visits by both observers were included the calculated arrival dates hardly varied from the actual data recorded in 1994, although where they did vary, not surprisingly, the calculated arrival dates were 0-2 days later (Table 1.3.6). The arrival dates calculated on the basis of observer A's visits only showed some marked deviations from the original data (Table 1.3.6).

Both sets of calculated arrival dates for 1994 were used to repeat the comparisons with 1993 (made on page 25) to see if observer effort explained the differences in arrival dates found. When using the data calculated on the basis of all visits to the study site in 1993, all the conclusions remained unchanged: there was still a significant difference in arrival dates between years, for all birds combined, and adult males and females treated separately. However, using the data calculated on the basis of observer A's visits altered the conclusion for adult females, suggesting that arrival dates were similar in both years (1993=75, 69-85; 1994=73, 68-85: M.W.T.: Z=1.3, n.s.).

Thus, it would appear that both the weather and observer effort account for variation in arrival dates between years. To control for this variation, all further analyses were conducted on deviations from the annual median date of arrival (18 March 1993, 12 March 1994). These data were normalised by log-transformation and referred to as “corrected arrival dates”.

Table 1.3.6. The median date of arrival with inter-quartile range (I.R.) for Lapwings of each age group (years) and sex in 1994 (1=1 January; 60=1 March; 91=1 April): A=original data (as in Table 1.3.1); B=calculated arrival dates based on the regime of visits to the study area in 1993; C=calculated arrival dates based on the regime of visits by observer A only in 1993. "All"=all age groups, plus individuals of unknown absolute-age (see General Methods). Sample sizes are as in Table 1.3.1.

		Arrival dates for Lapwings aged									
		One		Two		Three		Four		All	
		Median	I.R.	Median	I.R.	Median	I.R.	Median	I.R.	Median	I.R.
Male	A	79	70-88	68	63-85	66	63-79	65	63-80	70	64-83
	B	79	71-88	68	65-85	68	65-79	67	65-80	71	65-84
	C	85	73-105	68	65-85	68	65-85	67	65-85	73	65-85
Female	A	89	80-100	72	66-79	71	68-79	75	68-84	79	68-87
	B	90	80-102	73	68-79	71	68-79	75	68-85	79	68-87
	C	105	85-105	76	68-85	73	68-85	78	68-90	85	68-105

The effect of sex and age on arrival date

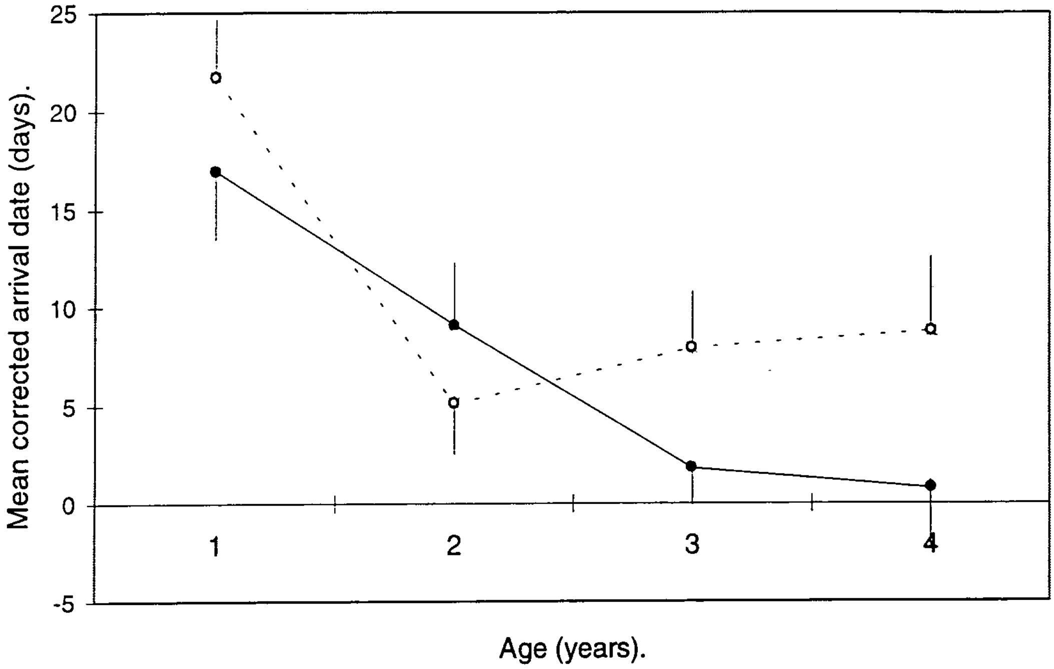
A two-way-ANOVA, comparing variation in arrival dates due to age (1-4 years) and sex, shows that both have a significant effect (sex: $F_{1,407}=8.6$, $P<0.01$; age: $F_{3,407}=15.1$, $P<0.001$; 2-way interaction: $F_{3,407}=1.6$, n.s.). The relationship between arrival dates and these two variables is illustrated in Figure 1.3.2. The greatest discrepancy between the sexes occurred in four-year-olds, with males arriving about eight days before females. The relationship between arrival date and age for males was best described by a linear equation (quadratic term was not significant: b=0.04 ±0.03; t=1.4, n.s.); that for females was best described by a quadratic equation (quadratic term was significant: t=3.7, $P<0.001$): -

Males: $r^2=0.09$, $F_{1,217}=21.6$, $P<0.0001$; log (corrected) arrival date= -0.14 ±0.03(age) + 1.41.

Females: $r^2=0.11$, $F_{2,193}=11.8$, $P<0.0001$; log (corrected) arrival date= -0.60 ±0.14(age) + 0.11 ± 0.03(age^2) + 1.90.

Thus, among males arrival date advances with successive age increases between one and four years, whilst among females, arrival date was earlier for two-year-olds than for younger and older females. The greatest discrepancy in arrival dates for males was between yearlings and 4-year-olds (12 days); for females it was between yearlings and 2-year-olds (15 days). However, although the quadratic term in the equation above for females was significantly different from zero, it was not significantly different from the quadratic term for males ($t_{411}=1.5$, n.s.), suggesting further investigation is needed to confirm the above relationships.

Figure 1.3.2. Mean corrected arrival date (deviation from annual median, in days) with S.E. for male (•) and female (o) Lapwings of different ages, 1993 and 1994. Sample sizes for each age group (1 to 4 years, respectively) are, males: 72, 65, 60, 22; females: 59, 52, 59, 26.



It could be argued that the above variation in arrival dates is due to differences between cohorts rather than age groups, given the small number of cohorts included in the analysis (maximum of two for any age group). In order to consider this possibility, the arrival dates of the same individuals returning to Upper Teesdale in both years of study were compared (i.e. after an increase in age of one year - "longitudinal comparison"). In both sexes, individuals arrived significantly earlier as 2-year-olds than as yearlings (males: 11 days, paired t-test on transformed data, $t_{22}=2.8$, $P<0.01$; females: 14 days, $t_{14}=2.6$, $P<0.02$). Among the older age groups the difference in arrival dates (1994 minus 1993) ranged between 4 days (2-3 year-old males) and -4 days (2-3 year-old females), but all comparisons were not significant.

This suggests that no major change in arrival date with age occurred after two-years of age, concurring with the general “cross-section” pattern illustrated in Figure 1.3.2. However, more data regarding the effects of further increases in age within these cohorts would elucidate the matter further.

The difference in arrival dates between yearling and older Lapwings may not be the result of age *per se*, but perhaps due to a difference in breeding experience or a negative association between arrival date and survival. The first of these possibilities was investigated by comparing the arrival dates of two-year-old Lapwings in 1994 (sexes combined to increase samples) that had either bred or not in their first year (1993). The median arrival date for two-year-olds breeding for the first time (inexperienced individuals, n=10) was six days later than for those breeding a second time (experienced individuals, n=17), although this was not significant (corrected, transformed data, $t_{25}=1.4$, n.s.). The longitudinal analysis of arrival dates for individuals between one- and two-years of age suggests that individuals advance their date of arrival in their second year, regardless of their initial arrival date. This would not be expected if changes in median arrival dates between years were the result of differential mortality of individuals. Furthermore, no evidence of a negative association between arrival date and survival was found (see below). Thus, it seems likely that an increase in age causes the advanced arrival of two-year-olds as compared to yearlings.

Arrival date and breeding status

Uncorrected arrival dates of breeding and non-breeding Lapwings are summarised in Table 1.3.7. Using a factorial ANOVA on transformed,

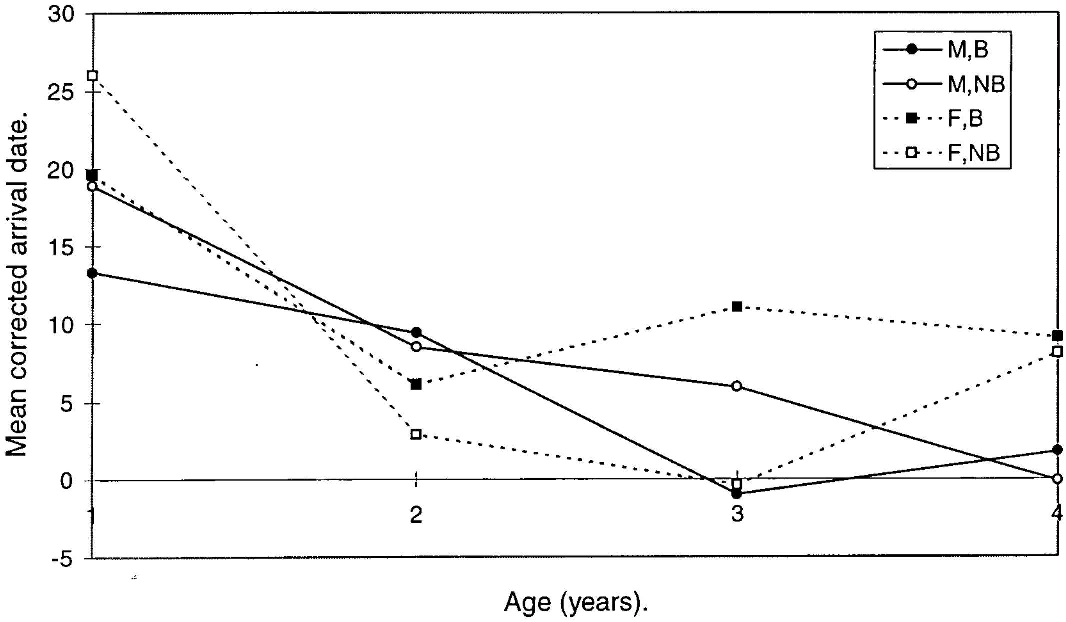
Table 1.3.7. Median date of arrival with inter-quartile range (I.R.) and sample size (n) for breeding (B) and non-breeding (NB) Lapwings. (1=1 January; 60=1 March; 91=1 April; 120=1 May).

		Adult male		Adult female		Yearling male		Yearling female	
		B	NB	B	NB	B	NB	B	NB
1993	Median	73	80	75	76	77	78	87	103
	I.R.	69-85	73-94	69-103	69-78	73-128	76-106	79-112	76-136
	n	62	41	69	30	7	22	16	8
1994	Median	68	66	70	79	76	79	89	88
	I.R.	63-79	63-71	67-79	67-87	68-93	70-87	79-100	81-115
	n	69	39	79	16	18	25	23	12

corrected data whilst controlling for age and sex, shows there is no difference in arrival dates between breeders and non-breeders ($F_{1,414}=0.0$, n.s.). The three-way-interaction between age, sex and breeding status was not significant, although there was only about a 6% probability of obtaining the observed outcome by chance ($F_{3,414}=2.4$, $P<0.07$). In order to aid the interpretation of this result, the relationship between the three variables is illustrated in Figure 1:3.3. This reveals a confusing pattern of changing relations between arrival dates of males and females, and breeders and non-breeders, with advancing age, particularly after 2-years of age. However, the final age group consists of a single cohort which may bias the conclusion for four-year-olds.

It is possible that any effect of breeding status is compromised by the criteria used here to define non-breeders. Some individuals in this category may be transients moving through the study site to breed in other areas (see General Methods). Although no evidence has been found to date to suggest this happens, it should be addressed. This was done by comparing the arrival dates of breeders and non-breeders who remained on the study site for at least one month (i.e. non-transients). Using the same procedure as that described above, breeding status still does not influence arrival dates ($F_{1,237}=0.4$, n.s.).

Figure 1.3.3. Mean corrected arrival date in relation to age, sex and breeding status for individually marked, known-age Lapwings, 1993 & 94. M=male, F=female, B=breeding, NB=non-breeding. Mean standard error=4.1 (range 1.9-6.1); mean sample size=25.9 (range 7-47).



Arrival date and breeding site

Uncorrected arrival dates of Lapwings breeding in improved or unimproved fields, and high- (≥1pair/ha) and low-density (<1pair/ha,) fields, are summarised in Table 1.3.8 and Table 1.3.9 respectively. Again, using a factorial ANOVA on transformed, corrected data to control for age and sex, there were no differences in arrival dates between individuals breeding in improved or unimproved fields, or between those breeding in high-density and low-density fields (improved/unimproved: $F_{1,175}$=0.0, n.s.; high-/low-density: $F_{1,175}$=0.1, n.s.). None of the higher order interactions were significant.

Table 1.3.8. Median arrival dates with inter-quartile range (I.R.) and sample size (n) for Lapwings later found breeding in either improved or unimproved fields. Date of arrival is first sighting on the study site, not necessarily in the breeding field. Data for male and female yearlings have been combined to increase sample sizes. M=Male, F=Female. 1=1 January, 60=1 March, 91=1 April.

				Arrival dates for Lapwings breeding in	
Year	Age	Sex		Unimproved fields	Improved fields
1993	Yearling	Sexes combined	Median	78	85
			I.R.	69-85	73-112
			n	11	3
	Adult	M	Median	73	73
			I.R.	69-80	65-75
			n	29	15
		F	Median	73	73
			I.R.	69-85	68-81
			n	30	14
1994	Yearling	Sexes combined	Median	86	78
			I.R.	77-92	73-101
			n	11	10
	Adult	M	Median	66	66
			I.R.	63-70	63-85
			n	38	19
		F	Median	68	71
			I.R.	93-79	68-83
			n	42	20

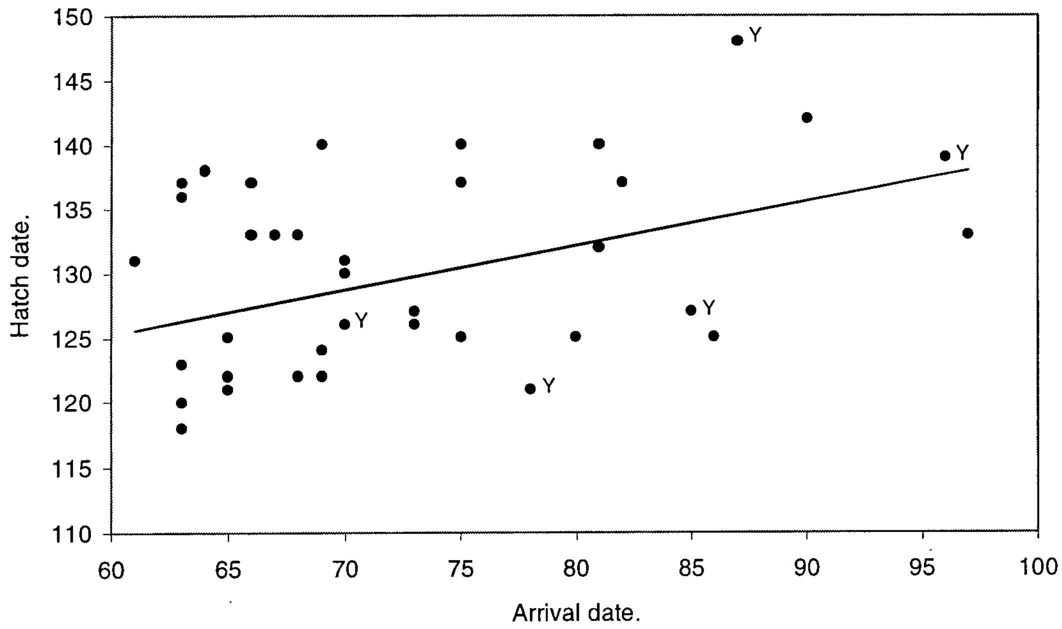
Table 1.3.9. Median date of arrival with inter-quartile range (I.R.) and sample size (n) for Lapwings later breeding in fields with a high or low density of pairs. Date of arrival is the first sighting on the study site, not necessarily in the breeding field. Data for male and female yearlings have been combined to increase sample sizes. M=Male, F=Female. 1=1 January, 60=1 March, 91=1 April.

				Arrival dates for Lapwings breeding in	
Year	Age	Sex		High density fields (≥1 pair/ha)	Low density fields (<1 pair/ha)
1993	Yearling	Sexes combined	Median	85	79
			I.R.	74-87	70-117
			n	9	4
	Adult	M	Median	72	77
			I.R.	69-80	65-104
			n	34	7
		F	Median	73	85
			I.R.	69-81	75-103
			n	33	7
1994	Yearling	Sexes combined	Median	83	92
			I.R.	74-92	76-102
			n	15	7
	Adult	M	Median	66	68
			I.R.	63-70	64-84
			n	38	14
		F	Median	68	77
			I.R.	63-76	68-86
			n	43	14

Arrival date and the timing of breeding

Those females whose nesting attempt was monitored, and for whom the arrival date was known, were included in a regression analysis of the effect of arrival date on the timing of hatching. This relationship was not significant in either year (1993: r^2=0.19, $F_{1,16}$=3.5, n.s.; 1994: r^2=0.16, $F_{1,21}$=3.8, n.s.), and not significantly different between the two years (t_{35}=-0.4, n.s.). Thus, the data have been combined to produce Figure 1.3.4. The linear equation for this relationship is Hatch date=0.29±0.11(arrival date) + 109.36: r^2=0.14, $F_{1,38}$=5.9, $P<0.02$. The result holds after controlling for age. This means that a delay in arrival of about three days results in a delay in hatching (and therefore laying) of one day.

Figure 1.3.4. Regression of hatch date by arrival date for individually-ringed females, 1993 and 1994. Points marked with a "Y" represent yearling females, all others are adults. 1=1 Jan; 60=1 March; 91=1 April; 121=1 May; 152=1 June.



Arrival date and survival

The influence of arrival dates on the subsequent survival of individual Lapwings was investigated by comparing the frequency of resightings in 1994, for individuals arriving in 1993 before or after the median date of arrival for the group (classified by age and sex). This section assumes there were no differences in site-fidelity between groups (Thompson *et al.* 1994). There were no significant associations between arrival date and survival for adults (greater than one-year-old) of both sexes (Table 1.3.10: all $G_1<2.9$, n.s.). However, only 56% of yearling males arriving before 19 March were seen in 1994, compared to 100% of those arriving after this date (Table 1.3.10: $G_1=9.4$, $P<0.01$).

Table 1.3.10. The number (and %) of Lapwings seen in 1994 in relation to their date of arrival in Upper Teesdale in 1993. Early=arrived before the median arrival date; late=arrived after the median arrival date.

	Age (years), sex and relative arrival date											
	One				Two				Three			
	Male		Female		Male		Female		Male		Female	
Status in 1994	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late
No. seen	9 (56%)	13 (100%)	8 (67%)	7 (58%)	15 (71%)	10 (59%)	11 (65%)	10 (67%)	14 (82%)	5 (50%)	13 (68%)	11 (61%)
No. not seen	7	0	4	5	6	7	6	5	3	5	6	7

1.4 DISCUSSION

On average, Lapwings arrived six days earlier in 1994 than in 1993, with particularly marked advances in arrival in 1994 among adult males. Evidence suggested that harsh weather conditions influenced the return of adult Lapwings to Teesdale in 1993, but also fewer visits to the study site in 1993 may have resulted in a “false” delay in arrival for some groups in that year. This problem illustrates the basic need to use standardised field techniques in order to eliminate such observer effects.

The influence of weather on the arrival date of waders is widely documented, particularly with reference to snow cover, with Holmes (1966), Nettleship (1973) and Green *et al.* (1977) reporting that the date of territory establishment was closely correlated with that of snow melt. Byrkjedal (1980) showed that artificial nests set up between snow patches suffered higher predation than those established when there was no snow present, and suggested that waders benefited by commencing breeding only after all snow had melted.

There is obviously a great deal of within-year variation in arrival dates for Lapwings returning to Upper Teesdale. Much of this was attributed to the differences between the sexes and age-groups, with males arriving before females and adults arriving before yearlings. The early arrival of males on the breeding grounds is a well-documented strategy among birds: e.g. songbirds: Pied Flycatcher *Ficedula hyperleuca* (Sternberg 1989; Lundberg & Alatalo 1992), Swallow *Hirundo rustica* (Møller 1994), Red-winged Blackbird *Agelaius phoeniceus* (Searcy & Yasukawa 1995), waterfowl: Shelduck *Tadorna*

tadorna (Patterson 1982), shorebirds: Dunlin *Calidris alpina* (Holmes 1966), Least Sandpiper *C. minutilla* (Page 1974; Myers 1981), Western Sandpiper *C. mauri* (Holmes 1971), and Ruff *Philomachus pugnax* (Van Rhijn 1991). However, this is not the only strategy utilised by shorebirds, as both sexes have been shown to arrive together in other species: e.g. Red Phalarope *Phalaropus fulicarius* and Sanderling *C. alba* (Myers 1981), and females usually arrive before males in the Snowy Plover *Charadrius alexandrinus* (Warringer *et al.* 1986) and Spotted Sandpiper *Actitis macularia* (Oring & Lank 1986). Previous studies that refer to the arrival times of Lapwings have produced different conclusions. Rinkel (1940) suggested that both sexes probably arrive simultaneously, whereas Spencer (1953 - cited in Cramp & Simmons 1983), and Galbraith (1989), reported males arriving before females. This tentatively raises the possibility that different populations adopt different strategies, although further comparative studies of different populations would be needed to investigate this.

Yearling Lapwings arrived eight days later than adults in Upper Teesdale, a pattern also reported by Imboden (1974) in his study utilising European ringing-recoveries. Young birds have also been shown to arrive later than older individuals in other species: e.g. Kittiwake *Rissa tridactyla* (Coulson & White 1958), Manx Shearwater *Puffinus puffinus* (Harris 1966), Arctic Tern *Sterna paradisaea* (Coulson & Horobin 1976), Blue-eyed Shag *Phalacrocorax atriceps* (Shaw 1985), Pied Flycatcher (Sternberg 1989; Lundberg & Alatalo 1992).

Differences in arrival dates between sex and age classes could be a result of one, or a combination of, the following: the classes may segregate such that one group winters further from the breeding grounds than the other; the classes may winter in similar areas, but one may depart before the other; they may depart together, from similar areas, but one may require longer for the journey (e.g. more stopovers) than the other. Imboden (1974) showed that adult and juvenile Lapwings breeding in Britain wintered at different distances from the breeding grounds, with the juveniles travelling, on average, further than adults (particularly those that move onto the continent). He also suggested that adult Lapwings leave the wintering grounds before the juveniles. Therefore, it seems likely that at least part of the discrepancy in arrival dates between yearlings and older Lapwings was due to differences in the relative distance to wintering sites. By implication therefore, the advanced arrival of two-year-old Lapwings may be the result of individuals switching to wintering sites closer to the breeding grounds after their first winter, and/or the advanced departure from the breeding grounds.

It has been suggested that the segregation of age groups and sexes on the wintering grounds is the result of the desire to remain close to the breeding grounds, modified by the competitive exclusion of subordinate groups or individuals (Pienkowski & Evans 1985). One advantage of maintaining proximity to the breeding grounds is that by doing so, individuals could return to the breeding grounds earlier than competitors and thereby secure valuable resources needed for breeding (e.g. holes for protected nest-sites, von Haartman 1968; territories, Myers 1981; mates, Ezaki 1990; Møller

1994). However, in this study the only effect of arrival date was that on the timing of breeding, with a delay in arrival of a female of three days resulting in a 1-day delay in hatching (and hence laying) of the first clutch. This could have important consequences for an individuals breeding success as Thompson *et al.* (1994) showed that late-hatched (31 May to 14 July) Lapwing chicks in Upper Teesdale had a 30% lower chance of returning to the study area in the following year, than earlier-hatched chicks. They suggested this was due to a lower rate of post-fledging survival. Similar effects have been demonstrated in other species: Harris (1967) showed that Oystercatchers *Haematopus ostralegus* laid progressively smaller clutches which produced fewer young through the season. Parsons (1975) and Parsons *et al.* (1976) demonstrated a seasonal decline in clutch size, egg volume, hatching success and fledging success in the Herring Gull *Larus argentatus*; Verhulst & Tinbergen (1991), and Barba *et al.* (1995), showed a reduction in clutch size, fledging success, nestling weight and recruitment of late-hatched Great Tits *Parus major*; and Birkhead (1991) showed that 20% fewer late-hatching Magpie *Pica pica* chicks survived to one-year-old than early chicks.

The date of arrival did not appear to influence the breeding status of individual Lapwings. This implies that it did not affect an individuals ability to find and occupy a territory, nor to mate. Neither were arrival dates associated with the site in which an individual bred, thus, contradicting expectations according to von Haartman (1968), Myers (1981), Ezaki (1990) and Møller (1994). It is possible that arrival dates have more subtle effects than those investigated here. For example, late arriving individuals may suffer a decline in social status, as in the Red-winged Blackbird (Cristol 1995), or the date of return may influence the quality of territory gained, with quality varying according to parameters not monitored here.

Yearling male Lapwings arriving in Teesdale before the median date of arrival for this group in 1993, showed a decrease in survival over the following year of 44% when compared to later arriving yearling males. This suggests that early arrival on the breeding grounds may be hazardous for at least some individuals in this age group, so why don’t all yearling males return later? The obvious suggestion would be that early arriving males enjoyed some form of advantage over those returning later, but no evidence of this was found. Møller (1994) found that early arrival was particularly hazardous for males of poor quality (low body mass) as these individuals were more likely to succumb to harsh weather. This suggests that the male Lapwings that failed to return in their second year, may have been in poor condition and suffered increased mortality as a result of the stresses experienced during the period after arrival in their first year. This area would benefit from further study: does the relationship between arrival date and survival hold true for yearling males in all years or is it associated with environmental conditions? Does it ever appear in the older age groups?

2. The social mating system of the Lapwing.

2.1 INTRODUCTION

The term "mating system" is used here in reference to the associations between individuals during the breeding season, and the behaviour exhibited by the sexes, pertaining to reproduction. The distinction between social and genetic mating systems is made, given that social associations between the sexes in birds do not always result in exclusive mating relationships and therefore may not represent the true flow of gametes (Westneat *et al.* 1990; Birkhead & Møller 1992; Avise 1996; Reynolds 1996).

The Lapwing is usually regarded as a monogamous breeder (one male paired with a single female during a breeding season), with only occasional incidences of males paired with more than one female (polygyny) (Cramp & Simmons 1983). This view has been challenged recently by studies involving individually-recognisable Lapwings. Berg (1993) and Byrkjedal *et al.* (1997) showed that 50% and 35% respectively of territorial males were polygynous in Sweden and Norway. These figures exceed the 5% threshold used by Verner and Willson (1966) to indicate a polygynous species.

Lapwings have also been assumed to be single brooded, laying one clutch each season with replacement clutches in the event of failure (Cramp & Simmons 1983). Double-clutching was defined by Erckmann (1983) as the laying of two clutches in rapid succession by one female with the eggs and chicks of the first clutch tended by the male, and the eggs and chicks of the second tended by the female. Blomqvist and Johansson (1994) recently demonstrated the occurrence of "double-clutching" in the Lapwing, with three of 36 (8%) individually-marked females producing second clutches. These Lapwings did not conform to Erckmann's (1983) definition of double-clutching, however, as incubation of the first clutch was shared by both sexes and the second clutch was laid at about the time of hatching of the first clutch. Such behaviour is more closely akin to double-brooding, which is the term used in this section. These findings suggest that Lapwings have a more varied mating system than was originally thought, with different strategies open to them.

This section describes the mating system of Lapwings in Upper Teesdale. In addition to the usual monogamous pairs, evidence of polygyny, polyterritoriality, polyandry and attempted double-brooding was found. Polyterritoriality is where a single male defends two or more separate territories in a season, and polyandry occurs when a female pairs with more than one male in a season (sequentially or simultaneously). Polyterritoriality and polyandry have not been reported previously in the Lapwing. The occurrence of polygyny is investigated in detail and in particular an attempt to answer the following questions is made:

1) Which factors determine the mating status of different males?

2) What are the consequences for male and female Lapwings with different mating systems?

2.2 METHODS

This study was conducted during 1993-95. For a description of the study area, and details regarding the identification and marking of individuals, and of census methods, see General Methods.

In addition to colour-ringed individuals, eight males were individually identifiable in 1995 by differences such as plumage (mottling on the breast patch, variation around the face) and damaged legs, and because all were mated with at least one individually ringed female. Similar methods were used by Galbraith (1988a), Berg (1993), Blomqvist and Johansson (1995) and Byrkjedal *et al.* (1997).

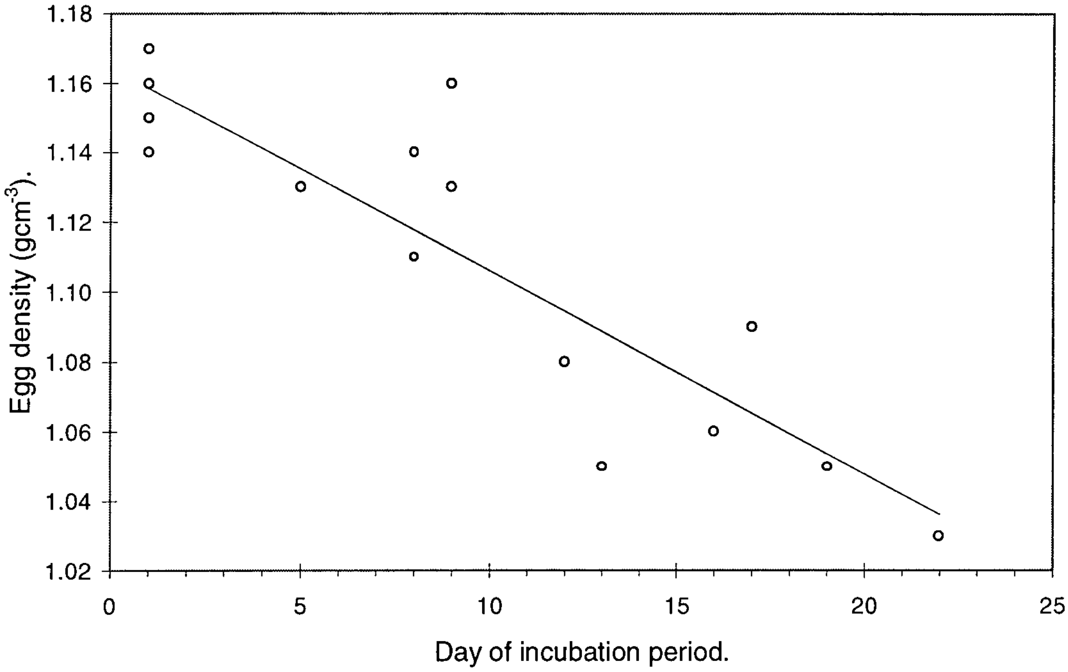
Mating status (i.e. the number of mates per individual in a season) was recorded for each individual during regular censuses.

Nests of ringed females were located during regular censuses and once found, were marked if there were no natural features to aid relocation, using wooden posts about 30-40cm long, placed 10-15 metres from the nest in line with some prominent feature, such as a gate post or observation hide. This method was used rather than placing the marker at a fixed bearing to the nest in order to minimise the regularity of the procedure, which may have enabled predators to learn to use posts as cues to finding nests. However, Picozzi (1975) showed that Crows *Corvus corone* learned to use markers as cues to finding artificial nests on moorland, even though posts were apparently oriented randomly with regard to nests. Crows were unlikely to pose a serious threat to Lapwing clutches in Upper Teesdale however, as they were controlled effectively (see General Methods). Also, Galbraith (1987) suggested that marking Lapwing nests on his arable site in Scotland did not affect the rate of predation, although he employed a less rigorous approach than that of Picozzi (1975). When natural features were present (e.g. ditches, patchy vegetation etc.), notes were made relating them to the position of the nest. All nests were visited to check contents, or observed from a distance to check for incubating adults, every 2-4 days.

Lapwings did not incubate frequently or for prolonged periods until egg-laying was completed (Cramp & Simmons 1983). Therefore the majority of clutches were discovered after clutch completion: 92% of 49 clutches in 1993, 83% of 48 in 1994, and 78% of 164 in 1995. This meant that the date on which the first egg was laid was seldom recorded by direct observation, so laying dates were calculated from the date of hatching. This was done by assuming 25 days for incubation (the period from clutch completion to hatching) and an interval of 1.5 days between the laying of eggs. Of 17 clutches of known laying and hatching date, the average period for incubation was 25.4 (±1.7 S.D.) days. Also, the relationship between egg density (mass/volume) and time from laying (illustrated in Figure 2.2.1) predicts an incubation period of approximately 25 days. Only one clutch was monitored daily in Teesdale from the laying of the first egg to the fourth. The second egg was laid within 48 hours of the first, the third within 24 hours of the second and the fourth egg within 48 hours of the third. A range of values have been published for the incubation and egg-laying periods of Lapwings: Jackson and Jackson (1975) reported incubation periods averaging just 21 days in southern England, whilst Nethersole-Thompson (in Cramp & Simmons 1983) found a mean of 28.1 days in Scotland. Eggs were laid daily according to Klomp (1951) and at 2.8-day intervals according to Heim (1974). The figures used here fall within the range of published values.

During 1995, measures of egg density were used to estimate laying dates. All eggs were measured (length and breadth) to the nearest 0.05mm with Vernier callipers and some clutches were weighed at intervals throughout the incubation period, to the nearest 0.5g with a Pesola balance. These data were used to construct a regression equation of egg density (gcm^{-3}) with time, for those clutches of known lay-date (n=18) (Figure 2.2.1). Each point represents the mean egg density for the clutch (all of four eggs), and each clutch was included only once. Laying dates were then estimated in other weighed clutches. The equation was: egg density (gcm^{-3})= -0.0058 (±0.0007) x (day from clutch completion) + 1.1651; r^2=0.82, $F_{1,16}$=74.6, P<0.0001.

Figure 2.2.1. The change in egg density during the incubation period (day 0=clutch completion). Taken from a sample of 18 Lapwing clutches of known lay date, 1995.



The measures of reproductive success investigated were the proportion of clutches producing at least one chick (i.e. number of successful clutches divided by the total number of clutches - “traditional method”, see Chap. 3), the proportion of chicks which hatched that subsequently fledged per brood and the total number of chicks which fledged per clutch laid. Chicks were recorded as fledged if seen flying, or if they reached 20 days of age. After this age, pre-fledging mortality was constant (P.S. Thompson, pers. comm.). The first measure of reproductive success provides an estimate of success to hatching, the second is a measure of fledging success independent of hatching success and the number of chicks fledging per clutch provides a composite measure of reproductive success over the whole breeding cycle, and is an estimate of an individuals contribution to the next generation. Data regarding the latter two measures did not conform to a normal distribution and were resistant to normalisation via transformation. Therefore non-parametric statistics were used and data were summarised as medians and inter-quartile ranges (I.R.).

Time-activity budgets were compiled in 1995 using a protocol developed in 1993 and 1994. Recognisable individuals were observed continuously for a period of ten minutes, during which the time of initiation and termination of all behavioural acts was recorded to the nearest 15 seconds ("focal sampling and continuous recording": Altmann 1974; Martin & Bateson 1993). Often it was possible to observe more than one individual simultaneously (e.g. one male and his two mates). Data were summarised as the proportion of time spent performing each behaviour, not including periods when the individual was out of sight. All behaviour was categorised as maintenance or reproductive, including mating and parental behaviour (Table 2.2.1). (maintenance behaviour included that which could not be ascribed to reproduction). For the purposes of this study territorial behaviour is regarded as a form of reproductive behaviour, although it will also serve to secure resources essential to maintenance. The characteristic flight display of the Lapwing (Dabelsteen 1978) and vigilant behaviour are categorised under reproductive behaviour, but are described separately, due to the potential duplicity of their intent. Dabelsteen (1978) described the circumstances of the occurrence of flight displays and suggested their main function was in territorial establishment and defence, although there was also a clear role in mate attraction (Dabelsteen 1978; Cramp & Simmons 1983). Vigilant behaviour was often performed in response to the appearance of predators or the activities of mates and neighbours (pers. obs.), so was impossible to categorise accurately.

Data were collected from a total of 107 individuals of different mating status during 531 observation sessions of approximately 10 minutes duration (Table 2.2.2). Observations were conducted throughout the breeding season, from shortly after territory establishment to the chick-rearing period, and between 0800-1700. For the purpose of analysis the breeding season was divided into six stages: pre-mating, pre-laying, egg-laying, incubation I (days 0-12 of incubation), incubation II (remainder of incubation) and chick dependence (Table 2.2.3). The chick-rearing period was not further divided due to the difficulties in locating and observing the mobile older chicks, resulting in few data for these individuals. The stage of the breeding season was known in 93% of cases and, on average, individual Lapwings were included in 2.7 ± 1.6 (S.D.) stages.

Table 2.2.1. Classification of Lapwing behaviour, 1995. Reproductive behaviour has been divided into mating and parental behaviour. Flight display is described separately under mating behaviour, and vigilance is described separately under reproductive behaviour, because of the duality of their use (see text).

Category	Behavioural description
Maintenance behaviour	
Foraging	Searching for prey; standing with head cocked (often vibrating one foot on the ground); probing the ground with the bill; consuming prey.
Roosting	Standing or sitting in hunched posture, often with eyes closed.
Preening	Preening feathers with the bill; stretching; bathing.
Reproductive behaviour	
Vigilance	Standing upright (occasionally sitting) in alert posture, turning head.
Mating behaviour	
Mate attraction	Rocking display and nest scraping (no females on territory) (Cramp & Simmons 1983).
Pair formation	Nest scraping and carrying of nest material (females present); courting behaviour: rocking display (females present), upright posture, forward-hunched run (Cramp & Simmons 1983); copulation.
Territory defence	Antagonistic behaviour: forward-hunched run, parallel walk, upright posture (Cramp & Simmons 1983).
Flight display	Complex string of flight patterns and vocalisations, mainly for territory establishment and defence (Dabelsteen 1978).
Parental behaviour	Incubation; brooding young; attending young (leading and contact calls); defence (chasing and mobbing potential predators, distraction displays).

Table 2.2.2. The number of individuals of different mating status included in the analyses, 1995. Bigamous males were paired with two females and trigamous males with three.

Mating status	No. individuals	No. observations	No. observations per individual (mean ± S.D.)
Males			
Unmated	7	22	3.1 ± 2.1
Monogamous	23	142	6.2 ± 4.3
Bigamous	15	87	5.8 ± 5.4
Trigamous	5	30	6.0 ± 6.9
All polygamous males	20	117	5.9 ± 5.6
Females			
Monogamous	20	92	4.6 ± 3.7
Polygamous	37	158	4.3 ± 4.1
Total	107	531	5.0 ± 4.3

Table 2.2.3. The number of individuals included in the analyses for whom the stage of the breeding cycle was known.

Stage	No. Individuals	No. observations	No. observations per individual (mean ± S.D.)
Pre-mating	28	49	1.8 ± 1.4
Pre-laying	52	127	2.4 ± 2.0
Egg-laying	32	47	1.5 ± 1.1
Incubation I	52	76	1.5 ± 0.8
Incubation II	50	84	1.7 ± 0.8
Chick dependence	50	91	1.8 ± 1.0

Data summarised as proportions are inherently non-normal due to the lack of independence between the sample mean and variance, and require arcsine transformation to correct this (Sokal & Rohlf 1995). In this study, all data remained non-normal (significantly right-skewed distribution) after arcsine transformation. Therefore, all analyses were conducted on raw data using non-parametric statistics and summaries are presented as medians with inter-quartile ranges (I.R.).

Territories were mapped by observing territory owners until eggs hatched and were based on the location of individuals and their interactions with neighbours. Locations were recorded on an aerial photograph (scale: 116mm=500m), and boundaries were drawn to include 95% of observed positions. The area occupied by a territory was estimated from the maps using an AM100 area meter (ADC Ltd., Hertfordshire).

2.3 RESULTS

THE MATING SYSTEM

Polygyny

All cases of polygyny were simultaneous, with one male breeding with up to three females during the same period within a breeding season (Table 2.3.1).

Table 2.3.1. The number of territorial, individually-recognisable, male Lapwings, breeding with different numbers of females in the same season. The number of males in each situation is expressed as a proportion (%) of the total number of males on the intensive site for that year in parentheses.

		No. of males with the following no. of mates:				% Poly-
Year	Total	None	One	Two	Three	gynous
1993	44	7 (16%)	28 (64%)	9 (20%)	0	20%
1994	38	11 (29%)	20 (53%)	7 (18%)	0	18%
1995	54	4 (7%)	26 (48%)	19 (35%)	5 (9%)	44%
Total	136	22 (16%)	74 (54%)	35 (26%)	5 (4%)	30%

1993 v. 1994: $G_3=2.2$, n.s.; 1995 v. 1993: $G_3=10.4$, $P<0.02$; 1995 v. 1994: $G_3=14.2$, $P<0.01$

In all, 33 (37%) of the 90 individually-recognisable males were polygynous at some stage during the study. On average, 20% of territorial males were polygynous in 1993 and 1994, but 44% were polygynous in 1995. It also follows from Table 2.3.1 that 40% of breeding females were mated polygamously in 1993 and 1994, but 67% mated polygamously in 1995, with 20% and 37% respectively, mating with an already-mated male, despite the presence in the area of unmated, territorial males.

There were 49 territorial, individually-recognisable males whose mating status was known in at least two years (Table 2.3.2). Where males were seen in consecutive years, unpaired males were likely to change status between years and gain a mate, whereas mated males (monogamous and polygynous) typically maintained their status (G_2=6.4, P<0.05). Male status did not influence the likelihood of an individual being seen the following year (G_2=1.4, n.s.), suggesting there was no association between male mating-status and survival.

Table 2.3.2. The relationship between the mating status of territorial male Lapwings in subsequent years, 1993-95. Data from 49 individuals providing 65 male-years.

Status in	Status in year t_{+1}			
year *t*	Unpaired	Mono.	Poly.	Not seen
Unpaired	1	4	2	6
Mono.	3	18	7	11
Poly.	0	3	6	4

Most yearling males remained unmated, whilst the highest proportion of polygynous males occurred among males over two years (Table 2.3.3: G_4=20.4, P<0.001).

Table 2.3.3. The number of female Lapwings per territorial-male in relation to male age, 1993-95. Males more than two-years-old and those with more than one female have been combined. Individuals present in more than one year were included once, after random selection. Figures in parentheses express the number of males as a percentage of the total for that age group.

Male age		No. of males with the following no. of mates:		
(years)	Total	None	One	More than one
One	15	10 (67%)	3 (20%)	2 (13%)
Two	27	4 (15%)	19 (70%)	4 (15%)
Over two	31	3 (10%)	18 (58%)	10 (32%)

Male polyterritoriality

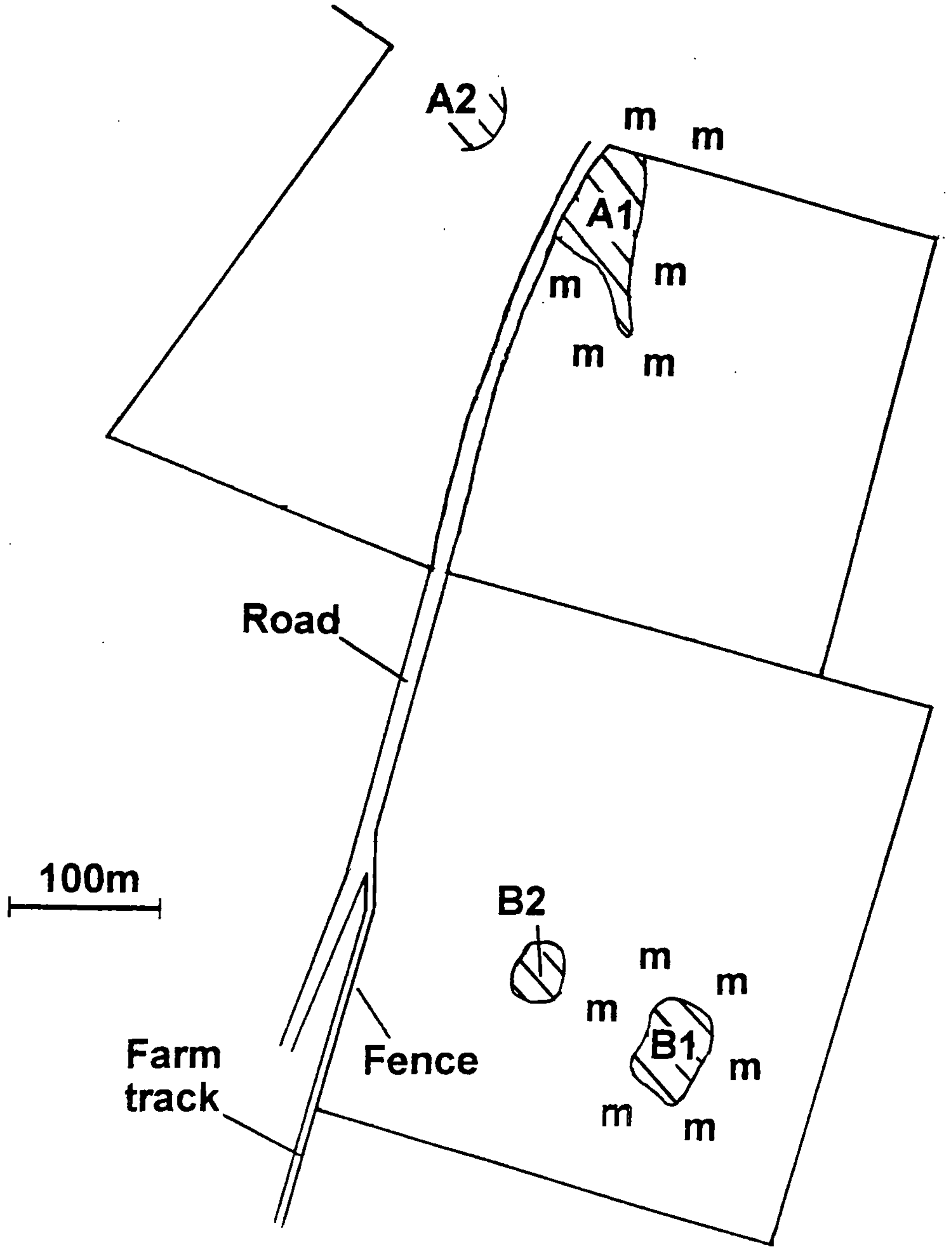
In 1995, two polygynous males simultaneously defended two separate territories (4% of 55 polygynous males; 1% of 136 male-years). The first, male A, was paired with two females on his original territory, both of whom began egg-laying by 6 April and were frequently seen incubating. This male established another territory about 65m away, in a neighbouring field (Figure 2.3.1). He was seen here on 9 and 13 April, defending this area against conspecifics, and courting a new female. On 9 and 12 April he was also seen on his first territory. After 13 April, male A was not seen on the second territory again.

Polygynous males with a single territory in other parts of the study site, were seen regularly at or near nests of the females with whom they were breeding. Thus, the absence of male A from his second territory after 13 April suggests he was either unsuccessful in his courting attempts there, or that the breeding attempt was unsuccessful. Eggs in one of the nests on the first territory hatched by 7 May and a single chick fledged. Eggs in the second nest were taken by a predator (24 April) and a replacement clutch was laid, but later abandoned.

The second case of polyterritoriality involved male B. He had a single mate on his initial territory, who began egg-laying by 9 April, but this clutch was lost on 4 May. On 13 May, male B was incubating a clutch on a second territory about 60m away (Figure 2.3.1). Egg-laying had begun in this nest by 30 April and involved a second female. She had not been seen with any male until 13 May, after which she associated with male B only. From 13 May, male B was seen defending the second territory against neighbours, and was still frequenting his first territory. The lost clutch on the first territory was not replaced, although the female was frequently seen. The female on the second territory was seen with three chicks on 30 May.

The areas in between the two territories of male A and also male B, were occupied and defended by other territorial males, thus discounting the possibility that the cases of polyterritoriality involved males with large territories that were unevenly frequented (Ford 1996).

Figure 2.3.1. Scale drawing showing the relative positions and sizes of the territories of polyterritorial males A and B, and the location of neighbouring territories. All field boundaries are dry-stone walls unless labelled otherwise. 1=the first territory occupied by a polyterritorial male, 2=the second territory occupied; m=neighbouring territorial male.



The fate of clutches

In total, 104 first clutches were laid on the intensive site from 1993-95, by 64 individually-ringed females (104 female-years). Of these clutches, 65 (63%) hatched. Of the 39 (38%) clutches that were lost, replacements were laid for 25 (61%), most of which (68%) were also lost. All but one (96%) of the females laying both first and replacement clutches remained with the same male throughout. In three cases a second replacement clutch was laid after the loss of the original replacement clutch; one of these hatched successfully. Four of the females laying successful clutches went on to lay second clutches, and two of them laid replacement clutches after the loss of their broods.

Attempted double-brooding

Of the 64 colour-ringed females whose breeding chronology was known, four attempted to produce second broods (6%, or 4% of 104 female-years): one in 1993 (3% of 37 breeding females), and three in 1995 (9% of 35). Information was collected regarding a further case found on the extensive site in 1994, and is included in Table 2.3.4. Each case is described in detail below.

1. 1993. Female A was a two-year-old bird and began laying her first clutch (four eggs) by 2 April. Incubation was carried out by both parents (her mate was an unringed male and it is unknown whether he was monogamous or polygynous). Four chicks hatched on 4 May and were ringed the following day. On 3 June, the female was seen incubating her second clutch (four eggs) within 50m of the first nest-site and within the same territory. The following day the remaining chick from the first clutch was caught and individually ringed, in the same territory. On 10 June the second nest was inspected and found to have failed.

2. 1994. On 2 May, female B (three-years-old) was found with one chick (1-3 days old) which was then ringed. Her mate was unringed. On 28 May, the same female was incubating a clutch of three eggs in the next field (date of laying estimated from hatch date at 20 May), with the chick from the first clutch nearby (<1m). Her mate for the second clutch was also unringed, so it is not known whether she remained paired with the male from the first clutch. The chick was again within 1m of the sitting female on 11, 13 and 15 June. On 22 June, the female was seen with two new chicks (1-3 days old) and the chick from the first clutch was nearby. The surviving chick from the second clutch was ringed on 3 July and seen on 13 July with the female and a colour-ringed, fledged chick (believed to be the first-brood survivor). On 28 July, the female was seen for the last time that year with the near-fledged chick from the second clutch.

3. 1995. Female C (two-years-old) began laying her first clutch (four eggs) on 8 April. She was paired with a monogamous, colour-ringed, two-year-old male. Four of eight observations of sitting adults showed the male incubating. The eggs hatched by 8 May, three chicks were seen on 9 May and by 12 May only one chick remained. On 2 June, the female was sitting on a second nest within the territory of her original mate (<20m from the first nest site) and the surviving chick was nearby. On inspection two days later, a broken egg was found close to the disturbed nest scrape.

4. 1995. Female D (five-years-old), paired with a monogamous, four-year-old, colour-ringed male, began laying her first clutch (four eggs) on 7 April. The male was incubating in six of nine observations of sitting adults. The eggs hatched on 6 May and three chicks were ringed. On 10 May, two chicks were seen and by 15 May, one remained. On 1 June, an adult (unidentified) was incubating a second clutch of four eggs about 20m from the first nest site. On two further visits the male was incubating at this nest. A near-fledged, ringed chick was present on and around the territory at this time, with the adults. Chicks of this age are usually repulsed when intruding (pers. obs.), so this was probably the survivor from the first brood. The male was incubating on 14 June, but the eggs disappeared and neither adult was seen thereafter.

5. 1995. Female E (five-years-old), paired to a bigamous male (unringed), began laying her first clutch (four eggs) on 7 April. The male was incubating in five of nine observations of sitting adults. All of the eggs hatched on 6 May and the chicks were ringed. One chick was taken by a Merlin *Falco columbarius* the following day, and on 10 May, two chicks were seen. From 15 May, one chick survived. On 23 May, the female and an unringed male were nest-displaying (scraping and moving nest material) 10m from the original nest site and in the same territory, and the female was apparently incubating. Neither adult was at the nest on 26 or 31 May, but the female was again sitting on 1 June. On inspection four days later, the nest cup was found to have been disturbed by a predator.

In all five cases where second clutches were laid, both sexes tended first-clutch chicks (e.g. vigilant, defensive or brooding behaviour) before the second clutch was laid. In the four cases where the female was known to have kept the same mate, this behaviour continued for the duration of the second clutch.

Three similar cases of attempted second broods in the Lapwing were reported by Blomqvist and Johansson (1994). The characteristics of these cases are compared with those from Teesdale in Table 2.3.4.

Polyandry

Of the 64 colour-ringed females whose breeding chronology was known, one bred with two males in succession in the same year. This represents 2% of the 64 individuals studied, or 1% of 104 female-years. This was a yearling female (female X), mated first with male C. He was a polygynous male, with three females on his territory, female X being the last of these females to begin laying her clutch (10 April). After 16 days the eggs were taken by a Stoat *Mustela erminea* and female X was not seen on the territory of male C thereafter, despite his presence on this territory for the remainder of the season. On 23 May female X was found in a neighbouring field, on the territory of male D (now a bigamous male), approximately 150m from the territory of her original mate. This was close to an area she had used frequently for feeding. She laid her second clutch on this territory (estimated from hatch date at 16 May), which was incubated by both male D and female X, and the eggs hatched on 9 June.

Table 2.3.4. Summary of the main characteristics of attempted second broods reported for Lapwings. The summary for Upper Teesdale includes the case found in 1994 on the extensive site. Figures in parentheses indicate the frequency of occurrence (e.g. 5/5 = 5 of 5 cases), except for row three, where sample sizes are shown.

	Blomqvist & Johansson (1988-90)	Upper Teesdale (1993-95)
Incubation of first clutch	Both parents (3/3)	Both parents (5/5)
Attendance of first-clutch chicks	Male only (3/3)	Both parents (5/5)
Mean no. days (±S.D.) between clutches[a]	35±9 (n=3)	47±4 (n=5)
Success of first clutch	Brood fledged[b] (3/3)	One chick fledged (5/5)
Success of second clutch	Chicks hatched in 2/2 cases[c], but no evidence of fledging	Chicks hatched in 1/5 cases, producing a single fledgling

[a] Period between completion of the first clutch, and initiation of the second.

[b] Not specifically given in Blomqvist and Johansson (1994). More than one chick fledged in each case.

[c] The fate of the second clutch of one of the females in the Swedish study was unknown, due to its location.

THE NATURE OF POLYGYNY

Males

No males were seen exhibiting territorial behaviour anywhere other than in the area where they bred and no intrusions were witnessed: all disputes involved neighbouring individuals. The date of territory establishment was taken as the first date on which a male was seen exhibiting territorial behaviour on the territory where he subsequently bred. This was known for 39 males in 1995. There was significant variation in the date of territory establishment between males of known age (Table 2.3.5), with establishment dates earliest for three-year-old males and latest for yearlings, although sample sizes were small.

Table 2.3.5. The mean (± S.E.) date of territory establishment in relation to the age (years) of male Lapwings, 1995. Sample sizes shown in parentheses. Day 1=1 January.

Date of territory establishment for males aged				
One	Two	Three	Four	Five
74.6 ±6.8 (n=5)	70.1 ±3.0 (n=10)	54.4 ±2.4 (n=5)	62.2 ±4.7 (n=6)	73.3 ±3.0 (n=3)

One-way-ANOVA: $F_{4,24}=3.4$, $P<0.05$; Tukey multiple-range test: ages 1 & 3 significantly different ($P<0.05$).

A factorial ANOVA was used to compare the dates of territory establishment for those males later found to be unpaired, monogamous or polygamous, whilst controlling for the above differences due to age (Table 2.3.6). Differences in timing in relation to mating status were not significant ($F_{2,22}$=0.9, n.s.).

Table 2.3.6. The mean (± S.E.) date of territory establishment in relation to the eventual mating status of male Lapwings, 1995. Sample sizes are shown in parentheses.

Date of territory establishment		
Unpaired	Monogamous	Polygamous
76.3 ±6.0 (n=6)	63.9 ±2.1 (n=18)	65.1 ±2.6 (n=15)

The area of 49 territories was known in 1995. There was no variation in territory size among the six fields included (one-way-ANOVA: $F_{5,41}$=0.5, n.s.), nor among the age groups for territory-holding males of known age ($F_{4,22}$=1.7, n.s.). Territory size did vary, however, according to the number of mates a male acquired (range=0-3): $F_{3,43}$=13.5, $P<0.001$. A Tukey multiple range comparison suggests unpaired and monogamous males have smaller territories than bigamous and trigamous males, $P<0.05$ (Table 2.3.7). When comparing only mated-males, the territories of trigamous males were also significantly larger than bigamous males: $F_{2,40}$=17.4, $P<0.001$ (Tukey test: all groups significantly different, $P<0.05$). Furthermore, a regression analysis confirms the linear nature of the increase in territory size with the number of mates for mated-male Lapwings, suggesting that for each additional female, territory size increases by 2468 ±419m^2 (r^2=0.46, $F_{1,41}$=34.7 P<0.001).

Table 2.3.7. Territory area (m^2) in relation to male mating status (no. of mates), 1995. The polygamous category combines data from bigamous and trigamous males.

Male mating status	Territory area (m^2)
Unpaired (n=4)	2116±687
Monogamous (n=21)	2636±226
Bigamous (n=17)	4932±633
Trigamous (n=5)	7730±809
Polygamous (n=22)	5568±574

There was no relationship between the date of territory establishment and territory size for 32 territories for which both were known (r=-0.15, n.s.).

A total of 47 behaviour-observation sessions were conducted on 26 males during the pre-mating period of the breeding season: seven of these males failed to attract a female, 14 became monogamous and five later paired with two or more females. There were no behavioural differences between the groups of males (Table 2.3.8).

The presence of more than one female on a territory might have influenced a male's behaviour: for example, vigilance duties might have been shared between territory mates such that polygamous males spent less time alert than their monogamous counterparts. Alternatively, the extra female(s) present might have resulted in polygamous males being more alert than their monogamous counterparts because of additional mate-guarding responsibilities. To examine this, the maintenance and reproductive behaviour of monogamous and polygamous males was compared at all stages through the breeding season (Table 2.3.9).

Table 2.3.8. Behaviour of male Lapwings during the pre-mating period 1995 in relation to their eventual mating status. K.W. is the test statistic from a Kruskal-Wallis one-way-ANOVA (d.f.=2 in all cases). I.R.=Inter-quartile range.

		Proportion of time allocated to					
				Reproductive behaviour			
Mating status		Maintenance		Mating behaviour		Vigilance	
	N	Median	I.R.	Median	I.R.	Median	I.R.
Unmated	7	0.73	0.49-0.83	0.11	0.00-0.19	0.21	0.05-0.35
Monogamous	14	0.68	0.30-0.90	0.03	0.00-0.23	0.10	0.03-0.40
Polygamous	5	0.45	0.02-0.87	0.08	0.00-0.47	0.16	0.02-0.55
K.W.		1.2 (n.s.)		0.3 (n.s.)		0.2 (n.s.)	

Table 2.3.9. The proportion of time allocated to different behaviour by monogamous (Mono.) and polygamous (Poly.) male Lapwings throughout the breeding season, 1995. Figures in parentheses replace medians of zero, showing instead the proportion of data equal to zero. I.R.=Inter-quartile range.

			Proportion of time allocated to							
					Reproductive behaviour					
			Maintenance		Mating behaviour		Parental behaviour		Vigilance	
Stage	Status	N	Median	I.R.	Median	I.R.	Median	I.R.	Median	I.R.
Pre-laying	Mono.	17	0.50	0.33-0.76	0.31	0.10-0.49	-	-	0.03	0.00-0.10
	Poly.	12	0.63	0.43-0.84	0.20	0.02-0.39	-	-	0.08	0.00-0.15
Egg-laying	Mono.	7	0.30	0.21-0.81	0.11	0.00-0.17	(70%)	0.00-0.39	0.12	0.00-0.27
	Poly.	7	0.53	0.20-0.80	0.14	0.07-0.41	(90%)	0.00-0.00	0.09	0.04-0.31
Incubation I	Mono.	12	0.58	0.00-0.90	(89%)*	0.00-0.00	(56%)	0.00-1.00	0.02	0.00-0.13
	Poly.	9	(54%)	0.00-0.74	(54%)*	0.00-0.06	0.23	0.00-1.00	(54%)	0.00-0.17
Incubation II	Mono.	13	0.36	0.00-0.78	0.03	0.00-0.06	(60%)	0.00-1.00	0.08	0.00-0.22
	Poly.	7	0.49	0.00-0.82	(58%)	0.00-0.05	0.04	0.00-0.95	0.02	0.00-0.15
Chick	Mono.	13	0.35	0.18-0.63	0.11	0.00-0.33	(92%)**	0.00-0.00	0.25	0.10-0.51
	Poly.	10	0.27	0.08-0.64	(56%)	0.00-0.11	(56%)**	0.00-0.76	0.14	0.03-0.35

Mann-Whitney U test, *P<0.05; ** P<0.01.

The majority of behavioural comparisons between monogamous and polygamous males revealed insignificant differences, with the exception of some reproductive behaviour: polygamous males apparently allocated more time to mating behaviour during early incubation and more time to parental duties during chick-rearing than monogamous males, although there were no differences between median values (Table 2.3.9). The difference in mating behaviour was the result of more time allocated to courting and flight displays by polygamous males during early incubation (polygamous males also allocated more time to flight displays during egg-laying), although again the differences were small (median values the same - all zero). The greater proportion of time allocated to parental behaviour by polygamous males during chick rearing was actually the result of more time spent incubating than monogamous males: a consequence of the asynchrony between nests on the territories of polygamous males. This also meant it was not possible to determine the apportionment of effort by polygamous males among the females on their territories. None of these differences were due to male age (Kruskal-Wallis one-way-ANOVA [KW-ANOVA]: all $\chi^2_4<5.9$, n.s.), although the sample sizes for some age groups were small.

One clear advantage of polygamy for males was the number of chicks fledged. There were no differences in productivity among years (all samples were non-normally distributed and resistant to transformation: KW-ANOVA, monogamous males: $\chi^2_2=0.6$, n.s.; polygamous males: $\chi^2_2=1.3$, n.s.), so samples have been pooled. Overall, polygamous males raised 1.0 extra chicks to fledging per season compared to monogamous males: Mann-Whitney U test: Z=2.2, $P<0.05$ (Table 2.3.10).

Table 2.3.10. The median (and mean) number of chicks fledged per season in relation to the mating status of male Lapwings, 1993-95. I.R.=Inter-quartile range. N=number of males.

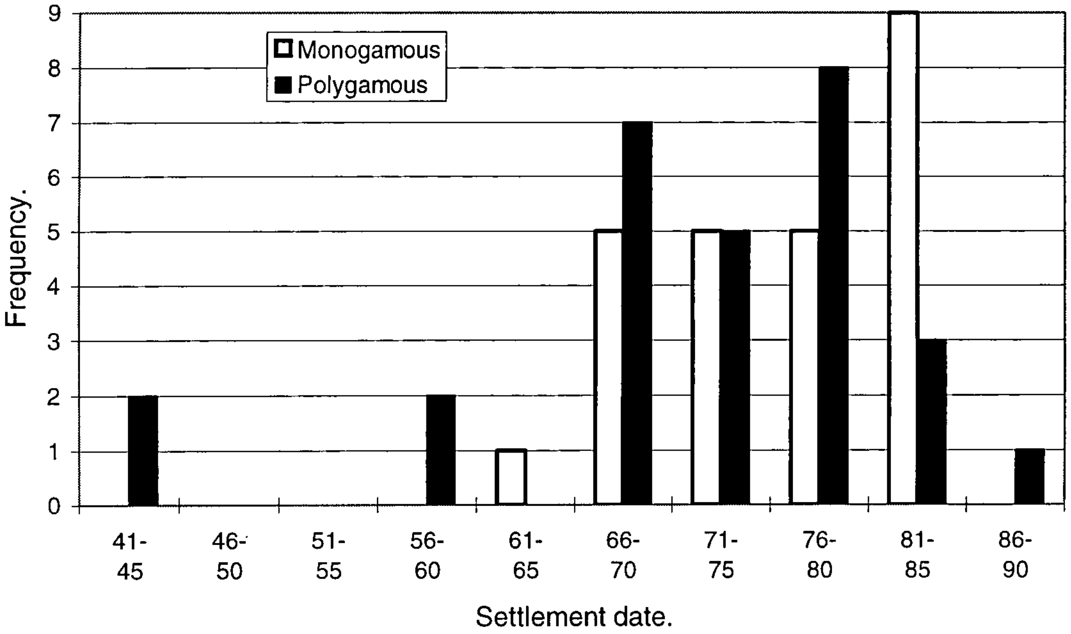
		Number of chicks fledged		
Status	N	Median	I.R.	Mean
Monogamous	48	1.0	0.0-2.0	1.2
Polygamous	25	2.0	1.0-3.0	1.9

Females

No females were seen courting males on territories other than that in which they bred and only one female was seen on more than one occasion on another male's territory before breeding. The date of settlement on a territory (the first date on which a female was seen on the site where she later bred) was known for 72 females from 1994 and 1995. There was no difference in settlement date between years (t_{70}=1.1, n.s.) and there was no variation due to female age (one-way-ANOVA: $F_{4,38}$=2.4, n.s.). Thus all data have been pooled. There was no significant difference in settlement dates between monogamous and polygamous females (t_{51}=1.9, n.s.), but Figure 2.3.1 shows a high degree of variation in settlement dates among polygamous females, with both the earliest and latest females to settle on a territory being polygamous. It was not possible to determine the order of settlement for the females on many territories due to the prevalence of unringed birds.

The date of settlement of females onto a territory was not related to the date of laying of the first clutch: r=0.25, n.s. (n=55).

Figure 2.3.1. The date on which monogamous (n=25) and polygamous (n=28) female Lapwings settled on the territories where they subsequently bred, 1994-95. Dates are days from 1 Jan (45=14 Feb; 60=1 March; 75=14 March; 90=31 March).



The behaviour of monogamous and polygamous females was compared at all stages throughout the breeding season (Table 2.3.11). The only significant difference in behaviour was during the pre-laying period, when monogamous females allocated 12% more of their time to maintenance behaviour than polygamous females. This was primarily the result of more time spent feeding, although none of the comparisons of the components of maintenance behaviour (see Table 2.2.1) revealed significant differences.

Polygamous females allocated more time to aggression, a component of mating behaviour (see Table 2.2.1), than monogamous females during this period, although the median values were equal (both zero). It was not possible to adequately control for age effects here due to the prevalence of unringed females. No aggression was recorded for monogamous females during this time. Of 10 aggressive acts involving polygamous females during the pre-laying period (counting aggression between females who were territory-mates once), only one could be classified as defence of the territory; four involved encounters between females resident on the same territory, three cases involved aggressive acts between female territory-mates but with the intervention of the male resulting in the cessation of conflict, and the last two cases concerned aggression between one female and the resident male.

To examine whether the difference in the allocation of time to feeding between monogamous and polygynous females reflected a difference in effort, the peck rates (number of pecks per minute) were compared for monogamous and polygamous females during the pre-laying period. The data were positively skewed with high variances relative to the mean, so analyses were conducted on log-transformed data. Using a factorial ANOVA to separate variation due to age and mating status, and with date entered as a covariate, none of the factors resulted in significant variation in peck rate (main effects: $F_{5,13}=1.4$, n.s.). The mean peck rate of monogamous females (n=15) was 7.8 ±1.1 pecks per minute, and of polygamous females (n=12) was 5.3 ±0.6 pecks per minute.

The aforementioned difference in the proportion of time allocated to feeding by monogamous and polygamous females, did not result in any differences in egg dimensions (t_{57} all <0.8, n.s.).

In terms of reproductive success, there were no differences between the first clutches of monogamous and polygamous females. There was no difference in the proportion of first clutches producing at least one chick (Table 2.3.12), no difference in the proportion of hatched chicks which fledged per brood nor in the total number of fledglings produced per clutch (sample distributions were skewed and resistant to transformation: Mann-Whitney U test: Z=1.5, n.s.; Z=1.5, n.s. respectively - Table 2.3.13). The two latter measures did not differ between years (monogamous females: Kruskal-Wallis one-way-ANOVA: χ^2_2=0.1, n.s.; χ^2_2=0.1, n.s. respectively; polygamous females: χ^2_2=3.0, n.s.; χ^2_2=3.3, n.s. respectively), so data were pooled. The mean number of chicks fledged per clutch laid has been given with the median value, in order to allow comparisons with measures of productivity in other studies. It should be emphasised, however, that the statistical tests used compare sample medians (and ranked distributions).

Table 2.3.11. The proportion of time allocated to different behaviour by monogamous (mono.) and polygamous (poly.) female Lapwings throughout the breeding season, 1995. Figures in parentheses replace medians of zero, showing instead the proportion of data equal to zero. I.R.=Inter-quartile range.

		Proportion of time allocated to							
				Reproductive behaviour					
		Maintenance		Mating behaviour		Parental behaviour		Vigilance	
Stage	Status	Median	I.R.	Median	I.R.	Median	I.R.	Median	I.R.
Pre-laying	Mono.	0.80*	0.68-0.99	(59%)	0.00-0.11	-	-	0.03	0.00-0.27
	Poly.	0.68*	0.39-0.89	0.03	0.00-0.12	-	-	0.10	0.00-0.33
Egg-laying	Mono.	0.05	0.00-0.79	(56%)	0.00-0.05	(67%)	0.00-0.53	0.18	0.00-0.38
	Poly.	0.51	0.00-0.80	(78%)	0.00-0.01	(67%)	0.00-0.80	0.10	0.00-0.26
Incubation I	Mono.	(77%)	0.00-0.10	(100%)	0.00-0.00	1.00	0.00-1.00	(88%)	0.00-0.00
	Poly.	(57%)	0.00-0.36	(93%)	0.00-0.00	0.60	0.00-1.00	(86%)	0.00-0.00
Incubation II	Mono.	(68%)	0.00-0.17	(79%)	0.00-0.00	0.75	0.00-1.00	(95%)	0.00-0.00
	Poly.	(70%)	0.00-0.03	(91%)	0.00-0.00	0.85	0.28-1.00	(79%)	0.00-0.00
Chick	Mono.	0.40	0.13-0.75	(60%)	0.00-0.04	0.08	0.00-0.70	0.15	0.02-0.42
	Poly.	0.45	0.03-0.71	(76%)	0.00-0.02	0.13	0.00-0.75	0.13	0.00-0.20

Mann-Whitney U test: *$P<0.05$.

Table 2.3.12. The proportion of first clutches producing at least one chick for monogamous and polygamous female Lapwings, 1993-95. Data for 1993 and 1994 were combined due to similar hatching-success rates (see Chap. 3). Figures in parentheses are the proportion (%) of successful clutches.

Year	Female status	Number of clutches: Hatch	Fail	Total
1993 & 94	Monogamous	25 (66%)	13	38
	Polygamous	12 (60%)	8	20
	Total	37 (64%)	21	58
1995	Monogamous	17 (57%)	13	30
	Polygamous	20 (42%)	28	48
	Total	37 (47%)	41	78

Association between female status and hatching success: 1993 & 94: G_1=0.2, n.s.; 1995: G_1=1.5, n.s.

Table 2.3.13. The median proportion of hatchlings which fledged per brood and the median (and mean) number of chicks which fledged per clutch, for monogamous and polygamous female Lapwings, 1993-95. Data for all years were pooled (see text). I.R.=Inter-quartile range. Sample sizes shown in parentheses.

Female status	Proportion of hatchlings fledging per brood: Median	I.R.	Number of fledglings per clutch laid: Median	I.R.	Mean
Monogamous	25% (n=45)	0-58	1 (n=50)	0-2	1.1
Polygamous	0% (n=45)	0-29	0 (n=49)	0-2	0.8

2.4 DISCUSSION

The mating system

In this study, 30% of territorial male Lapwings bred simultaneously with more than one female. This concurs with Berg (1993) and Byrkjedal *et al.* (1997), who reported 50% and 35% polygyny, respectively. Recognisable individuals had not been used in studies of the Lapwing until recently, suggesting that the high frequency of polygyny in this species had previously been overlooked.

Territory-holding adult males were more likely to obtain more than one mate in a season than territory-holding yearlings, most of whom remained unmated (67%). This suggests that yearling males were either unattractive to females, or obtained poor-quality territories which were themselves undesirable to females. The increase in the proportion of mated males among two-year-olds to 85% suggests that some form of maturation of the males has occurred, or that they changed territories between years, and thereby improved their chance of attracting a mate. Changes in territories between years occur in the Temminck's Stint *Calidris temminckii* (Hildén 1979) and the role-reversed Spotted Sandpiper *Actitis macularia* (Oring *et al.* 1991), with first-time settlers obtaining a poor territory and moving to a better one the following year. However, the high degree of between-year site-fidelity among adult males in Upper Teesdale (Thompson *et al.* 1994) and the high frequency of polygyny in this age group, suggests that a change in territory is not necessary to improve a male's mating success.

Two males were found defending two separate territories at the same time, an aspect of Lapwing breeding biology not previously reported. Lapwings often leave their territories to feed in nearby fields (Cramp & Simmons 1983; Galbraith 1989a), but no territorial or breeding behaviour takes place in such areas. Although not previously recorded in waders, polyterritoriality is common among passerines, with 37% of 46 polygynous species exhibiting polyterritoriality (Møller 1986). Alatalo *et al.* (1981) suggested that polyterritoriality concealed the mating status of mated-males from potential secondary females, a theory supported by Møller (1986). Winkel and Winkel (1984), however, proposed that this behaviour may serve to spread the risk of predation, whilst Slagsvold and Lifjeld (1986) suggested that maintaining a second territory would facilitate quick renesting in the event of first-clutch failure. Breiehagen and Slagsvold (1988) also suggested that polyterritoriality would increase male mating success by reducing female-female aggression. It is unlikely that the polyterritorial male Lapwings in this study could have deceived potential secondary females, as males indulge in conspicuous, aerial displays (Dabelsteen 1978) and the two territories, in both cases, were only 60-65m apart in open habitat. It also seems unlikely that these males were attempting to reduce the risk of predation by decreasing the clumping of nests, as all polyterritorial nests were still part of a larger aggregation of nests. Likewise, it would appear that polyterritoriality was unnecessary to induce hasty renesting as replacement clutches were laid frequently and quickly on other territories (Chapter 3). However, this behaviour may have been intended to reduce female-female aggression, given that female Lapwings sharing the territory of a single male were often aggressive towards their territory-mates early in the season, and that such aggression may deter other females from settling on a territory (see discussion of female aggression below). If female-female aggression resulted in reduced breeding success of the individuals involved (and thus their mates), males may benefit by trying to keep their females separated. Alternatively, males A and B may have resorted to polyterritoriality if they could not extend the boundaries of their original territories. Moreover, the initial territories of males A and B were both smaller than the average for other bigamous males.

Polyterritoriality could entail disadvantages, as males occupied on a second territory risk losing paternity of eggs laid on the first. The males in this study may have overcome this potential problem by waiting until egg-laying was underway on their first territories before establishing the second. There could also be an increased risk of losing clutches on a territory to predators if the male was frequently absent.

During this study, 6% of colour-ringed females attempted to produce second broods. This concurs with a frequency of 8% found in Sweden by Blomqvist and Johansson (1994). Such behaviour also occurs in some other shorebirds, e.g., the Mountain Plover *Charadrius montanus* (Graul 1976) and, in some areas at least, the Sanderling *Calidris alba* (Parmelee & Payne 1973). It is not always clear, however, whether this coincides with the changing of mates between clutches (e.g. polyandry), as in the Temminck's

Stint *Calidris temminkii* (Hildén 1975; Breiehagen 1989). In this study, four of the five females remained with the same male for both clutches.

The production of second broods is usually regarded as a means of increasing reproductive output, given the phylogenetic constraints preventing variation in clutch size in waders (Emlen & Oring 1977; Oring 1982; Erckmann 1983; Ligon 1993). This appeared to be the best interpretation for the cases reported in the Lapwing by Blomqvist and Johansson (1994), as the females deserted the first brood around the time of hatching to lay a second clutch of eggs. Female Lapwings in Teesdale laid their second clutches only after a period when their breeding efforts had been concentrated on tending the first brood. Here, second clutches may have been laid in response to the reduction of the first brood to a single chick. There were two cases in Upper Teesdale where females laid second clutches after the complete loss of a brood of young chicks, thus closely akin to the production of replacement clutches.

In this study, 25 (61%) females who lost their first clutch laid a replacement clutch and all but one remained with the same male. The one female which changed mates in the same season is the first polyandrous female reported for the Lapwing.

The nature of polygyny

Polygamous male Lapwings fledged, on average, 1.0 more chicks each year than monogamous males, suggesting a clear advantage to males able to secure more than one mate. This assumes there is no associated loss of fitness due to decreased survivorship or increased cuckoldry suffered by polygamous males. There was no evidence of decreased survival among polygamous males: over-winter return-rates apparently were independent of male mating-status. Assessing the frequency of cuckoldry was beyond the scope of this study. However, a review by Birkhead and Møller (1992) revealed a higher proportion of extra-pair fertilisations (EPF's) among polygynous than monogamous species. In a study of Red-winged Blackbirds, Gibbs *et al.* (1990) were able to determine the reproductive success of polygamous males (including EPF's gained and suffered by each individual). They showed that a male's reproductive success did not necessarily increase with harem size, but rather that individuals were either successful at fertilising females (on and off the territory) or not (Gibbs *et al.* 1990). However, a similar study by Westneat (1993), again on Red-winged Blackbirds, suggested that EPF's had little effect on the relationship between fledging success and harem size, but again there was the suggestion that some males were more successful at gaining both within-pair and extra-pair fertilisations than others. Likewise, for the polygynous Corn Bunting *Miliaria calandra* (Hartley *et al.* 1993) and Great Reed Warbler *Acrocephalus arundinaceus* (Hasselquist *et al.* 1995) EPF's did not significantly alter estimates of male reproductive success based on the number of putative offspring. Thus, the presumed increase in reproductive success with the number of mates on a male's territory may hold, but is not inevitable (Searcy & Yasukawa 1995).

Assuming rates of cuckoldry were similar for monogamous and polygamous males, the increased annual production of fledglings of polygamous males, together with the tendency for mated-males to maintain their mating status between years, would translate into higher lifetime reproductive success than monogamous males, asserting the advantage to males in obtaining more than one mate. Increased lifetime reproductive success of polygamous males, based on the production of putative young, was also found in the Pied Flycatcher (Sternberg 1989; Lundberg & Alatalo 1992) and Red-winged Blackbird (Searcy & Yasukawa 1995).

There was a positive association between the number of females on a territory and territory size for mated-male Lapwings, whilst the territories of unpaired and monogamous males were similar in size. Byrkjedal *et al.* (1997) found a similar relationship between territory size and harem size for Lapwings in Norway in three out of four years. This suggests that each female requires a minimum area in which to breed (around 2468m^2 in this study during 1995) which also implies that certain territorial resources are of importance to breeding female Lapwings. It is unlikely that the resource in question would be available nest sites, as these are simply scrapes in the ground and males often create several before a pair choose one in which to lay eggs (Cramp & Simmons 1983). Also, the nature of the habitat (predominantly featureless grass) suggests that a territory will provide little cover from predators and inclement weather. Thus a minimum area may be required by females to provide sufficient food (for herself and/or chicks). Significantly, this hints at the importance of male characteristics over those of the territory in determining the number of females per male: critical resources may be distributed evenly in the area so, to provide sufficient resources to attract more than one female, males have to compete to increase territory size. This contrasts with species where high-quality territories were smaller than others due to the uneven distribution of critical resources (e.g. Corn Bunting *Miliaria calandra*, Møller 1983). The linear relationship between territory size and male mating success in the Lapwing also suggests there was no benefit of polygyny via co-operation between female territory-mates or density effects (e.g. predator swamping) (Altmann *et al.* 1977), as clutches were no closer together than those of neighbouring monogamous females. Further study, preferably involving manipulations (e.g. of food abundance) would determine the resources critical to female fitness, and manipulations of these and male characteristics would determine the relative contribution of each in influencing male mating-status.

There were only minor differences in activity budgets between monogamous and polygamous males, indicating that polygamous males did not adjust their allocation of time amongst different behaviour in response to the number of mates on their territory. There were also no behavioural differences between males during pre-mating that indicated their subsequent mating status. However, polygamous males spent marginally, but significantly, more time indulging in courting behaviour and flight displays than monogamous males during the egg-laying and early incubation periods. This suggests that once mated, monogamous males decreased their mating effort, whereas polygamous males did not.

Although the mean dates on which females settled on a territory were similar for monogamous and polygamous females, variation in settlement dates was greater for polygamous females. These were both the earliest and latest females to take up residency on a territory. Often settlement dates are inferred when not recorded directly from laying dates (Lightbody & Weatherhead 1987; Stutchbury & Robertson 1987; Teather *et al.* 1988; Byrkjedal *et al.* 1997). In this study, there was no relationship between settling date and laying date for individual females, suggesting that if laying dates are to be used to predict settlement patterns justification should be given.

The only behavioural differences between monogamous and polygamous female Lapwings occurred during the pre-laying period. Monogamous females allocated 12% more of their time to maintenance behaviour (mainly feeding), whilst polygamous females spent more time involved in aggressive interactions (primarily with their female territory-mates) during this period. It is not known whether any feeding took place at night. There was no correlation between the allocation of time by females to aggressive behaviour and feeding during this period (r_s=0.06, n=37, n.s.), suggesting that the differences in behaviour of the two groups were independent. Overall, therefore, polygamous females did not pay an activity-budget cost during the breeding cycle: even if polygamous males preferentially attended one of their mates, there would be no reason to expect them to allocate a different amount of time to any behaviour than that allocated by a monogamous male during the breeding season. Therefore, the proportion of time allocated to each behaviour by polygynous females would be either equivalent to, or more than that allocated by monogamous females.

The fact that female Lapwings sharing a territory were aggressive towards one another during the early part of the breeding season, suggests they may have been unwilling to share a territory. However, the moment of settling on a territory was not witnessed in this study and so it was not possible to determine if the earliest settling females tried to prevent later females from settling at the same site. If it is disadvantageous for a mated female to allow another female to settle and share the resources on the territory, then mated females should attempt to prevent other females from settling (Wittenberger 1979; Davies 1991; Searcy & Yasukawa 1995). Alternatively, females may be defending mutual territories within that of the male whom they share as a mate, or aggressive interactions may establish a dominance hierarchy that could then determine the outcome of later confrontations over resources on the territory. Aggression between females sharing a territory has been found in a number of species (reviewed by Slagsvold & Lifjeld 1994) and it has been suggested that this prevents the settling of other females on the territory (LaPrade & Graves 1982; Hurly & Robertson 1984, 1985 for Red-winged Blackbird, but see Searcy & Yasukawa 1995; Hannon 1984; Davies 1985). However, a dominance hierarchy has also been demonstrated among female Red-winged Blackbirds sharing a territory (Roberts & Searcy 1988; Langston *et al.* 1990; Cristol 1995), and Hurly and Robertson (1984) suggested that female Red-winged Blackbirds maintained exclusive territories within a single male's territory. Casual observations indicate that female Lapwings may exclude their female territory-mates from certain areas of the main territory. However, the fact that the territory-holding male often intervened in disputes between females on his territory is more consistent with a settlement-deterrence function of female-female aggression: there would be little benefit to the male in interjecting unless there was a threat of losing a female (Searcy & Yasukawa 1995), or perhaps if female-female aggression reduced the breeding performance of those involved. This topic would reward further study.

That monogamous females spent more time feeding than polygamous females during the pre-laying period might suggest the former were in better condition before their breeding attempt, and thus able to invest more resources in their breeding effort (assuming similar periods spent feeding at night by both groups). Indeed, polygamous females did not compensate for spending less time feeding by increasing their peck rate. Alternatively, monogamous females may have needed to spend more time feeding because they were in a poorer condition than polygamous females, or because they were less efficient feeders, although it is difficult to understand how these causes could operate. Also, this may have been the result of an inadequate food supply on the territory of monogamous females. Whichever, the difference in feeding time between monogamous and polygynous females was small and did not result in any differences between monogamous and polygamous females in egg size.

There were no discrepancies between monogamous and polygamous females in terms of their seasonal breeding success. However, the comparisons made in this study were between monogamous females and all polygamous females. It is widely acknowledged that this can give a false impression of relative breeding success as no account of settling order of polygamous females is made (Wittenberger 1979; Vehrencamp & Bradbury 1984). This was not possible here as the settling date of unringed females was hard to determine. A variety of relationships can be predicted for the actual and relative breeding success of monogamous and polygamous females (Vehrencamp & Bradbury 1984; Davies 1989), and many have been reported. For example, where the male provides parental care, polygyny may result in the loss of assistance for secondary females and thus a decrease in breeding success (Webster 1991). In contrast, after manipulating the harem size of Red-winged Blackbirds, Searcy & Yasukawa (1995) suggested there was no net-cost of polygyny.

The causes of polygyny in the Lapwing

Lapwings, like most waders, produce precocial young which require little intensive parental care, a factor thought to facilitate the evolution of polygamy via reduced costs of desertion (Lack 1968; Emlen & Oring 1977; Oring 1982; Erckmann 1983; Davies 1991; Temrin & Tullberg 1995), and the lesser role of male Lapwings in parental care (see Chapter 4 for a more detailed discussion) results in a propensity for polygyny over polyandry. The tendency in this study for male Lapwings to delay breeding until two years-of-age, coupled with the despotic monopolisation by males of limited breeding habitat (see Chapter 3), may have resulted in an excess of reproductive females (despite unity in the tertiary sex ratio - Chapter 3), again leading to a propensity for polygyny (Murray 1984). However, it is hard to distinguish cause and effect here. Are both the occurrence of polygyny and the low proportion of breeding yearling males the result of limited breeding habitat? (Emlen & Oring 1977) (see General Discussion). According to Wittenberger (1976, 1979), the existence of territorial bachelors suggests that polygyny is due to variation in the abundance of food among territories. That these territorial individuals were but a small proportion of the total number of bachelors, however, lends support to the notion that polygyny was, in this study, due to the despotic monopolisation of limited breeding habitat (Wittenberger 1976, 1979). What is not clear is whether females exercise any choice when deciding which male to settle with (Verner 1964; Verner & Willson 1966; Orians 1969; Wittenberger 1976, 1979), or whether the distribution of females is random within the suitable habitat (Wootton *et al.* 1986; Lightbody & Weatherhead 1987, 1988). The high degree of philopatry and site-fidelity exhibited by Teesdale Lapwings (Thompson *et al.* 1994), and the apparent lack of sampling behaviour noted in this study, suggests that, at most, restricted choice takes place (which applies equally to males establishing a territory). Wootton *et al.* (1986) suggested that site-fidelity (and philopatry) could be the result of choice for a familiar habitat or breeding site which individuals have experienced previously. The mating success of male Lapwings in this study increased with age from yearlings to those three-years-of-age and older, despite high site-fidelity of adult males (Thompson *et al.* 1994). If female choice was occurring, this trend would suggest that territory characteristics were less important in determining the breeding situation quality than male characteristics (also suggested above by the linear increase in territory size with number of resident females), or that all territories in the study area were of sufficiently high quality to negate the need for discrimination. This may also explain why there were no differences in the dates of territory establishment between unpaired, monogamous and polygamous males (if polygyny was associated with high-quality territories, then there would be a premium on early residency). If active female choice does not occur, the trend of increased male mating-success with age could be due to competitive asymmetries among males which result in the despotic monopolisation of females. Taken together, the evidence suggests that polygyny in the Lapwing is primarily the result of competitive asymmetries among males for access to limited breeding habitat, with older males able to maintain larger territories and thereby secure more than one mate. Proof of this would require further detailed study of male and female settling patterns, including the identification and manipulation of territory and male characteristics influencing fitness (see Suggestions for Further Study).

3. The breeding biology of the Lapwing, with particular reference to the influence of age.

3.1. INTRODUCTION

In birds, the age of an individual often influences many aspects of its reproductive life (see reviews in Clutton-Brock 1988a; Newton 1989; Sæther 1990; Forslund & Pärt 1995; Fowler 1995; Martin 1995). Some long-lived birds do not breed in their first year(s) of life, often despite having reached sexual maturity and therefore being capable of breeding. The Procellariiformes provide a variety of examples of delayed breeding, with none breeding at two-years-old, most taking 5-6 years to reach maturity and the Royal *Diomedea epomophora* and Wandering *D. exulans* Albatrosses breeding for the first time at about 11-years of age (Warham 1990). In a review of the age of first breeding for shorebirds, Thompson *et al.* (1994) showed that in the 11 species for which data were available, seven typically bred at one-year-old, with the remainder breeding at two-years-old.

Age also seems to be of importance in mate selection, with many studies reporting a correlation between the ages of paired individuals (Reid 1988): e.g. the Kittiwake Gull *Rissa tridactyla* (Coulson 1966); Sparrowhawk *Accipiter nisus* (Newton *et al.* 1981); Blue-eyed Shag *Phalacrocorax atriceps* (Shaw 1985); Redshank *Tringa totanus* (Thompson & Hale 1991); Marsh Tit *Parus palustris* (Smith 1993) and Barnacle Goose *Branta leucopsis* (Black & Owen 1995).

When a bird breeds several times during its lifetime, within-season breeding performance has often been shown to improve with age, particularly in the early years of life (reviewed by Clutton-Brock 1988a; Newton 1989, 1995; Sæther 1990; Forslund & Pärt 1995; Fowler 1995; Martin 1995): e.g. seabirds: the Kittiwake Gull (Thomas & Coulson 1988); Short-tailed Shearwater (Wooller *et al.* 1990); Great Skua *Catharacta skua* (Hamer & Furness 1991) and Western Gull *Larus occidentalis* (Sydeman *et al.* 1991); song birds: the Collared Flycatcher *Ficedula albicolis* (Gustafsson & Pärt 1990); Blackbird *Terdus merula* (Desrochers & Magrath 1993); Marsh Tit (Smith 1993); Savannah Sparrow *Passerculus sandwichensis* and Tree Swallow *Tachycineta bicolor* (Wheelwright & Schultz 1994); waterfowl: the Lesser Snow Goose *Anser caerulescens* (Rockwell *et al.* 1983; Hamman & Cooke 1987; Rockwell *et al.* 1993; Robertson *et al.* 1994); Coot *Fulica atra* (Perdeck & Cavé 1992) and Barnacle Goose (Forslund & Larsson 1992; Black & Owen 1995); raptors: the Sparrowhawk (Newton *et al.* 1981; Newton 1988). In some species, success also falls again after reaching a peak: e.g. seabirds: the Short-tailed Shearwater (Wooller *et al.* 1990) and Great Skua (Hamer & Furness 1991); song birds: Collared Flycatcher (Gustafsson & Pärt 1990) and Blackbird (Desrochers & Magrath 1993); waterfowl: the Lesser Snow Goose (Rockwell *et al.* 1993) and Barnacle Goose (Black & Owen 1995); raptors: the Sparrowhawk (Newton *et al.* 1981; Newton 1988). Similar age effects have been found in shorebirds: yearling Semipalmated Sandpipers *Calidris pusilla* laid eggs approximately 5% smaller than those of older females, and hatched their eggs, on average, later than experienced females. In one year, significantly fewer yearlings hatched eggs than older females (Gratto *et al.* 1983). Experienced females of the polyandrous

Spotted Sandpiper *Actitis macularia* laid eggs earlier and gained more mates than inexperienced ones, and thereby fledged more chicks (Oring & Lank 1986; Oring *et al.* 1991). Experienced Greenshanks *Tringa nebularia* laid eggs earlier than inexperienced females (Thompson *et al.* 1986), as did experienced Redshank, which also produced larger eggs (Thompson & Hale 1991).

This section describes the breeding biology of the Lapwing, and in particular, how this is influenced by age.

3.2 METHODS

This study was conducted during 1993-95. For a description of the study area, and details regarding the identification and marking of individuals and of census methods, see General Methods.

Breeding behaviour, breeding status (i.e. breeding or not breeding) and mate(s) of ringed individuals were monitored during regular censuses (see General Methods).

The breeding success of female Lapwings was summarised in terms of parameters described in Chapter 2. Nests were located and monitored as also described in Chapter 2. The date of hatching or failure was taken as the mid-point between visits when not recorded directly, or estimated as in Chapter 2. Hatching success was the proportion of clutches laid which produced at least one chick ("traditional" method). Hatching success was also estimated using the Mayfield method (Mayfield 1961; 1975) for comparison. Although this method of calculating nesting success is considered the best means of eliminating biases (Johnson 1979; Willis 1981; Klett & Johnson 1982), inaccuracies can arise when the assumption regarding homogeneity of clutch survival rates is not met (Willis 1981; Klett & Johnson 1982). These assumptions apply equally to any method of calculating hatching success where groups of clutches are pooled. The validity of these assumptions was investigated in 1995 by controlling for season, stage of the incubation period and field. In 1993, the distance from nests to the nearest field boundary was measured. In 1994 and 1995 the location of nests was recorded on an aerial photograph of the study site (scale: 116mm=500m). Both methods allowed the investigation of hatching success in relation to the distance to the field boundary, and thereby the control of another potential confounding variable in hatching success calculations.

All eggs found were measured (length and breadth), and eggs in some nests were weighed, as described in Chapter 2. These measurements were used to calculate shape index (length/breadth) and egg volume, using the equation, volume (cm^3)=0.457 x L (cm) x B^2 (cm), where L=length and B=breadth (Galbraith 1988). This assumes the preceding formula is generally applicable to Lapwings: at worst, measurements will be accurate for relative comparisons.

In order to investigate the roles of heredity and the environment in determining laying dates and egg dimensions, indices of repeatability were calculated (Falconer 1981) using the protocol of Lessells and Boag (1987). Average values from a clutch (4-eggs) were used for egg size.

In 1994, spot observations were used to estimate the spatial use of fields by individuals, whereby the location of each bird was recorded as <10m, 10-20m or >20m from the field boundary when first seen, or during scan samples of whole fields or field sections.

3.3 RESULTS

The proportion of breeders in each age group

In 1993 and 1994, the proportion of individually-ringed Lapwings of different age-classes that were breeding was known for the whole of the study site (Table 3.3.1).

Table 3.3.1. The proportion (% ± standard error) of individually-ringed Lapwings of different age (years) and sex classes present in the study area and which were breeding in 1993 and 1994. Adult=individuals ringed as adults, and therefore of unknown absolute-age (see General Methods). Figures in parentheses are sample sizes (breeders+non-breeders).

		Proportion of breeders aged				
Year	Sex	One	Two	Three	Four	Adult
1993	Male	24±8%	68±6%	44±10%	-	68±7%
		(29)	(38)	(27)		(43)
	Female	67±10%	63±9%	65±8%	-	82±7%
		(24)	(32)	(37)		(34)
1994	Male	42±8%	56±10%	73±8%	46±11%	77±8%
		(43)	(27)	(33)	(22)	(26)
	Female	66±10%	75±10%	86±8%	73±9%	96±4%
		(24)	(20)	(22)	(26)	(27)

Examination of Table 3.3.1 reveals some interesting patterns in the proportion of breeders among age groups and cohorts, and between sexes and years. Each is considered in turn below.

Sex - Overall, 55% of males and 75% of females bred, a highly significant difference (G_1=20.0, P<0.001). This trend was maintained in each age group in both years (Table 3.3.1) with the exception of 2-year-olds in 1993, where it was reversed (although not significantly so). In seven comparisons of each known-age group (three in 1993, four in 1994), a higher proportion of breeding females was found in four of them, the remainder being not significantly different. The difference in the proportion of male and female breeders for those individuals ringed as adults was not significant.

Year - Combining all data and comparing the two years suggests there was no difference in the proportion of breeders between the two years (G_1=2.5, n.s.). However, having demonstrated a difference in the proportion of breeders between sexes and in order to eliminate possible confounding effects of age, it is necessary to analyse each age group and sex separately. Three-year-old males had proportionately more breeders in 1994 than 1993 (G_1=5.0, P<0.05). No other groups showed significant differences, although Figures 3.3.1 and 3.3.2 (illustrations of the proportions of breeders from Table 3.3.1) suggest there is generally greater variation in the proportion of breeders between years for males than for females.

Age - In both years there was a significant association between age and the proportion of breeders, but only for males (1993: G_2=13.7, P<0.01; 1994: G_3=7.9, P<0.05). Table 3.3.1 suggests this is due to more non-breeders than breeders in the youngest and oldest (3-years-old in 1993, 4-years-old in 1994) age categories, with the reverse pattern in the middle age-groups. It is notable that the “adults” in Table 3.3.1 have the highest proportion of breeders. These were individuals caught after having successfully established or settled on a territory (see the consideration of cohort effects below).

Cohort - This analysis compared the proportion of breeders within the same group of individuals in different years (i.e. shows the effect of an increment in age of one year on the same individuals). For those Lapwings ringed in 1990 (aged three and four years in 1993 and 1994 respectively) and those ringed in 1991 (two- and three-years-old respectively), there were no significant differences in the proportion of breeders between years (i.e. no effect of an increase in age of one year), for both sexes. Not only was the proportion of breeders consistent between years for the 1990 cohort, but the males showed a remarkably low percentage of breeders compared with the other male age groups. The cohort ringed in 1992, however, showed a 30% increase in the proportion of breeding males between 1993 and 1994 (i.e. from one- to two-years-old), though not in females (males: $G_1=6.4$, $P<0.02$; females: $G_1=0.4$, n.s.). The data suggest there is greater variation in the proportion of breeders within cohorts (i.e. between years) among females, with males two years and older showing a greater degree of consistency from one year to the next (Figures 3.3.3 & 3.3.4).

Figure 3.3.1. Proportion of ringed male Lapwings breeding in the study area in each age group in 1993 and 1994.

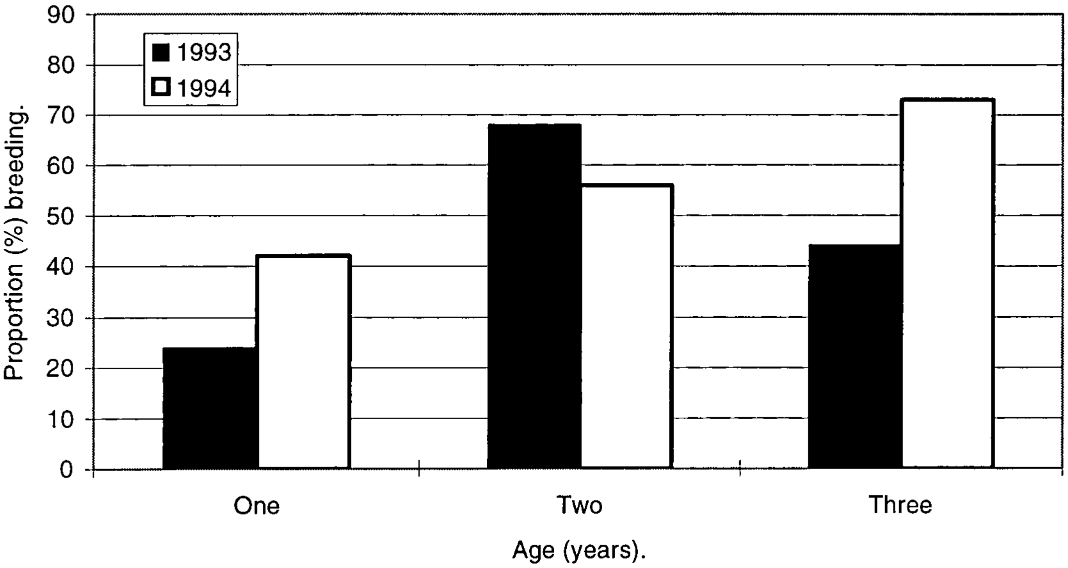


Figure 3.3.2. Proportion of ringed female Lapwings breeding in the study area in each age group in 1993 and 1994.

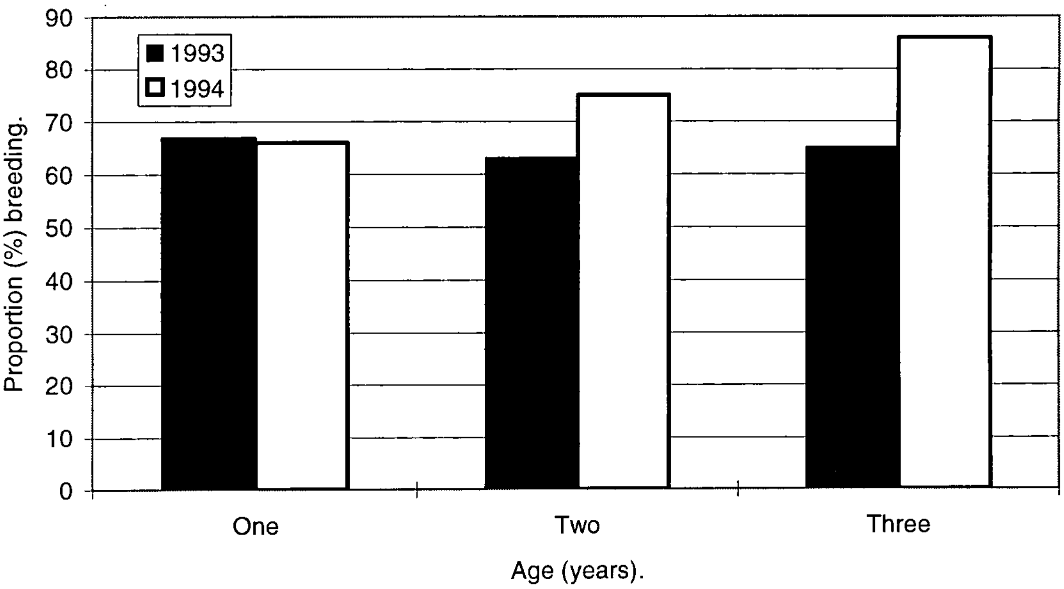


Figure 3.3.3. Proportion of ringed male Lapwings breeding in the study area in 1993 and 1994, from cohorts ringed in 1990, 1991 and 1992.

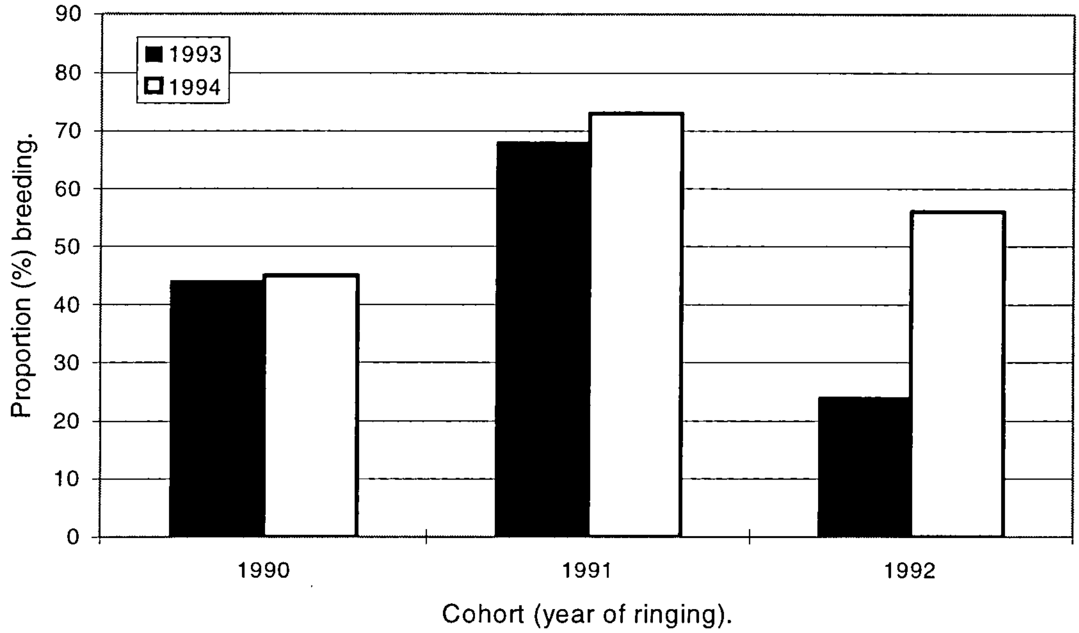
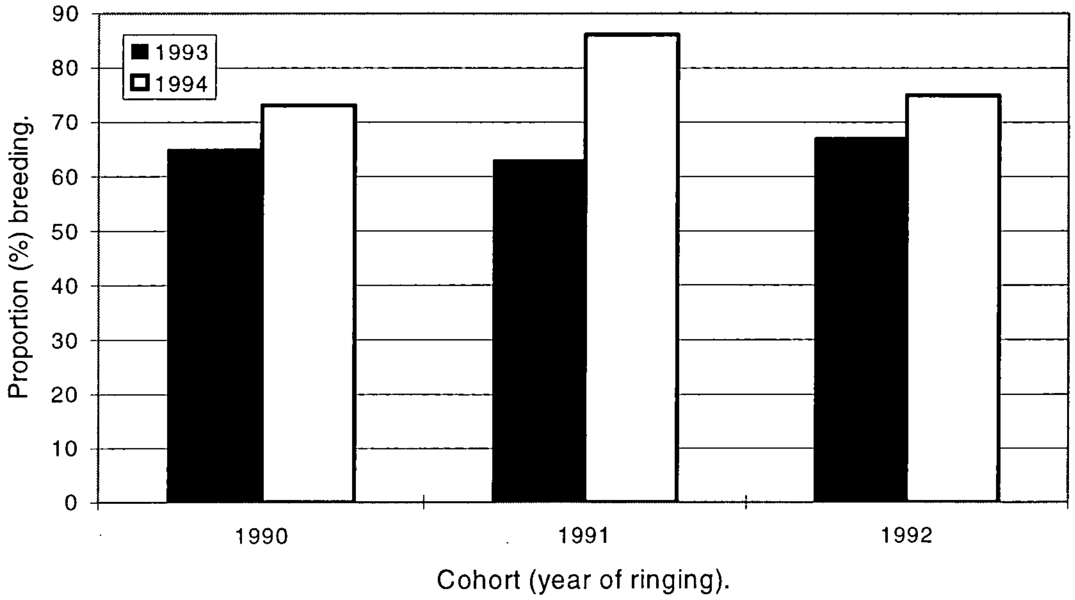


Figure 3.3.4. Proportion of ringed female Lapwings breeding in the study area in 1993 and 1994, from cohorts ringed in 1990, 1991 and 1992.



Further consideration will be given below to the effect of sex and cohort on the proportion of breeders.

Sex - Consistently greater proportions of female Lapwings bred each year than males. The rates of philopatry and survival of Lapwings do not differ between the sexes, at all ages (Thompson *et al.* 1994; P.S. Thompson, pers. comm.) and so cannot have caused this pattern. Here, the following possibilities were investigated: 1) that a skewed sex-ratio in the whole population resulted in more males than females, 2) that polygynous males, that bred with more than one female, account for the extra breeding females. If the first possibility was the sole cause of the discrepancy in the proportion of breeders between the sexes, the sex ratio of the whole population of Lapwings on the study site would be male-biased (more than one male per female), whilst that among breeding Lapwings would be equal. Conversely, if polygyny was the cause, the sex ratio of the whole population would be equal but that for breeders would be unequal (in this case more than one female per male).

Table 3.3.2 shows the sex ratio of Lapwings in the study population in Upper Teesdale, in relation to age. The sex ratio for ringed Lapwings does not differ significantly from equality (all categories), although there is an excess of males overall in both years (Table 3.3.2). However, these data refer to ringed Lapwings. In order to confirm that the sex ratio of ringed Lapwings reflects that of those that are unringed, census data for 1994 from the intensive site were broken down into the numbers of ringed and unringed Lapwings seen each fortnight throughout the season. Each two-week period was analysed separately, comparing the ratio of ringed and unringed Lapwings, for both males and females (Table 3.3.3).

Table 3.3.2. The sex ratio (females per male - F/M) of individually-ringed Lapwings in the whole study population in Upper Teesdale, in relation to age (years). Adult=individuals ringed as adults (unknown absolute-age - see General Methods). Total=no. of individuals of each sex when all categories are combined. G_1=two-sample test for homogeneity - all n.s.

		No. of individuals			
Year	Age (years)	Female	Male	Ratio (F/M)	G_1
1993	One	24	29	0.83	0.5
	Two	32	38	0.84	0.5
	Three	37	27	1.37	1.6
	Adult	34	44	0.77	1.3
	Total	127	138	0.92	0.5
1994	One	35	43	0.81	0.8
	Two	20	27	0.74	1.1
	Three	22	33	0.67	2.2
	Four	26	22	1.18	0.4
	Adult	27	26	1.04	0.0
	Total	130	151	0.86	1.6

Table 3.3.3. The ratio of ringed to unringed Lapwings (R/U) on the intensive site, 1994. Period one=1-15 April; two=16-30 April; Three=1-15 May; Four=16-31 May; Five=1-15 June. Overall=the whole sample period. G_1=test of association (2x2 contingency table) between sex and ringed status (ringed or unringed) for each age group - all n.s.

	No. of individuals						
	Male			Female			
Period	Ringed	Unringed	Ratio (R/U)	Ringed	Unringed	Ratio (R/U)	G_1
One	61	49	1.24	41	42	1.02	0.7
Two	46	26	1.77	40	29	1.38	0.6
Three	65	49	1.33	63	59	1.07	0.7
Four	56	30	1.87	55	46	1.20	2.3
Five	30	21	1.43	30	26	1.15	0.3
Overall	258	175	1.47	229	202	1.13	3.7

All of the tests for an association between sex and ringed status (ringed or unringed) in Table 3.3.3 were not significant. Thus, the sex ratio of individually ringed Lapwings (shown in Table 3.3.2) can reliably be used in reference to all Lapwings on the study site. Therefore, it is reasonable to conclude that the sex ratio of Lapwings on the study site does not differ significantly from equality, rejecting the possibility that a skewed sex ratio was the cause of the discrepancy between the proportion of male and female breeders. However, although not significant, there is the suggestion in Table 3.3.3 of a lower ratio of ringed to unringed females than males in the study area. This may indicate a difference in the degree of emigration between the sexes (more ringed females leaving the area than males, to be replaced by unringed immigrants). This cannot be pursued further in this study, but if true could also help explain the discrepancy in the proportion of breeders between ringed male and female Lapwings.

Data in Chapter 2 show that many breeding males were polygynous during the period of study. This is reflected in the sex ratio of breeding birds, as previously predicted (Table 3.3.4). In six out of nine age groups, and overall in both years, breeding females outnumber breeding males, with up to 2.3 females for each male (Table 3.3.4). However, this is significant only for 3-year-olds in 1993, although the probability of obtaining the sex ratio for yearlings in 1993 and for 4-year-olds in 1994 by chance was less than 0.1. Therefore, it seems likely that the discrepancy in the proportions of male and female breeders was caused by some males breeding with more than one female.

Table 3.3.4. The sex ratio (females per male - F/M) for breeding, individually-ringed Lapwings in relation to age (years). Adult=individuals ringed as adults (unknown absolute-age - see General Methods). Total=all categories combined. G_1=test for homogeneity.

		No. of individuals			
Year	Age (years)	Female	Male	Ratio (F/M)	G_1
1993	One	16	7	2.29	3.5
	Two	21	26	0.81	0.5
	Three	25	12	2.08	4.6*
	Adult	28	27	1.04	0.0
	Total	90	72	1.25	2.0
1994	One	24	19	1.26	0.6
	Two	15	15	1.00	0.0
	Three	19	24	0.79	0.6
	Four	20	10	2.00	3.4
	Adult	26	20	1.3	0.8
	Total	104	88	1.18	1.3

Statistical significance: * $P<0.05$.

Cohort - The remarkable consistency in the proportion of breeders occurring within cohorts in subsequent years can be investigated further by comparing the breeding status of individually-ringed Lapwings found on the study site in both years of study (Table 3.3.5). Yearlings are excluded from this analysis as they tend to change status between years (particularly males, Fig. 3.3.3).

Table 3.3.5. Comparison of the breeding status of individually-ringed Lapwings seen on the study site in 1993 and 1994, except for yearlings. Data are proportions (%) ± 1 standard error.

		Proportion in 1994 that were	
Sex	Status in 1993	Breeding	Non-breeding
Male	Breeding (n=46)	78±6%	22±6%
	Non-breeding (n=18)	39±10%	61±10%
Female	Breeding (n=50)	94±3%	6±3%
	Non-breeding (n=12)	50±15%	50±15%

In both sexes there was a significant association between breeding status in 1993 and that in 1994 (males: G_1=8.5, P<0.01; females: G_1=11.0, P<0.001): i.e. both sexes tended to maintain their status between years, even where this was non-breeding. There were some differences here between the sexes, with male breeders in 1993 being more likely to become non-breeders in 1994, than breeding females (G_1=5.3, P<0.05), although non-breeding males were no more likely to remain non-breeders than non-breeding females (G_1=0.3, n.s.). This also explains why the “adults” in Table 3.3.1 had the highest proportion of breeders: these birds were caught as breeding adults and then maintained their status thereafter.

The age difference within pairs

In total, 74 pairs in which both individuals were individually ringed were observed between 1992 and 1995 and, in 39 pairs, both individuals were also of known age (the remainder having at least one individual ringed as an adult, and therefore of unknown absolute-age). Data from 1992, and some from 1993 and 1994, were collected by P.S. Thompson. Table 3.3.6 shows the frequencies of age combinations from 33 known-age pairs (discounting repeat sightings of the same pair in more than one year) at the time of pair formation, or when first recorded. 39% of the pairs in Table 3.3.6 include individuals of equal age: 67% are of equal age, or differ by one year. In 15 pairs (45%) the male is older than the female, whereas in only 5 pairs (15%) the female is older than the male. The difference in age within pairs (male age – female age) varied from -3 to 2 years, with a mean (±S.D.) of 0.4 ±1.3 years. However, the limited range of known ages present in this study prevents greater differences occurring. Thus, most individuals were of a similar age to their mate, but where one was older than the other, this was usually the male (sign test, $P<0.05$).

Table 3.3.6 suggests that many adult male Lapwings take yearling females as mates, with yearling males pairing only with yearling females. In all, 33% of pairs were between adult males and yearling females. No adult females paired with yearling males. This pattern deviates significantly from random ($G_1=6.9$, $P<0.01$).

Table 3.3.6. Frequencies of age combinations from 33 known-age pairs of Lapwings at the time of formation, or when first recorded, from 1992-95. Shaded squares indicate pairs of equal age.

		Age of male (Years)						
		One	Two	Three	Four	Five	Six	Seven
Age of female (Years)	One	4	5	6				
	Two		5	2	1			
	Three		1	4				
	Four		2	1				
	Five		1					1

Nest-site selection in relation to field boundaries

The position of 216 nests was recorded between 1993-95 in relation to the distance to the field boundary (dry-stone wall or fence). The distribution of nests was not significantly different between years (G_4=4.0, n.s.). There was a strong avoidance of the field edge during nest-site selection (Table 3.3.7). The fields studied ranged in size from 4.1-12.5ha. Thus, between 22% and 66% of the fields was avoided by nesting Lapwings.

Table 3.3.7. The spatial distribution of Lapwing nests in relation to the distance from the field boundary (dry-stone wall or fence), 1993-95. Expected values calculated on the basis of area.

	Distance from field boundary			
	<10m	10-20m	>20m	
Nests found	4	10	202	G_2=57.7,
Nests expected	28.5	27.2	160.2	*P*<0.001
Percent of expected nests found	14%	37%	126%	

This is reflected in a general avoidance of the field edge by individual Lapwings during the breeding season (Table 3.3.8).

Table 3.3.8. The spatial distribution of individual Lapwings during the breeding season, estimated from spot observations in 1994. Expected values calculated on the basis of area.

	Distance from field boundary			
	<10m	10-20m	>20m	
Birds seen	28	70	588	G_2=96.7,
Birds expected	99.4	94.9	491.7	*P*<0.001
Percent of expected seen	28%	74%	120%	

The date of laying, clutch size, egg volume and hatching success of first clutches

Only the effect of female age is considered here. Given the tendency demonstrated above for individuals of similar age to pair together, it would be impossible to separate the effects of the two sexes without large numbers of pairs in which both individuals were of known-age. Up to 31 such pairs were available for each section of the analysis. Due to the incomplete nature of information from some clutches and the inclusion of unringed females in certain analyses, sample sizes vary throughout this section.

Multiple regression analyses have been used in the following sections (but see *clutch size*) in order to statistically control confounding variables. The regression slope is given ± 1 standard error (S.E.).

Date of laying - The date on which the first egg was laid is used as a measure of timing of the breeding attempt. There were no differences in laying dates between years (one-way-ANOVA, $F_{2,99}$=0.8, n.s.), so data from 1993-95 have been pooled (Figure 3.3.5). Lapwing first clutches were laid with a high degree of synchrony: mean laying date (1993-95)=8 April ±6 days (S.D.). Figure 3.3.6 shows laying dates in relation to female age. This suggests a trend, with mean laying dates of two-year-olds being slightly earlier than those of younger and older females, although the maximum difference is only 4-5 days. A one-way-ANOVA shows this is not statistically significant ($F_{5,63}$=1.3, n.s.), and a t-test comparing laying dates of yearlings with those of all adult females combined, shows an insignificant difference using a two-tailed test (t_{67}=1.7, n.s.), although this is significant when applying one-tailed assumptions (i.e. that yearling females will lay later than older females). Using multiple regression analyses to control for differences between fields, shows that neither female age nor field affect laying date (model fit: r^2=0.00, $F_{2,55}$=0.0, n.s.). This conclusion is not altered when substituting relative female-age (i.e. yearling or adult) for absolute female age (r^2=0.02, $F_{2,55}$=0.6, n.s.).

Figure 3.3.5. Laying dates (days from 1 January) for 100 first-clutches of individually-ringed Lapwings, 1993-95.

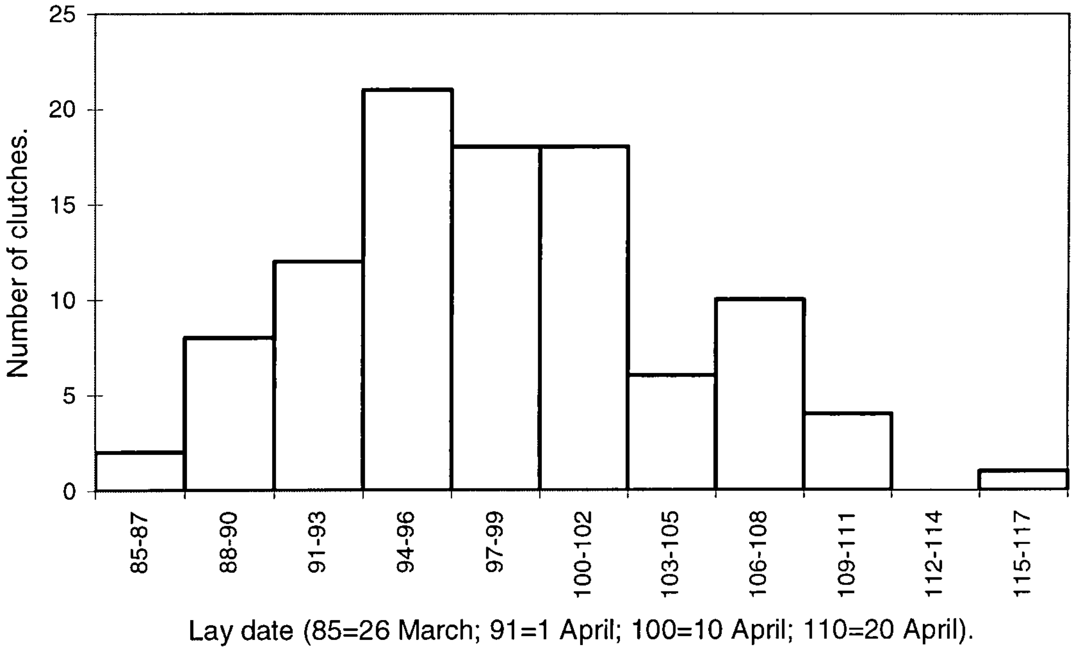
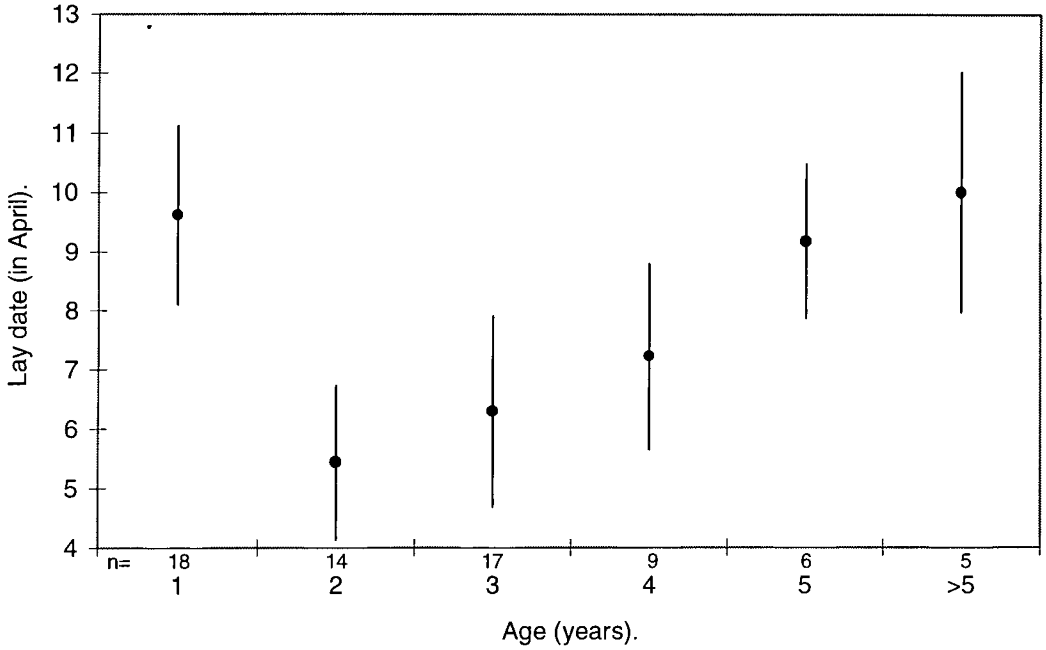
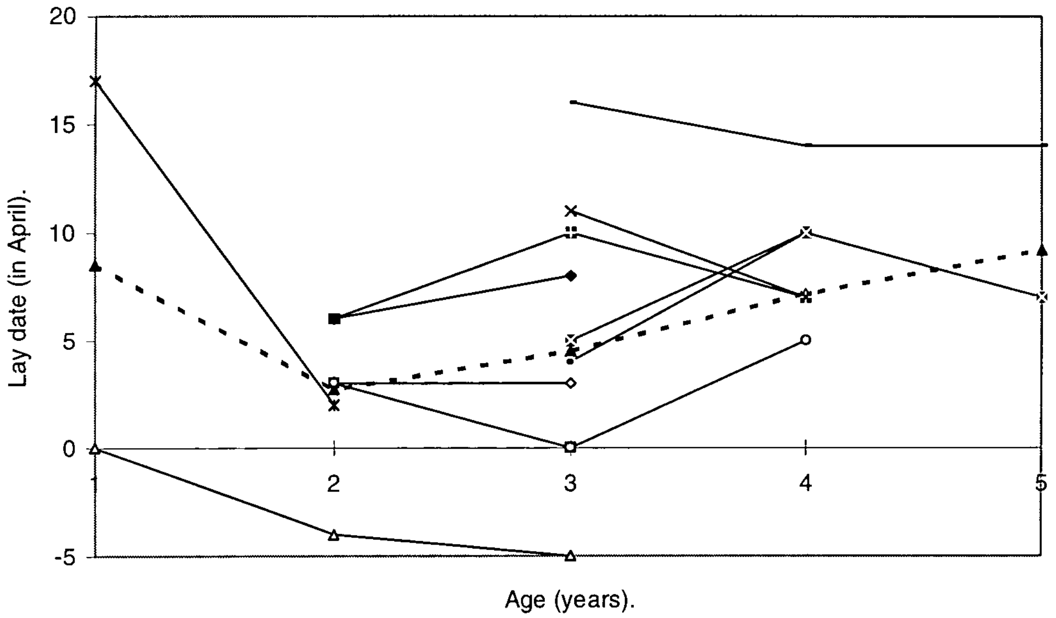


Figure 3.3.6. Mean (±S.E.) laying dates (days in April) for known-age female Lapwings, 1993-95. Sample sizes are below the X-axis. The >5-year-old category includes females ringed as adults - see General Methods.



That female age does not influence first-clutch laying dates is supported by the findings from 13 individual females whose laying dates were known in more than one year (all bred in the same field: change of mate cannot be controlled in this instance due to the prevalence of unringed males) (Figure 3.3.7). This shows that much of the apparent variation between ages suggested by the trend line is caused by differences between females. A one-way-ANOVA, conducted on the data from the 13 individuals monitored during more than one year, suggests there is no difference in laying dates in subsequent years, whilst significant differences do occur between individual females (69% of variation in laying dates explained by between-female differences: $F_{12,19}=3.5$, $P<0.01$). Thus, there is no firm evidence to suggest that age of females influences the date of laying for the first clutch. Rather, the data suggest a degree of synchrony between all individuals, and consistency of laying date between years for individuals. Moreover, the index of repeatability (see methods) was 0.5, reiterating this point.

Figure 3.3.7. Laying dates for 11 known-age female Lapwings seen in more than one year (consecutively). The bold, dotted line shows the mean laying date at each age (includes data from the two extra females not shown individually, that were present in non-consecutive years). Dates are days in April.



Clutch size - Clutch size was taken as the maximum number of eggs found in a nest, and was known for 106 first-clutches of ringed females. This definition does not exclude the possibility that some clutch sizes were the result of partial losses occurring before the nest was found. Overall, 86% of first-clutches contained four eggs. Table 3.3.9 shows the frequency of clutch sizes during the three years of study, and Table 3.3.10 shows the frequency of clutch sizes for females of different ages.

Table 3.3.9. Clutch-size frequencies for individually-ringed female Lapwings in each year of study. All age groups combined. Figures in parentheses express the frequency of each clutch size as a percentage of the total for that year.

		Frequencies of the following clutch sizes				
	Total	Two	Three	Four	Five	Mean
1993	35	1 (3%)	6 (17%)	27 (77%)	1 (3%)	3.80
1994	33	0	6 (18%)	27 (82%)	0	3.82
1995	38	0	1 (3%)	37 (97%)	0	3.97

Table 3.3.10. Frequencies of clutch sizes for female Lapwings of known ages. Adult=females ringed as adults (unknown absolute-age - see General Methods). Data pooled for 1993-95.

		Frequencies of the following clutch sizes				
Age (years)	Total	Two	Three	Four	Five	Mean
One	22	1	4	17	0	3.73
Two	17	0	1	16	0	3.94
Three	17	0	5	11	1	3.76
Four	10	0	1	9	0	3.90
Five	7	0	0	7	0	4.00
Adult	33	0	2	31	0	3.94

There was no significant difference in clutch size between years (G_6= 11.0, n.s.) or between age groups (G_{15}=15.6, n.s.).

Egg size - Egg length and breadth measurements were taken from a total of 148 clutches between 1992 and 1995, from which a shape index (length/breadth) and egg volume were calculated. Variation in egg size was greater between the clutches of different females than within (Table 3.3.11), so the average value for the clutch was used in all analyses.

Table 3.3.11. Variation in egg biometrics between and within first clutches of four eggs, 1992-95, estimated from 1-way-ANOVAs. Data from 5, 40, 31 and 72 clutches of four eggs only.

	Percent of total variation in egg size due to differences between females, with F-ratio							
	Breadth		Length		Shape index		Volume	
Year	%	F	%	F	%	F	%	F
1992 d.f.=4,15	49%	3.6*	84%	19.3****	62%	6.0***	87%	26.2****
1993 d.f.=39,120	64%	5.4****	51%	3.2****	62%	4.9****	54%	3.6****
1994 d.f.=30,93	69%	6.8****	62%	5.0****	60%	4.7****	69%	7.0****
1995 d.f.=71,216	80%	12.4****	63%	5.2****	62%	5.0****	80%	12.4****
Total d.f.=147,444	73%	8.5****	62%	4.8****	62%	4.8****	72%	7.9****

*$P<0.05$; **$P<0.02$; ***$P<0.01$; ****$P<0.001$.

None of the variables differed significantly between years (one-way-ANOVA: all $F_{3,146}<1.1$, n.s.), but egg length and shape index varied among fields ($F_{8,103}=2.6$, $P<0.02$ and $F_{8,103}=2.6$, $P<0.02$ respectively). Thus, in the following analyses data regarding egg biometrics are pooled for different years and clutch sizes, but the breeding field is statistically controlled. Table 3.3.12 shows the mean for each variable in relation to female age.

Table 3.3.12. Mean, with standard error (S.E.), egg biometrics (length, breadth, shape index [length/breadth] and volume) in relation to age of female Lapwings (known age only), 1992-95.

	Length (cm)		Breadth (cm)		Shape index		Volume (cm^3)	
Age (years)	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
One (n=33)	4.62	0.25	3.00	0.10	1.40	0.01	22.98	0.19
Two (n=23)	4.66	0.24	3.36	0.14	1.39	0.01	24.12	0.24
Three (n=23)	4.67	0.27	3.35	0.14	1.39	0.01	23.92	0.28
Four (n=13)	4.66	0.33	3.36	0.24	1.38	0.01	24.03	0.43
Five (n=8)	4.66	0.45	3.36	0.34	1.39	0.01	24.09	0.64

All the multiple regression analyses in the following section were conducted using female age and field as independent variables. Female age is investigated in two ways: first actual age is used and then relative age (adult or yearling). The results are summarised in Table 3.3.13. Both regression models show that increasing female age results in increases in egg breadth and volume (Table 3.3.13). It is not surprising that differences in egg breadth translate into differences in egg volume, as volume is proportional to the square of egg breadth. Table 3.3.13 does not elucidate the relative roles of actual and relative female age on egg dimensions, but Figure 3.3.8 suggests that relative age was the primary factor influencing egg size.

Figure 3.3.8. Mean (± I standard error) egg volumes for female Lapwings of known age, 1992-95. Sample sizes are shown above the X-axis.

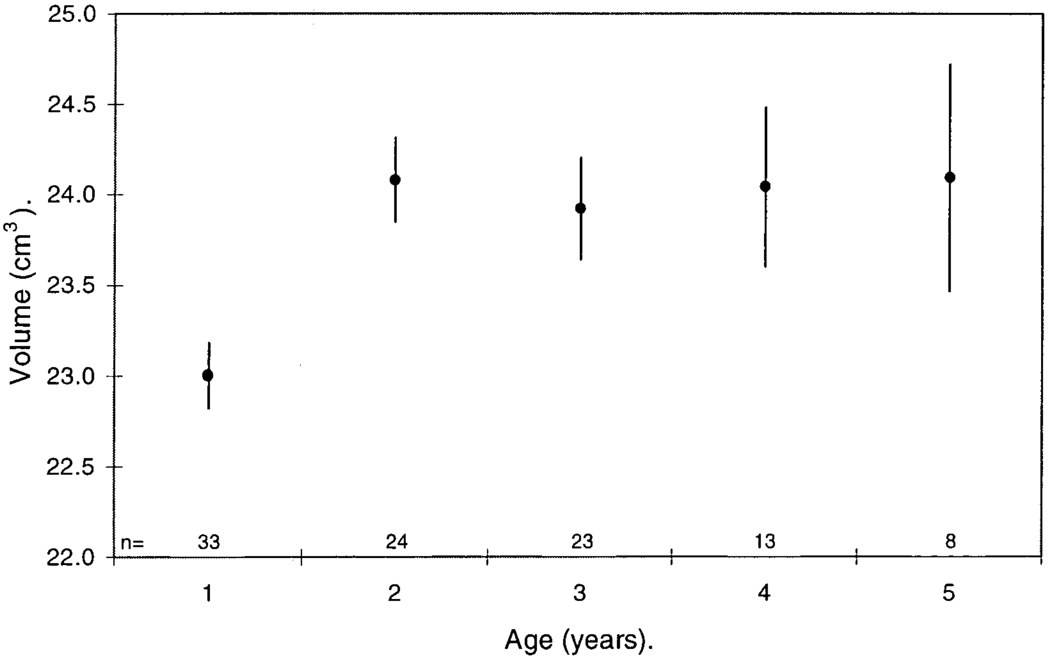


Table 3.3.13. Summary of multiple regression analyses (slope [b] ± 1 standard error [S.E.]), with egg length, breadth, shape index (length/breadth) and volume as dependent variables, and female age (model 1 only), relative female age (yearling or adult) (model 2 only) and field entered as independent variables. n.s.=no significant variables. Data from 1992-95, Lapwings of unknown absolute-age included in model 2 only.

	Regression coefficient (b ±S.E.) for significant variables	
	Model 1 (n=100)	Model 2 (n=143)
Length	n.s.	n.s.
Breadth	Female age: 0.16±0.06***	Relative age:0.68±0.15***
Shape	n.s.	n.s.
Volume	Female age: 0.28±0.11***	Relative age: 1.20±0.27***

Significance level: * *P*<0.05; ** *P*<0.02; *** *P*<0.01.

The mean volume for eggs laid by all adult females (including those of unknown absolute-age) was 24.19 ± 0.13cm^3 (n=110), 5% greater than that for yearlings: mean=22.98 ± 0.19cm^3 (n=33) (t_{141}=5.4, *P*<0.001). The trend for egg breadth and female age was similar to that in Figure 3.3.8.

Once again, some females for whom egg volumes were calculated (n=33) were present in more than one year. Therefore, the effect of age increases on egg volume can be examined longitudinally. There was a significant 5.5% increase in egg volume for individual female Lapwings between yearling and adult status (adult volume taken at 2-years-old if known, for two females adult volume was taken at 3-years-old) (n=7): paired t-test, $t_6=7.0$, $P<0.001$. Consistent with the situation found for laying dates, there was a high degree of consistency in egg size within older females. One-way-ANOVAs showed that 83% of the variation in egg breadth, length and volume between years was the result of among-female differences ($F_{32,48}>7.3$, $P<0.001$). Given the similarity between the ANOVAs for the different egg-size parameters, the index of repeatability (see methods) was calculated only for egg volume. This was found to be 0.72, but increased to 0.76 when between-year differences were considered only for females greater than 1-year-old. Thus much variation exists in egg size between similarly aged older females, but older individuals lay eggs of a similar size in successive years.

To test whether the difference in egg volume between adults and yearlings was due to breeding experience or age, the average volume of eggs laid by two-year-olds breeding for the first or second time were compared. Mean volume for inexperienced 2-year-olds=23.85 ±0.31cm^3 (n=3); experienced= 24.07 ±0.41cm^3 (n=6), an insignificant difference (Mann Whitney-U test: Z=0.65, n.s.). This suggests the difference in egg volume noted previously was due to the difference in age rather than experience. However, this analysis is impaired by the small sample sizes.

Hatching success - There were no differences in the estimates of hatching success (% clutches producing at least one chick) between the traditional and Mayfield methods: in all comparisons (Wilcoxon signed-ranks test) Z<1.6, n.s., with the biggest difference between estimates being just 8%. This suggests that the sample of clutches from which the traditional estimate of hatching success was calculated, was not biased towards successful clutches (Mayfield 1961, 1975). Thus, the methods are used interchangeably, employing whichever is most appropriate (see text). Mayfield confidence intervals and statistical tests are from Johnson (1979) and Hensler and Nichols (1981).

There are important assumptions which are normally made when calculating hatching success (using the Mayfield and other methods), which should be tested here before examining age differences between females. The basic assumption is that hatching success is constant throughout space and time (e.g. across a study site, throughout the breeding season and the breeding cycle). These assumptions are rarely tested. In this study, more of the appropriate data necessary for the calculation of nest survival rates were collected from a larger sample of nests (n=102) in 1995 than in the previous two years (e.g. laying dates assessed through egg-density measurements, nests of unringed Lapwings included), thus allowing the validity of the above assumptions to be tested.

On average, the proportion of clutches giving rise to at least one chick was significantly lower in 1995 than in the preceding two years (Table 3.3.14). Thus, 1995 will be treated separately from here on.

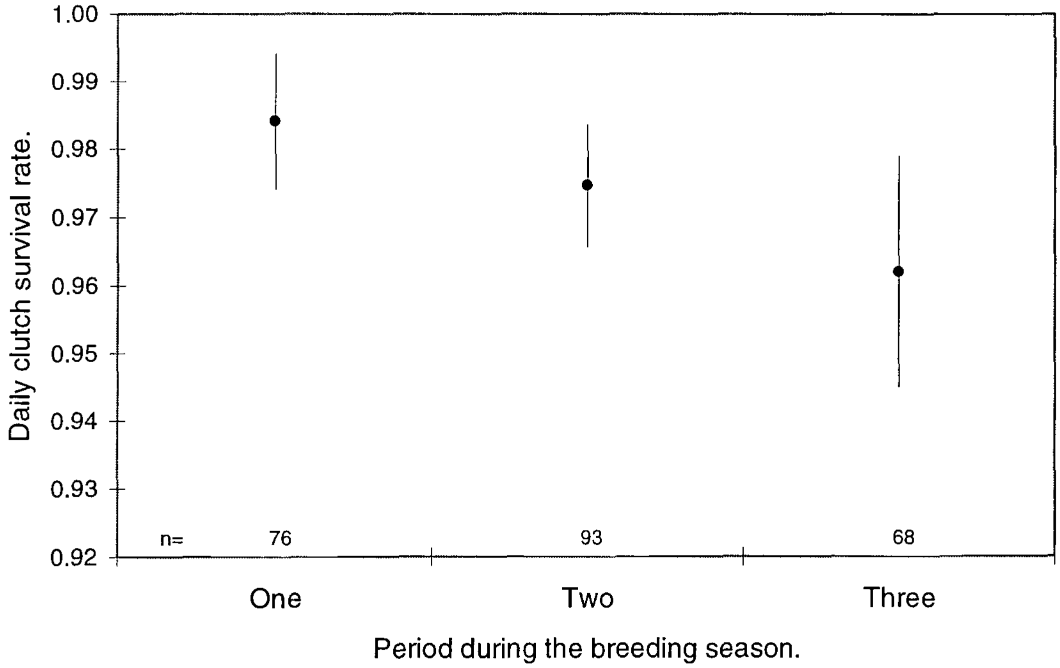
Table 3.3.14. Hatching success of Lapwing first-clutches during 1993-95. Includes unringed females and those of unknown absolute-age. Figures in parentheses are the proportion of clutches producing at least one chick.

	Number of clutches			
Clutch outcome	1993	1994	1995	Total
Hatch	25 (68%)	25 (71%)	49 (48%)	99 (57%)
Fail	12	10	53	75
Total	37	35	102	174

Association between hatching success and year: G_2=8.2, *P*<0.02.

In order to investigate intra-year variation in hatching success with time, the 1995 breeding season was divided into three periods (1-15 April, 16-30 April and 1-31 May) and Mayfield survival rates for clutches during each period were compared (Figure 3.3.10). The Mayfield method was used here to give an estimate of the likelihood of a clutch surviving from one period to the next. Many clutches appear in more than one period. As there is no allowance for multiple statistical comparisons with this method (Johnson 1979; Hensler & Nichols 1981), 95% confidence intervals are shown to facilitate the comparison of periods. The differences in clutch survival rate between periods illustrated in Figure 3.3.10 were analysed using pairwise comparisons (Johnson 1979; Hensler & Nichols 1981). Only periods one and three demonstrated a statistically significant difference (t=2.1, *P*<0.05).

Figure 3.3.10. Daily clutch survival rates in relation to the time of season, 1995. Period one=1-15 April; two=16-30 April; three=1-31 May. 95% confidence intervals are shown to aid the comparison of periods. Sample sizes (n) are the number of clutches included in each period. Most clutches were present in more than one period.



The effect of changing survival rates during the 1995 breeding season was reflected in the survival rates of clutches through the "egg cycle" (=egg laying + incubation), in those nests for which the date of laying of the first egg was known (Figure 3.3.11). Again, 95% confidence intervals are given to aid the comparison of periods.

Figure 3.3.11. Daily clutch survival rates (±95% confidence interval) for different periods of the egg cycle (egg laying + incubation) in 1995. Period 1=1-8 days after commencement of egg laying; 2=9-16 days; 3=17-24 days; 4=25 days-end of egg cycle. Sample sizes (n) are the number of nests in each period (most clutches were included in more than one).

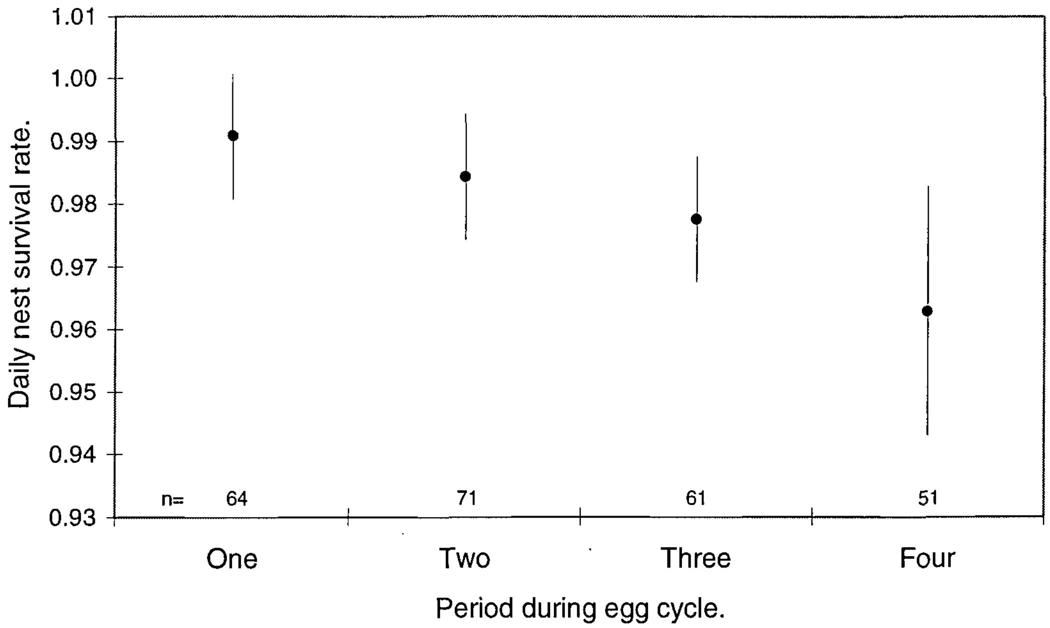


Figure 3.3.11 suggests periods one and four of the egg cycle show significantly different clutch survival rates. This was supported by pairwise comparisons (Johnson 1979; Hensler & Nichols 1981): t=2.19, *P*<0.05. No other combinations were significantly different.

Significant variation in hatching success was also found on a spatial scale (between fields) in 1995, with a low success rate in fields 35, 74 and 76, and higher rates in fields 20, 34 and 65 (Table 3.3.15).

Table 3.3.15. Hatching success of Lapwing clutches in relation to the field in which they were laid (no. 20-76), 1995. Figures in parentheses are the proportion of clutches producing at least one chick.

Clutch outcome	Number of clutches in field no.							
	20	34	35	36	65	74	76	Total
Hatch	8	17	5	7	7	1	4	49
	(62%)	(65%)	(31%)	(47%)	(70%)	(14%)	(27%)	(48%)
Fail	5	9	11	8	3	6	11	53
Total	13	26	16	15	10	7	15	102

Association between hatching success and field: $G_6=14.3$, $P<0.05$.

Even on a smaller spatial scale, variation in hatching success may exist. For example, the proximity of the field boundary (e.g. fence or dry-stone wall) may be important. Indeed, in 1995 (the year with the lowest overall success rate), 28% fewer of these clutches laid within 25m of the field boundary, hatched at least one chick compared to those laid further away (Table 3.3.16). Note, different distance classes were used here to those in Tables 3.3.7 and 3.3.8 because too few clutches were present in the categories nearest the boundaries to analyse.

From the preceding section it is clear that the assumption of homogeneity in hatching success (both temporal and spatial) is not valid in this case. However, most of the problems this raises were overcome for the investigation of hatching success in relation to female age. Variation in hatching success with the time of season was not important due to the synchrony in laying dates noted above: females of all ages were likely to be experiencing similar conditions. Likewise, the low success rate of clutches laid close to field boundaries in 1995 could be ignored as this applies to only 12% of all clutches. The greatest problem arose from the variation in hatching success between fields: insufficient numbers of females from each age group nested in each field to allow the independent analysis of fields, so data from all fields have been pooled.

Table 3.3.16. Hatching success of Lapwing clutches in relation to the proximity of the field boundary (fence or dry-stone wall). Figures in parentheses are the proportion of clutches hatching.

	Clutch outcome	Number of clutches		
		≤25m	>25m	Total
1993 & 1994	Hatch	9 (69%)	31 (70%)	40 (70%)
	Fail	4	13	17
	Total	13	44	57
1995	Hatch	4 (25%)	42 (53%)	46 (48%)
	Fail	12	38	50
	Total	16	80	96

Association between hatching success and proximity to the field boundary: 1993 & 1994: $G_1=0.1$, n.s.; 1995: $G_1=4.2$, $P<0.05$.

Bearing in mind the above caveat, Table 3.3.17 suggests there was no variation in hatching success with female age (with clutches from different fields pooled). This result holds when yearlings, two-year-olds and older females are compared, and when yearling and all older females are compared. It is also unaffected by the pooling of all three years (G_4=3.3, n.s.).

Table 3.3.17. Hatching success of Lapwing clutches in relation to female age (individuals of known age only). Figures in parentheses are the proportion (%) of successful clutches.

	Clutch	Number of clutches for females aged						
	outcome	One	Two	Three	Four	Five	Adult	Total
1993	Hatch	9 (60%)	7 (70%)	10 (77%)	3 (60%)	-	21 (72%)	50 (69%)
& '94	Fail	6	3	3	2		8	22
	Total	15	10	13	5		29	72
1995	Hatch	3 (30%)	4 (44%)	1 (33%)	4 (80%)	6 (75%)	4 (36%)	22 (48%)
	Fail	7	5	2	1	2	7	24
	Total	10	9	3	5	8	11	46

Association between hatching success and absolute female age: 1993 and 1994: G_3=0.9, n.s.; 1995: G_4=6.1, n.s.

Fledging success - Fledging success was measured as described in Chapter 2: the proportion of hatched chicks which subsequently fledged provided a measure of success independent of that to hatching; the number of chicks produced per clutch laid (including clutches which did not hatch) provides a composite measure of hatching and fledging success, and an estimate of total productivity. For all samples, distributions were significantly, positively skewed. All samples were also resistant to transformation.

Therefore non-parametric statistics were used and summaries presented as medians with inter-quartile ranges. Mean values have been reported too in order to allow comparisons of productivity with previous studies. There was no variation between years in either measure of fledging success (Kruskal-Wallis one-way-ANOVA: proportion of hatched-chicks fledging: χ^2_2=0.7, n.s.; number of chicks fledging: χ^2_2= 2.3, n.s.), so data were pooled. The proportion of hatched-chicks which fledged and the number of chicks fledged did not differ between females of different ages (Table 3.3.18). This result held when comparing yearlings and two-year-olds with older females, and when comparing yearlings with all older females (including a one-tailed test).

Table 3.3.18. The median proportion (%) of successfully-hatched chicks which subsequently fledged per brood (P), and the median (and mean) number of chicks fledging per clutch laid (No.), in relation to the age of female Lapwings: first clutches only, 1993-95. Adult=individuals of unknown absolute age (see General Methods). I.R.=Inter-quartile range. Figures in parentheses are the number of females.

		Fledging success for females aged					
		One	Two	Three	Four	Five	Adult
P	Median	0% (14)	0% (15)	13% (16)	13% (6)	25% (5)	25% (32)
	I.R.	0-50	0-33	0-94	0-100	0-63	0-66
No.	Median	0.0 (15)	0.0 (15)	1.0 (17)	1.0 (7)	1.0 (5)	1.0 (33)
	I.R.	0.0-2.0	0.0-1.0	0.0-2.0	0.0-3.0	0.0-2.0	0.0-2.0
	Mean	0.9	0.7	1.1	1.4	1.0	1.1

Kruskal-Wallis one-way-ANOVA (females of known absolute-age only): % chicks fledging: χ^2_4=2.1, n.s.; number of chicks fledging: χ^2_4=1.9, n.s.

Replacement clutches

Of 104 first clutches laid on the intensive site by 64 individually-ringed females (i.e. 104 female-years) between 1993-95, 65 (63%) hatched at least one egg. Four of the females laying successful clutches went on to lay second clutches (attempted double-brooding - Chapter 2), and two more of them laid replacement clutches after the early loss of broods. Of the 39 (38%) clutches that were lost, replacements were laid for 25 (61%), most of which (68%) were also lost. In three cases, a second replacement clutch was laid after the loss of the original replacement clutch: one of these hatched successfully.

Frequency of relaying - Sample sizes may differ here from those given previously in reference to the number of clutches lost. This is because this section deals only with those first clutches where it was known whether or not a replacement clutch was laid. Sample sizes also differ within this section because of the incomplete nature of the information from many clutches. There was no difference in the frequency with which first-clutch losses were replaced between adult and yearling female Lapwings (Table 3.3.19).

Table 3.3.19. The frequency with which first-clutch losses were replaced in relation to relative female age (adult or yearling) in the Lapwing, 1993-95. Adult includes females of unknown absolute-age (see General Methods).

	No. of first-clutch losses	
Age	Replaced	Not replaced
Yearling	7 (70%)	3
Adult	17 (68%)	8

Association between female age and the frequency of relaying: G_1=0.1, n.s.

The frequency of replacement of first-clutch losses was also independent of the date of failure of the first clutch (Table 3.3.20). This was reflected in the mean date of failure of the first clutch for those females that went on to lay a replacement clutch, and those that did not: mean fail date for 21 replaced first clutches=29 April ±1.8 days; mean fail date for 10 clutches not replaced=29 April ±1.7 days: t_{29}=0.1, n.s.

Table 3.3.20. The frequency with which Lapwing first-clutch losses were replaced in relation to the date of failure of the first clutch, 1993-95. Early=first clutch failed on-or-before 27 April (median fail date); late=first clutch failed after 27 April.

	No. of first clutch losses	
Fail date	Replaced	Not replaced
Early	10 (63%)	6
Late	11 (73%)	4

Association between frequency of relaying and fail-date of first clutch: G_1=0.5, n.s.

The frequency of relaying was not associated with the period between initiation and failure of the first clutch (here termed "age of first clutch at failure" - Table 3.3.21). This was confirmed by the mean periods between laying and failure of the first clutch: mean period for 16 females replacing first-clutch losses=21.5 ±1.6 days; that for seven females not laying replacement clutches=18.7 ±1.9 days (t_{21}=1.0, n.s.). That these periods were greater than 16 days (the mid-point of the egg-laying and incubation period) confirms the increased frequency of clutch losses in the later periods of the egg cycle (see above).

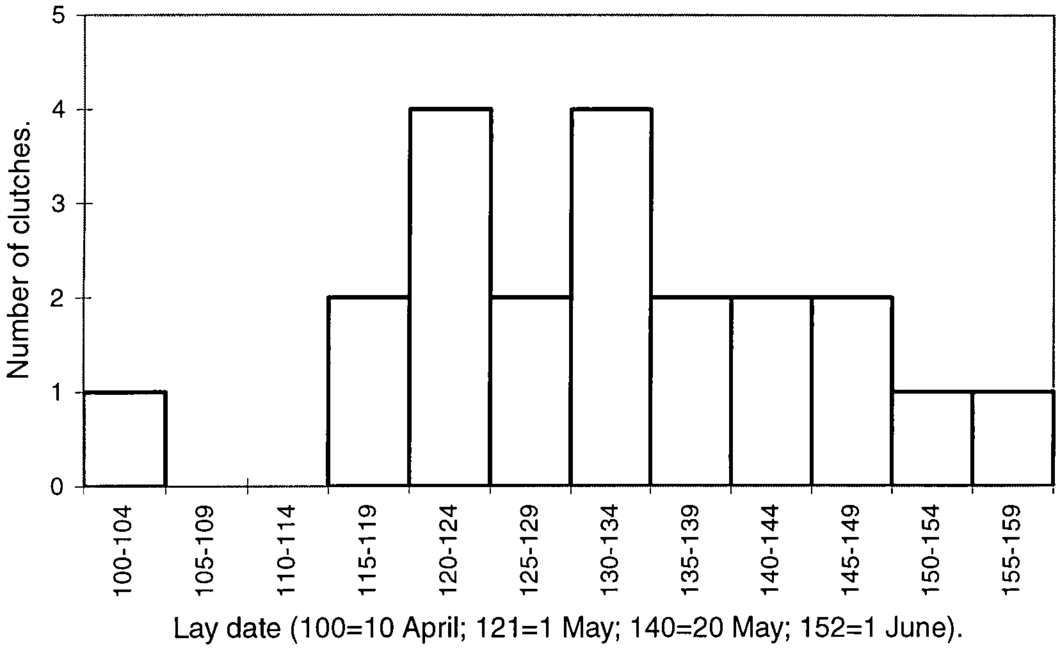
Table 3.3.21. The frequency with which Lapwing first-clutch losses were replaced in relation to the age of the first clutch at failure, 1993-95. Short period=periods ≤20 days (=median period); long periods=periods >20 days.

	No. of first-clutch losses	
Period	Replaced	Not replaced
Short	7 (58%)	5
Long	9 (82%)	2

Association between frequency of relaying and age of first clutch at failure: G_1=1.4, n.s.

Date of laying - The date of laying was known for 21 replacement clutches. There was no difference in laying date between years (one-way-ANOVA: $F_{2,18}$=0.0, n.s.) and data from 1993-95 have been pooled (Figure 3.3.12). The average laying date for replacement clutches was 7 May (±13 days, S.D.), and the average period between failure of the first clutch and laying of the replacement was 7.8 days (±4.6 days S.D.) for 18 females for whom both dates were known. There was no relationship between the age of the first clutch at failure, and the period between failure of the first clutch and the laying of the replacement (r_{13}=0.0, n.s.).

Figure 3.3.12. Laying dates for 21 replacement Lapwing clutches, 1993-95.



There were 14 females of known age for whom the laying date for their replacement clutch was known. A multiple regression analysis with female age and field entered into the model suggests that neither variable influenced laying date (model fit: r^2=0.22, $F_{2,9}$=1.3, n.s.). The mean date of laying of replacement clutches for yearling females was 8 May ±6 days, n=6, and for adults was 8 May ±3 days, n=14 (includes females ringed as adults).

Clutch size - Overall there was no difference in clutch size between 19 first and replacement clutches laid by the same female (Wilcoxon test for matched pairs: Z=0.7, n.s.), with clutch sizes the same in thirteen (68%) pairs.

There were no differences in the size of replacement clutches among females of different ages (Kruskal-Wallis one-way-ANOVA: χ^2_4=1.5, n.s.) and no confounding variables influenced replacement-clutch size.

Egg size - Egg biometrics (length, breadth, shape index [length/breadth] and volume) for replacement clutches (n=19) were compared to those of first clutches laid by the same female (i.e. paired comparison). The mean value for the clutch was used (Table 3.3.22). Egg volume for replacement clutches was on average 4% smaller than in first clutches, the result of a significant decrease in egg length (1.8%) and breadth (1.1%) in replacement clutches. The index of repeatability (see methods) for egg volume between first and replacement clutches laid by the same females was just 0.19, indicating much variation within females.

Female age did not influence the biometrics of eggs in replacement clutches (one-way ANOVA: all $F_{4,13}$<1.0, n.s.). No other variables affected the biometrics of eggs in replacement clutches.

Table 3.3.22. Summary of mean (±S.E.) egg biometrics (length, breadth, shape index [length/breadth] and volume) for 19 replacement and first clutches laid by the same individually-ringed female Lapwings, 1993-95. Statistical comparisons were made using paired t-tests (t_{18}).

	Average egg biometrics for		
	First clutch	Replacement	t_{18}
Length (mm)	46.43 ±0.30	45.59 ±0.28	2.62**
Breadth (mm)	33.44 ±0.15	33.07 ±0.13	2.55*
Shape	1.39 ±0.01	1.38 ±0.01	1.06
Volume (cm^3)	23.74 ±0.27	22.80 ±0.27	3.16***

Statistical significance: * $P<0.05$; ** $P<0.02$; *** $P<0.01$; no asterix=n.s.

Hatching success - The hatching success of replacement clutches was not significantly different between years (Table 3.3.23) and data for replacement clutches were pooled.

Table 3.3.23. Hatching success of Lapwing replacement clutches in each year of study (1993-95).

Clutch	Number of clutches			
outcome	1993	1994	1995	Total
Hatch	5 (45%)	2 (29%)	2 (20%)	9 (32%)
Fail	6	5	8	19
Total	11	7	10	28

Association between hatching success and year: G_2=1.7, n.s.

In 1995, the success rate of first clutches was no higher than that of replacements, but in 1993 and 1994 37% more first clutches produced at least one chick than replacements (Table 3.3.24).

Table 3.3.24. Hatching success of Lapwing first and replacement clutches. Figures in parentheses are the proportion (%) of clutches producing at least one chick.

	Number of clutches		
Clutch	First clutches		Replacement
outcome	1993 & 94	1995	clutches
Hatch	50 (69%)	49 (48%)	9 (32%)
Fail	22	53	19
Total	72	102	28

Hatching success of first and replacement clutches: 1993 & 94 first clutches vs. replacement: G_1=11.3, P<0.001; 1995 vs. replacement: G_1=2.2, n.s.

There was no difference in the proportion of replacement clutches producing at least one chick between adult and yearling females (there were insufficient data to compare all age groups): adults hatched 27% of 11 replacement clutches whilst yearling females hatched 50% of 6 replacement clutches (G_1=0.8, n.s.).

The productivity of Lapwings in Upper Teesdale

Overall, the median number of chicks raised per female on the study site (64 individually-recognisable females, 92 female-years), from 1993-95 was 0.5, inter-quartile range=0.0-2.0 (mean=1.0). This does not include chicks fledging from replacement clutches as insufficient data were available to estimate fledging success. However, it is not likely that this would invalidate the above approximation given the low hatching success of replacement clutches.

3.4 DISCUSSION

The marked avoidance of the field edge by Lapwings during the breeding season is in accordance with Lapwing behaviour during the winter, when individuals feeding in flocks form denser aggregations, in the centre of the field, when foraging in small fields compared to large ones (Thompson & Barnard 1983; Barnard & Thompson 1985). Similarly, Shrubb (1988) noted a marked avoidance of small fields by wintering Lapwing, with the majority (79%) of flocks found in fields greater than 16ha. Lapwing and Golden Plover *Pluvialis apricaria* were also more responsive to alarm stimuli, and tended not to resettle in the same field once disturbed, when feeding in smaller fields (Thompson & Barnard 1983; Barnard & Thompson 1985). These authors attributed this behaviour to the degree of vulnerability to avian predators (Kestrel *Falco tinnunculus*, Sparrowhawk *Accipiter nisus*, Carrion Crow *Corvus corone* and Rook *Corvus frugilegus*) perceived by the Lapwings, which increased when close to cover at the field edge. Sparrowhawks often use cover such as hedges and walls to approach prey unseen (Newton 1986). In Upper Teesdale, the principle avian predators were Kestrel, Sparrowhawk, Peregrine *Falco peregrinus*, Merlin *Falco columbarius* and Carrion Crow, and the first four species were all seen attacking Lapwings at some time. Indeed, Sparrowhawks and Merlins were regularly seen flying low over the ground close to the dry-stone walls. Thus, Lapwings may minimise their risk of attack from avian predators by avoiding cover at the edge of fields. Hatching success was also found to be lower close to the field boundary in one year (see below), suggesting that they may attempt to minimise clutch losses (primarily to mustelids in this study) by avoiding field edges. Alternatively, the avoidance of dry-stone walls may be an inherited response to some form of selection pressure which is no longer acting (e.g. clutch losses due to fox predation).

Overall, 67% of pairs at the time of formation, or when first recorded, consisted of individuals of a similar age. This concurs with the findings of many studies on other species; e.g., Coulson (1966) found 49% of paired Kittiwakes were within one year's breeding experience; Newton *et al.* (1981) found that 83% of Sparrowhawk pairs were either yearling-yearling or adult-adult; Shaw (1985) showed that 57% of paired Blue-eyed Shags were within one year in age; in 39% of Redshank pairs the individuals had the same number of years breeding experience (Thompson & Hale 1991); in the Barnacle Goose, individuals were of the same age in 96% of first-time pairings, and in 46% of re-pairings after the loss of the first partner (Black & Owen 1995); and Heitmeyer (1995) reported significant assortative mating by age (adult or yearling) in dabbling ducks. In the current study, where the age of paired Lapwings did differ, there was a significant tendency for males to be 1-2 years older than their mates (45% of pairs), with an associated high frequency of yearling female-adult male pairings (33% of pairs). This is probably because more females bred as yearlings than males. This is similar to the situation found by Heitmeyer (1995) who showed that where the age of paired dabbling ducks was not similar, the most common pairing was between adult males and yearling females.

Overall, 20% more female Lapwings bred than males in Upper Teesdale between 1993-94. This was probably due to many breeding males taking more than one mate, as suggested by the female-biased sex ratio among breeding Lapwings, and as shown in Chapter 2. There was no difference in the proportion of females which bred among different age groups. Males, however, showed significant variation in the proportion of breeders with age, particularly between one and two-years of age, when the proportion of males breeding within the same cohort increased by 30%. This was because yearlings had the lowest proportion of breeders in any year of all male age groups. Crawford (1980) reported a similar situation in the American Coot *Fulica americana* where only 58% of all yearlings bred, compared to over 96% for older age groups. Newton (1989) also found that 58% of yearling female Sparrowhawks, trapped at nesting territories, did not attempt to breed. Likewise, in a review of studies on the Red-winged Blackbird, Searcy and Yasukawa (1995) found that non-breeding rates in sub-adults were extremely high, often 100% in some populations.

The low proportion of breeding yearling males could have resulted from a lack of experience required for successful breeding (e.g. reproductive or maintenance skills, familiarity with topography or neighbours, familiarity with mate) (constraint hypothesis). Alternatively, they may have decided to delay their first breeding attempt in order to increase their chances of success in a later year (or to increase their longevity), assuming an inverse relationship between reproductive effort and fitness (Williams 1966) (restraint hypothesis), or finally, the nonbreeders among this age group were of poor quality, and so unable to breed at one-year-old (bad quality hypothesis) (Curio 1983). As the proportion of males breeding, within a cohort, increased so markedly between one- and two-years of age, the latter hypothesis can be rejected. The remaining two hypotheses are harder to separate as reproductive performance will increase with age under both scenarios. The constraint hypothesis requires the demonstration of the lack of breeding opportunities, skills or experience in yearlings that are present in older males, and the restraint hypothesis suggests that first-time breeders of different ages would show differences in success and/or longevity (Curio 1983; Forslund & Pärt 1995). This is beyond the scope of this study, but some of the life-history characteristics of the Lapwing (i.e. relatively high adult mortality, cessation of adult growth) would predict that breeding restraint would not be expected if lifetime reproductive success were to be maximised (Charlesworth & Leõn 1976; Charlesworth 1980). However, the high, stable nature of the population in Upper Teesdale is one factor potentially selecting for reproductive restraint (Charlesworth & Leõn 1976; Charlesworth 1980). Primarily, reproductive restraint of yearling Lapwings is highly unlikely given that the Lapwing is a relatively short-lived species. The constraint hypothesis is generally accepted as the most likely cause of age-specific reproductive performance in birds (see Charlesworth 1980, p. 259), and is supported in the majority of studies (Martin 1995), although the restraint hypothesis is rarely disproved. It is conceivable that both hypotheses operate simultaneously but in different individuals.

An apparent reduction in the proportion of breeding males in the older age groups was revealed as a cohort effect. Such effects are rarely considered in studies of age-specific reproductive performance (Desrochers & Magrath 1993; Martin 1995) and can obscure actual age effects, or suggest age-related variation when none is present. Consistency in the proportion of breeders between years within the same cohort was due to a tendency among older individuals (in both sexes) to maintain their breeding status in different breeding seasons. If this pattern were repeated between each breeding season, it would mean that some individuals that were non-breeders in their second year could potentially remain so for their entire lives. A similar situation has been reported by Ens *et al.* (1992, 1995) in the Oystercatcher *Haematopus ostralegus*, where some individuals, capable of breeding, remain as non-breeders for a number of years before their first breeding attempt. Ens *et al.* (1992, 1995) invoked a queuing system to explain this, whereby individuals could not obtain a high-quality territory until they had acquired experience regarding the topography and individuals in the area. Such a strategy may be conceivable in a long-lived species such as the Oystercatcher (mean annual survival rate=0.902, Safriel *et al.* 1984), but in the Lapwing such a system would surely be too risky: assuming the over-winter survival rate of yearlings to be 0.595, and the annual survival rate of adults to be 0.752 (Peach *et al.* 1994), an individual Lapwing chick has only a 0.25 chance of reaching four-years of age.

Perhaps the consistency in breeding status in older males, and the low proportion of breeding yearling males, can both be explained by the same constraint. The Lapwing population in Upper Teesdale has been stable since at least 1990, and can be regarded as relatively dense at 80-88 pairs per km^2 (Thompson *et al.* 1994) when compared to other grassland areas (Cramp & Simmons 1983). Therefore, some yearling males may have been competitively excluded from territory ownership, assuming that (i) territories are limiting and (ii) at least a minor discrepancy occurs in competitive ability between yearlings and older males. Thereafter, non-breeding status could be maintained between years if males were site-faithful, and territory holders had some form of resident advantage (e.g. Krebs & Davies 1993). Site-fidelity at the scale of individual fields was demonstrated by Thompson *et al.* (1994) in Upper Teesdale and would appear to operate at a smaller scale too (pers. obs.). Therefore, it could be that males in the 1990 cohort, which had a consistently low proportion of breeders in 1993 and 1994, were presented with few vacant territories as one-year-olds. However, this does not explain why persistent non-breeders did not obtain a territory in later life when natural vacancies arose. Nor does it explain non-breeding among female Lapwings. Alternatively, persistent non-breeders in other cohorts may have been inherently poor competitors (i.e. low quality individuals), with few individuals able to take a territory even when a vacancy arose. Or, individuals unable to obtain a territory in early life may have been affected by this experience such that they remained non-breeders, although it is hard to envisage how this might happen. The persistence of non-breeding in females was harder to demonstrate given the smaller proportion of non-breeders to start with. Here, non-breeding in any year may be condition dependent (Chastel *et al.* 1995, and refs. therein), rather than determined by breeding vacancies, such that females below a certain condition (i.e. in terms of nutrient resources for example) cannot breed. Persistent differences between individuals were found by Arcese (1987; 1989) in male Song Sparrows *Melospiza melodia*, where competitive differences among individuals were maintained throughout life, and males who did not obtain territories in their first year were more likely to lose their territory in later life. This has serious implications for an individuals lifetime reproductive success, as Smith (1988) found that those male Song Sparrows who did not secure a territory in their first year, raised the fewest young. Likewise, Harris and Wanless (1995) found that some Common Guillemots *Uria aalge* were persistent non-breeders, a trait which seemed to be associated with the loss of their breeding site in a previous year. They suggested that these may have been low-quality individuals (Harris & Wanless 1995).

No effect of female age was found with regard to laying dates, clutch size or success of the first clutch in this study. The date of laying of all first clutches was found to be relatively synchronised, as suggested by Thompson *et al.* (1994). This seems to contradict the findings of Chapter 1 where lay date was weakly, but positively correlated with date of arrival on the breeding grounds. Given that yearling females arrive around 15 days later than adults (Chapter 1), lay dates of yearlings would be expected to be significantly later than those of adults, particularly as no difference in the frequency of non-breeding was found between early and late arrivers (Chapter 1). That yearlings were as productive as adults contradicts the findings for many other species (see refs. in introduction) and requires further investigation to confirm. This may have been a false conclusion based on small samples. This seems unlikely, however, as sample sizes here compare favourably with those in other studies. Perhaps conditions in Upper Teesdale were, on average, sufficiently amenable to facilitate successful breeding by all ages. Several studies have shown that age-specific breeding performance only becomes apparent under stressful environmental conditions, such as food shortages (e.g. Hamer and Furness 1991), or that age-specific effects can be obscured when conditions are improved, for example by the provision of supplementary food (e.g. Desrochers 1992). Alternatively, the effect of age on breeding performance in the current study may have been masked by another factor negatively influencing the success of all females, such as Mustelid clutch predation. Stoats *Mustela erminea* and Weasels *M. nivalis* were frequently seen in the study area and caused significant clutch losses (pers. obs. and P.S. Thompson, pers. comm.). At present it is not possible to distinguish between these two possibilities. It is not surprising that no difference was found in clutch sizes between females of different ages, given the apparent conservatism in clutch size among shorebirds (Maclean 1972; Ligon 1993).

Individual female Lapwings aged two years and over, laid eggs on average 5.5% larger (by volume) than they did as yearlings. This was reflected in an average 5% difference in egg volume between adult and yearling females in a "cross-section" analysis. Having tentatively ruled out reproductive restraint as the cause of age-specific breeding performance (see above), the difference in egg volume could be due to the increase in age *per se* or a correlated factor, such as breeding experience (Curio 1983; Sæther 1990; Forslund & Pärt 1995; Pärt 1995). In this study, it was not possible to distinguish between the two hypotheses due to the tendency for most females to breed as yearlings, thus providing prohibitively small numbers of older first-time breeders. It was also not possible to eliminate the effect of the duration of the pair bond (Fowler 1995; Cézilly & Nager 1996), due to the prevalence of unringed males within pairs, and the short-term nature of this study. The increase in egg size in older birds was not due to individuals moving to areas of superior quality after their breeding effort as yearlings, as six of the seven females included in the longitudinal analysis were monitored in the same field on both occasions. The increase in egg size in older females could have resulted from morphological changes which permitted the formation and laying of larger eggs. Alternatively, older female Lapwings may have been more efficient foragers, a tendency noted in many species (Burger 1988; Marchetti & Price 1989). Thus, yearling females, as less efficient foragers than older females, had fewer resources to devote to egg production. This raises the question, however, of why yearling females did not delay egg-laying in order to allow more time to increase reserves, and thus compensate for low foraging efficiency? Perhaps there is significant selection pressure for early laying in the Lapwing to optimise the timing of breeding (Lack 1954; Perrins 1970), or this may be a consequence of the apparent heritability of lay dates (see below). Another possibility that could result in yearling females having fewer resources to devote to egg production, stems from their late arrival on the breeding grounds. Yearling females may have to sacrifice some pre-laying foraging time, and therefore egg size, in order to lay their clutch sufficiently early. This assumes there is a premium on the early laying of the clutch and that yearling females have not spent more time feeding on the wintering grounds than adults, which could potentially compensate for their late arrival. Egg size has been shown to vary with age and/or experience in a number of bird groups. Coulson *et al.* (1969) found a 12% difference in egg volume between 2- and 8-year-old female Shags *Phalacrocorax aristotelis*; Davis (1975) found a significant, positive correlation (r=0.76) between clutch volume index (length x breadth^2) and female age in Herring Gulls *Larus argentatus*, for females between five and 8-9 years-old; Coulson & Horobin (1976) demonstrated an 8% difference in egg volume between the youngest (3-years-old) and oldest (≥8-years-old) breeding Arctic Terns *Sterna paradisaea*; Gratto *et al.* (1983) found a 5% difference in egg volume between yearling and adult female Semipalmated Sandpipers; and Thompson & Hale (1991) found a significant, positive correlation (r=0.20-0.34) between egg volume and female breeding experience in the Redshank. In accordance with this study, Robertson *et al.* (1994) were able to demonstrate a 4% increase in egg size within individuals between the ages of 2- and 5-years in the Lesser Snow Goose.

Variation in egg size between the clutches of different females was greater than within, and individual females laid eggs of a similar size in consecutive years, with high indices of repeatability. Laying dates for individual females were also repeatable between years. High indices of repeatability may reflect heritability of a trait (Falconer 1981), or the temporal consistency of environmental conditions experienced by individuals (Leblanc 1989). This would be facilitated by between-year site-fidelity (Thompson and Hale 1991), as found in Lapwings (Thompson *et al.* 1994). I suggest that heredity was the primary cause of high repeatabilities in this case: habitat differences within a field appear slight due to the management regime, so variation in egg size within fields is likely to result from other sources. Also, despite differences in egg shape and length between fields, breadth and volume did not vary consistently, suggesting no uniform effect of habitat. That the repeatability indices were less than 1.0 indicates the influence of other effects (such as female age) on these traits. Galbraith (1988), and Blomqvist and Johansson (1995), found significant within-year correlations between egg volume and female body condition. In the current study, the possibility that body condition was also partly determined by heredity cannot be eliminated (Galbraith 1988). That environmental conditions did have some effect on egg size was indirectly suggested by the 4% decline in egg volume between first and replacement clutches. A similar decline was noted by Galbraith (1988b) for Lapwings nesting on grassland but not for those nesting on arable areas (a habitat considered to offer greater food availability). Heritability of laying dates was suggested by Hildèn and Vuolanto (1972) for the Red-necked Phalarope *Phalaropus lobatus* and by Thompson *et al.* (1986) for the Greenshank *Tringa nebularia*, although both studies also commented on significant environmental effects, reflecting the situation found in this study. Similarly, the heritability of egg size was suggested for five species of waders by Väisänen *et al.* (1972), for the Whimbrel *Numenius phaeopus* (Grant 1991) and for the Redshank *Tringa totanus* (Thompson and Hale 1991). A proper investigation of the determinants of egg size would require the determination of the degree of correlation between mother-daughter egg biometrics, whilst simultaneously controlling for body condition.

Galbraith (1988b) found that large Lapwing eggs produced chicks structurally larger than those from small eggs and with greater nutrient reserves (although the nutrients were unidentified). In 92% of 38 species reviewed by Williams (1994) there was also a positive correlation between egg size and chick size at hatching, primarily the result of varying nutrient stores. Thus, it seems reasonable to assume that adult females in this study produced larger chicks than yearlings. The effect of egg size on the fitness of the chicks is less clear, but chick growth and survival during the early chick-rearing period were positively related to egg size in 8 of 10, and in 4 of 5 studies respectively reviewed by Williams (1994). Therefore, adult Lapwings in this study may have had greater fledging success than yearlings as a result of their larger eggs. This could result from larger body mass and/or greater nutrient reserves in chicks hatched from larger eggs, which facilitate growth and survival during periods of nutrient or environmental stress (Williams 1994). This was not supported by the investigation of fledging success in this study, which suggested no significant difference in the proportion of chicks fledged between adults and yearlings.

Although no effect of age was found with regard to hatching success, this analysis was hampered by significant differences between years, in different periods of the breeding season and egg cycle, and differences between fields. The significantly lower success rate of clutches in 1995 was probably related to an increase in that year of Stoat sightings in most study fields (pers. obs.), which probably also lead to the noticeable "edge effect" on hatching success in that year. Differential occurrence of Stoats across the study area may also account for differences in the success rate of clutches in different fields, although farming practices were probably important too. Differences in the hatching success of clutches laid on grassland through the season were also found in the Lapwing, Black-tailed Godwit *Limosa limosa*, Redshank and Oystercatcher by Beintema & Müskens (1987), although they found success rates highest in mid-season. This was attributed to the early loss of exposed nests which were easy for predators to locate, and/or the provision of cover by increasing vegetation height later in the season. They also showed lower success rates during egg-laying than during clutch incubation (Beintema & Müskens 1987). However, a study of grassland-nesting Lapwings by A. Aunins (pers. comm.) revealed no variation in clutch survival rates with date. Fraga & Amat (1996) demonstrated a decrease in clutch survival through the season in Kentish Plovers *Charadrius alexandrinus* nesting around a salt lake in southern Spain, which was attributed to increased exposure of clutches to mammalian predators with changing environmental conditions. Variability in clutch survival rates was also found by Klett & Johnson (1982), who showed that early-laid clutches of Mallard *Anas platyrhynchos* and Blue-winged Teal *A. discors* experienced the highest losses, although there was also variation with date (i.e. breeding season) and nest site. The decrease in clutch survival rates through the season found in this study mirrored the situation found by Fraga & Amat (1996), although there were no obvious changes in the environment which may have resulted in increased exposure of nests to predators in Upper Teesdale later in the season. Alternatively, this pattern may reflect the intensity of predation by Stoats as their breeding season progressed, leading to a presumed increase in the demand for food: 4-9 young Stoats are born in April and May and are weaned within 5 weeks (Corbet & Southern 1977). This analysis illustrates the need to justify the pooling of groups across time and space in studies of hatching success. Further investigation of age-specific hatching success, including a larger number of yearlings, would be beneficial as the lack of a demonstrable effect here may simply reflect the small sample sizes and problems outlined above.

Around 70% of both yearling and adult female Lapwings laid replacement clutches when their first clutches failed. The frequency of replacement of first-clutch losses was found to be independent of the date of failure of the first clutch. Clearly, all first-clutch losses occurred early enough to allow the laying of a replacement. Replacement clutches were also laid independently of how far into incubation the loss of the first clutch had occurred.

Eggs laid in replacement clutches were on average 4% smaller than those in first clutches laid by the same females, and hatching success was 37% lower for replacement clutches in two of the three years when compared to first clutches. Thus, few replacement clutches produced chicks, and those chicks produced may have had a lower chance of survival by way of their smaller size at hatching (Williams 1994) and later hatching date (Thompson *et al.* 1994).

Overall, a median of 0.5 chicks (I.R.=0.0-2.0) were produced per female on the intensive site from 1993-95 (mean=1.0), although this estimate does not include replacement clutches and so can be regarded as conservative. The two most recent studies reporting Lapwing breeding success on similar grassland habitats, found the mean productivity to be 0.8 and 0.86 chicks per female respectively (Galbraith 1988a; Baines 1989). Thus, the productivity of Lapwings in this study reflects that found by these authors and would be enough to maintain the population (Galbraith 1988a; Baines 1989). It should be noted, however, that the fields comprising the intensive site were predominantly unimproved. It is therefore likely that this estimate of productivity would not be reflected ubiquitously and so should not be taken as a measure of the "health" of the Lapwing population in Upper Teesdale.

4. The roles of male and female Lapwings during reproduction: time-activity budgets.

4.1 INTRODUCTION

Among birds, as in most groups, the sexes rarely invest in reproduction in the same manner. Generally, males compete for the right to mate with females as male reproductive success usually increases proportionately with the number of matings, whilst females invest more resources in their gametes and offspring (parental investment) to improve their reproductive success (Bateman 1948; Trivers 1972; Clutton-Brock 1991; Arnold & Duvall 1994). Parental investment includes any investment by the parent that increases offspring survival at the expense of the parent's ability to invest in other offspring (Trivers 1972). This is distinct from the term *parental care*, which is descriptive and refers to any behaviour likely to increase the fitness of offspring (Clutton-Brock 1991).

The nature of any individual's investment in reproduction will depend on the costs and benefits of investing in mating or parental effort. For this reason, investment varies with mating systems (Emlen & Oring 1977; Maynard Smith 1977; Erckmann 1983). For example, if the opportunity for males to gain multiple matings is high then they will maximise their reproductive success by pursuing such opportunities instead of remaining with their first mate and investing in the care of the offspring. If, however, by doing so they jeopardise the survival of their offspring, then they would benefit by ignoring other mating opportunities and taking care of the young instead (Maynard Smith 1977). Thus, male investment in parental care generally increases from promiscuous mating systems, via polygyny and then monogamy, to polyandry, where males often assume all parental duties whilst females mate with as many males as possible (Clutton-Brock 1991).

Moreover, within any mating system the degree of parental care is often found to be variable. For example, in the monogamous Kentish Plover *Charadrius alexandrinus* males perform much of the parental care of chicks as the females often desert the brood (Lessels 1984; Fraga & Amat 1996). However, in the Oystercatcher *Haematopus ostralegus*, another monogamous species, both parents are required to feed young chicks and so must invest heavily in parental care (Ens *et al.* 1991; Ens *et al.* 1995).

This section aims to describe the behavioural roles of male and female Lapwings during the reproductive cycle, to identify any trade-offs which may exist between the allocation of time to different behaviour and thereby determine the mode of investment in reproduction by the sexes.

4.2 METHODS

This study was conducted during 1995. For a description of the study area, and details regarding the identification and marking of individuals, and of census methods, see General Methods.

The location and monitoring of nests, and the protocol for behavioural observations were described in Chapter 2.

4.3 RESULTS

The behaviour of male and female Lapwings was compared at all stages throughout the breeding cycle (see Chapter 2 for description of breeding cycle stages). Very few behavioural differences were found in relation to the mating system (i.e. monogamous or polygamous, see Chapter 2) so this was not considered here.

Maintenance behaviour

The allocation of time to maintenance behaviour peaked during the pre-laying period of the breeding cycle for male and female Lapwings, accounting for around 60% and 74% of their time respectively (Table 4.3.1). This proportion declined significantly to around 30-40% for males during the remainder of the cycle (Kruskal-Wallis one-way-ANOVA [KW-ANOVA]: $\chi^2_4=10.1$, $P<0.05$). A multiple range test (MRT, Siegel & Castellan 1988) showed that the proportion of time allocated during the pre-laying and chick-rearing periods were significantly different ($P<0.05$). Females showed a dramatic decline in the proportion of time allocated to maintenance behaviour during the egg-laying and incubation periods, when median values fell to zero. During the chick-rearing period this proportion rose again to 42% and overall the variation in time allocated to maintenance behaviour was significant (KW-ANOVA: $\chi^2_4=24.4$, $P<0.001$), with significant differences between the incubation periods and all other periods during the breeding cycle (MRT, $P<0.05$).

Females allocated around 14% more of their time to maintenance behaviour than males during pre-laying, but during early and late incubation, males allocated 28% and 45% respectively more time to maintenance behaviour than females (Table 4.3.1). The proportions were not significantly different during the two remaining periods of the breeding cycle.

The principle component of maintenance behaviour, during all stages, was feeding (Figure 4.3.1). This is reflected in the correlation between the proportion of time spent feeding and in all maintenance behaviour during observations: males r_s=0.91, n=281, P<0.001; females r_s=0.93, n=250, P<0.001. Roosting was not recorded for males during pre-laying, egg-laying or early incubation, and for females during all stages after pre-laying. The significant differences between the sexes recorded above for maintenance behaviour translate into significant differences in time allocated to feeding (Figure 4.3.1), except during the pre-laying period, where the probability value was 0.052.

Table 4.3.1. The median proportion of time allocated to different behaviour by male and female Lapwings throughout the breeding cycle, 1995. Figures in parentheses replace medians of zero, showing instead the proportion of data equal to zero. I.R.=Inter-quartile range. N=number of individuals.

			Proportion of time allocated to					
			maintenance behaviour		Mating behaviour		Parental behaviour	
Stage	Sex	N	Median	I.R.	Median	I.R.	Median	I.R.
Pre-laying	Male	29	0.60**	0.38-0.80	0.22****	0.08-0.46	-	-
	Female	23	0.74**	0.49-0.90	0.03****	0.00-0.11	-	-
Egg-laying	Male	14	0.39	0.24-0.80	0.14****	0.04-0.19	(80%)	0.00-0.00
	Female	18	0.23	0.00-0.78	(70%)****	0.00-0.03	(67%)	0.00-0.53
Incubation I	Male	21	0.28*	0.00-0.88	(74%)***	0.00-0.03	(52%)	0.00-1.00
	Female	31	(64%)*	0.00-0.30	(96%)***	0.00-0.00	0.65	0.00-1.00
Incubation II	Male	20	0.45****	0.00-0.78	0.02****	0.00-0.05	(56%)*	0.00-1.00
	Female	30	(69%)****	0.00-0.11	(87%)****	0.00-0.00	0.82*	0.03-1.00
Chick-rearing	Male	23	0.30	0.15-0.63	0.06***	0.00-0.23	(78%)****	0.00-0.00
	Female	27	0.42	0.12-0.71	(68%)***	0.00-0.03	0.11****	0.00-0.71

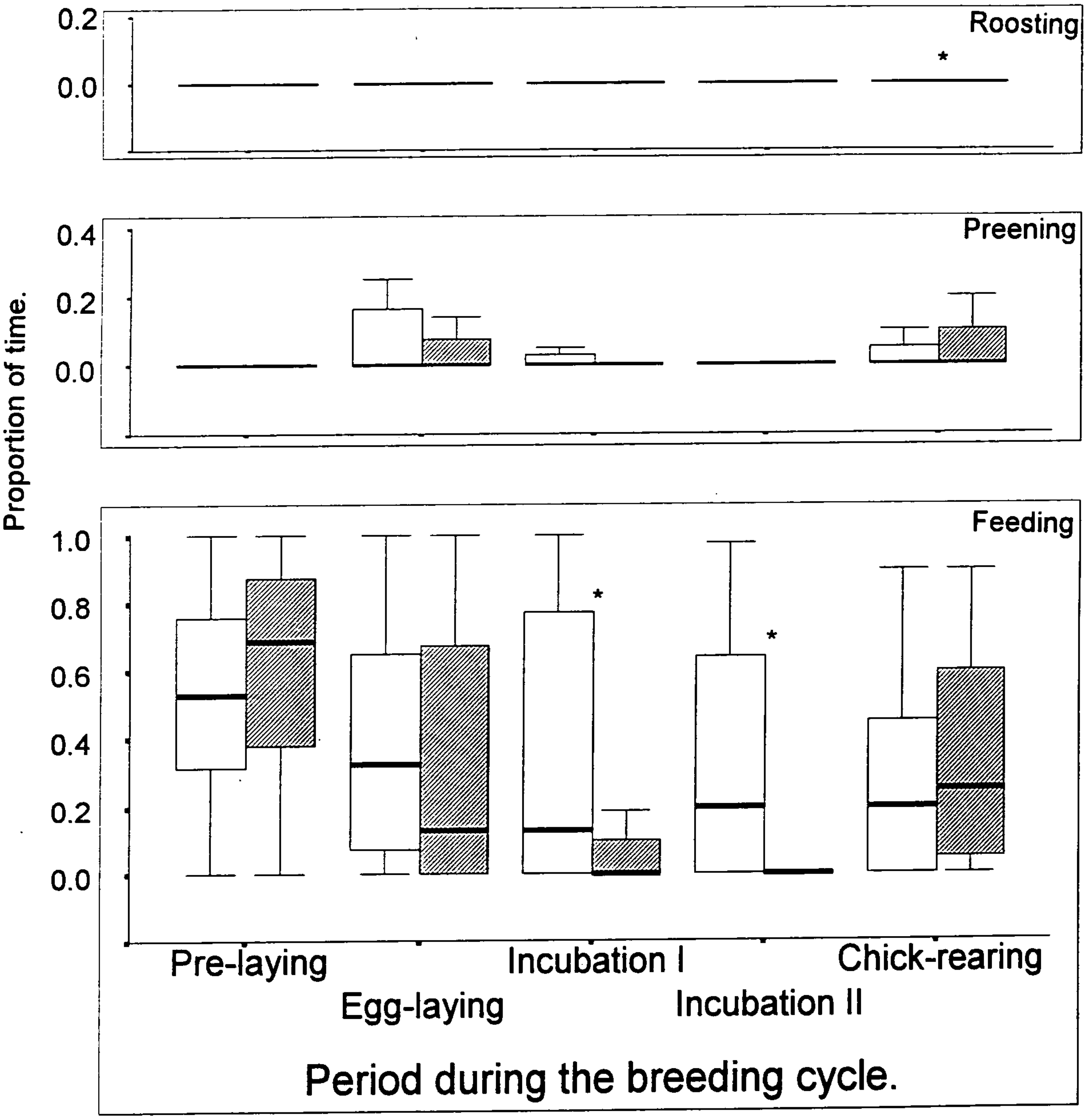
Comparison of sexes via Mann-Whitney U test: *$P<0.05$; **$P<0.02$; ***$P<0.01$; ****$P<0.001$.

Table 4.3.1. (Continued). Vigilant behaviour and time spent away from the territory (absence) cannot be described exclusively under maintenance or reproductive behaviour. Figures in parentheses replace medians of zero, showing instead the proportion of data equal to zero. N=number of individuals.

			Proportion of time allocated to			
			Vigilant behaviour		Absence	
Stage	Sex	N	Median	I.R.	Median	I.R.
Pre-laying	Male	29	0.05	0.00-0.13	(94%)	0.00-0.00
	Female	23	0.08	0.00-0.28	(91%)	0.00-0.00
Egg-laying	Male	14	0.12	0.00-0.30	(80%)	0.00-0.00
	Female	18	0.10	0.00-0.29	(85%)	0.00-0.00
Incubation I	Male	21	(52%)****	0.00-0.13	(100%)***	0.00-0.00
	Female	31	(87%)****	0.00-0.00	(71%)***	0.00-0.35
Incubation II	Male	20	0.05****	0.00-0.18	(94%)*	0.00-0.00
	Female	30	(85%)****	0.00-0.00	(75%)*	0.00-0.06
Chick-rearing	Male	23	0.23	0.10-0.47	(88%)	0.00-0.00
	Female	27	0.13	0.00-0.29	(94%)	0.00-0.00

Comparison of sexes via Mann-Whitney U test: *$P<0.05$; **$P<0.02$; ***$P<0.01$; ****$P<0.001$.

Figure 4.3.1. The proportion of time allocated to the components of somatic behaviour for male (open bars) and female (hatched bars) Lapwings, 1995. The horizontal line represents the median value, the bar is the inter-quartile range (I.R.) and the "whiskers" show the outliers within 1.5 times the I.R. Sample sizes are as in Table 4.3.1. *=significant difference between the sexes (Mann-Whitney U test, *P*<0.05).



Reproductive behaviour: mating

The proportion of time allocated to mating behaviour by males was highest during the pre-laying and egg-laying stages of the breeding cycle (22% and 14% respectively) and lowest during the incubation and chick-rearing periods (median=0-6%) (Table 4.3.1). This variation was significant (KW-ANOVA: χ^2_4=49.9, P<0.001) with time spent in mating behaviour during the pre-laying period significantly higher than during the incubation and chick-rearing periods, and that during egg-laying higher than early incubation (MRT, P<0.05).

The peak allocation of time to mating behaviour by female Lapwings occurred during the pre-laying period (3%) and declined thereafter (0%) (Table 4.3.1) (KW-ANOVA: χ^2_4=35.8, P<0.001). A MRT reveals that time allocation to mating behaviour during pre-laying was significantly higher than during both incubation periods (P<0.05).

During all stages of the breeding cycle males allocated significantly more time than females to mating behaviour, with differences between the sexes greatest during pre-laying and egg-laying where the discrepancy reached 19% and 14% respectively (Table 4.3.1).

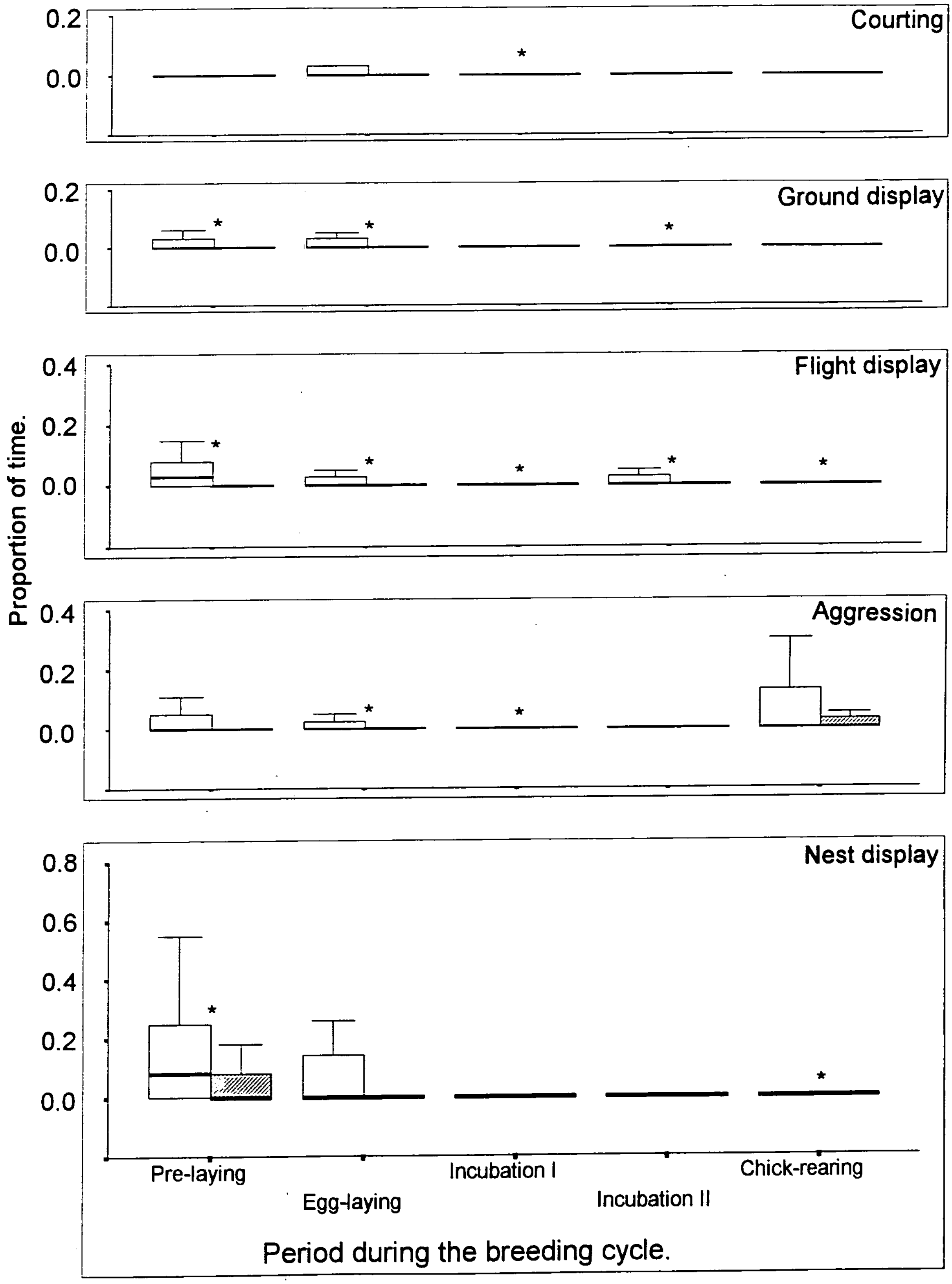
No single component of mating behaviour accounted for the variation witnessed at the composite level (Figure 4.3.2). No female was recorded performing the flight display at any stage during the study and ground displays were not performed during egg-laying and incubation periods. Likewise, no aggressive acts were recorded by females during early incubation, nor nest displays during chick-rearing. In contrast, all mating behaviours were recorded for males during all stages, with the single exception being ground displays during early incubation. Not surprisingly, all mating behaviour was concentrated mainly within the pre-laying and egg-laying periods of the breeding cycle (Figure 4.3.2), with the exception of aggressive behaviour. An increased proportion of time was allocated to aggression during chick-rearing by both sexes. This was probably associated with the movements of chicks, particularly when this involved relatively large translocations via other bird's territories. In all cases where a significant difference was found between the sexes in time allocated to different mating behaviour, time allocated by males was greater than by females (Figure 4.3.2).

Reproductive behaviour: parental

The pre-laying period has been excluded from this analysis as no behaviour was regarded as parental for the purposes of this section. The allocation of time to parental behaviour by males peaked during the incubation periods, although median values were zero throughout the breeding cycle (Table 4.3.1). Nonetheless their allocation of time to parental behaviour varied significantly (KW-ANOVA: χ^2_3=11.6, $P<0.01$), although a MRT suggests that no two periods were significantly different.

For females too, maximum allocation of time to parental behaviour occurred during incubation (65-82%) but they also maintained a relatively high allocation during chick-rearing (11%) (Table 4.3.1). This variation was also significant (KW-ANOVA: χ^2_3=21.2, $P<0.001$), but here a MRT revealed that all periods were significantly different from each other ($P<0.05$).

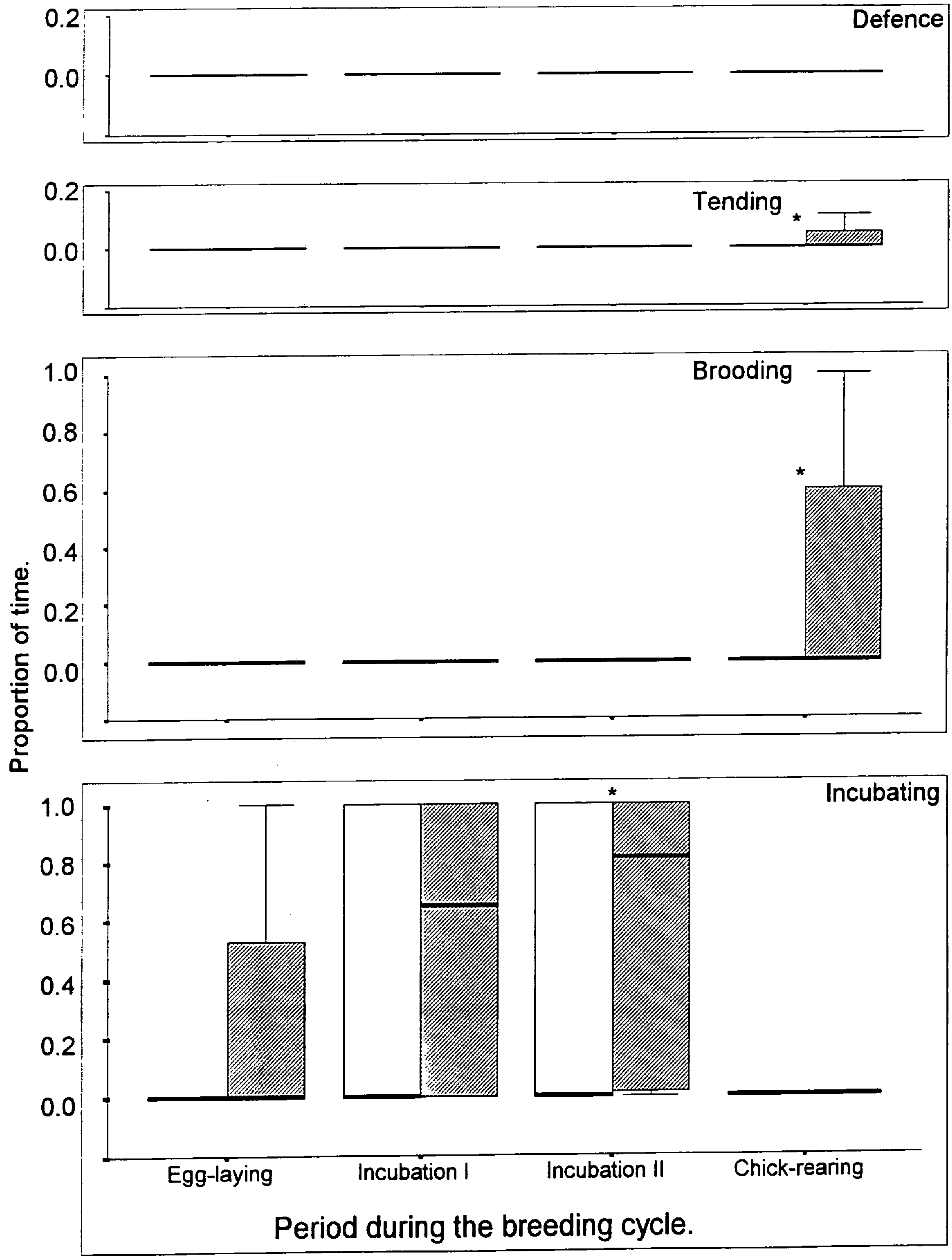
Figure 4.3.2. The proportion of time allocated to the components of mating behaviour for male (open bars) and female (hatched bars) Lapwings, 1995. Horizontal lines, bars and "whiskers" as in Figure 4.3.1. Sample sizes as in Table 4.3.1. *=significant difference between the sexes (Mann-Whitney U test, $P<0.05$).



The allocation of time to parental behaviour was similar for both sexes during egg-laying and early incubation, but the allocation by females exceeded that of males by around 82% and 11% respectively during late incubation and chick-rearing (Table 4.3.1).

Predictably, the main form of parental care during all egg stages was incubation and during chick-rearing was brooding (Figure 4.3.3). There was no difference in the frequency of incubation between the early and late incubation periods (males: $G_1=0.1$, n.s.; females: $G_1=0.7$, n.s.), nor before and after noon (males: $G_1=2.7$, n.s.; females: $G_1=1.7$, n.s.). Thus females were more likely to be found incubating than males at any time during the incubation period ($G_1=9.9$, $P<0.01$), as males were recorded sitting on the clutch in only 35% of 133 observations of incubating adults. Some incubation behaviour was recorded for males during the chick-rearing period, the result of asynchrony between clutches laid by polygamous females sharing a territory (Chapter 2). Anti-predator behaviour was not recorded for females during egg-laying and late incubation, and for males during late incubation. At no stage did male Lapwings allocate more time to any form of parental behaviour than females (Figure 4.3.3).

Figure 4.3.3. The proportion of time allocated to the components of parental behaviour by male (open bars) and female (hatched bars) Lapwings, 1995. Horizontal lines, bars and "whiskers" as in Figure 4.3.1. Sample sizes as in Table 4.3.1. *=significant difference between the sexes (Mann-Whitney U test, $P<0.05$).



Vigilant behaviour and absence from the territory

The allocation of time to vigilance in male and female Lapwings was highest during chick-rearing (23% and 13% respectively) and lowest during the incubation periods (maximum of 5% for males, zero for females) (Table 4.3.1). For males, variation between the chick-rearing period and the pre-laying and incubation periods was significant (KW-ANOVA: χ^2_4=27.0, $P<0.001$, with MRT, $P<0.05$), and for females the proportion of time allocated to vigilance was significantly lower during the incubation periods than during all other periods (KW-ANOVA: χ^2_4=68.0, $P<0.001$, with MRT, $P<0.05$).

Male and female Lapwings allocated similar proportions of time to vigilance during pre-laying, egg-laying and chick-rearing, but males were more vigilant during both incubation periods (Table 4.3.1).

The proportion of time spent away from the territory was low for both male and female Lapwings throughout the breeding cycle (Table 4.3.1). All median values were zero. The proportion of time spent away from the territory did not vary through the breeding cycle for males (KW-ANOVA: χ^2_4=8.0, n.s.), but females seemed to spend more time away from the territory during incubation (KW-ANOVA: χ^2_4=14.5, $P<0.01$), although a MRT revealed no differences between any two periods. This was reflected by significant differences between males and females during both incubation periods (Table 4.3.1).

Time constraints and associated trade-offs

Considering the associations among the components of maintenance behaviour first, males showed a significant, but weak, negative correlation between the allocation of time to feeding and roosting behaviour (Table 4.3.2). There were no such associations for female Lapwings (Table 4.3.2).

Table 4.3.2. Spearman correlation coefficients for the components of maintenance behaviour, from observations of male (n=281) and female (n=252) Lapwings throughout the breeding cycle, 1995.

		Behaviour	
Sex	Behaviour	Preening	Roosting
Male	Feeding	-0.06, n.s.	-0.15, $P<0.02$
	Preening	-	0.12, n.s.
Female	Feeding	0.10, n.s.	0.03, n.s.
	Preening	-	0.08, n.s.

In six of nine associations between the components of mating behaviour, males demonstrated significant positive associations (Table 4.3.3), whilst females did so in just one of six (Table 4.3.3). This suggests that males employ many different behaviours in close association during mate attraction and pairing. Also, the weak, but significant positive correlation between the proportion of time allocated to flight displays and aggressive behaviour by males, and the positive associations between flight display and other mating behaviour, illustrates the use of flight displays in both mate attraction and territorial defence.

Table 4.3.3. Spearman correlation coefficients for the components of mating behaviour, from observations of male (n=281) and female (n=250) Lapwings throughout the breeding cycle, 1995. F.D.=flight display; G.D.=ground display; N.D.=nest display; Conflict=aggressive behaviour.

		Behaviour			
Sex	Behaviour	F.D.	G.D.	N.D.	Conflict
Male	Court	0.13, $P<0.05$	0.00, n.s.	0.21, $P<0.001$	0.01, n.s.
	F.D.	-	0.28, $P<0.001$	0.27, $P<0.001$	0.14, $P<0.02$
	G.D.		-	0.15, $P<0.02$	0.00, n.s.
	N.D.			-	0.10, n.s.
Female	Court	x	-0.04, n.s.	0.21, $P<0.01$	0.08, n.s.
	G.D.	x	-	0.03, n.s.	-0.06, n.s.
	N.D.	x		-	0.08, n.s.

Conversely, there were no significant associations between the components of parental behaviour for males, but significant positive associations in two of four comparisons for females (Table 4.3.4).

Table 4.3.4. Spearman correlation coefficients for the components of parental behaviour, from observations of male (n=281) and female (n=250) Lapwings throughout the breeding cycle, 1995. Defence=anti-predator behaviour.

		Behaviour		
Sex	Behaviour	Brooding	Incubation	Defence
Male	Attending	0.00, n.s.	-0.03, n.s.	-0.02, n.s.
	Brooding	-	-0.03, n.s.	-0.02, n.s.
	Incubation		-	-0.06, n.s.
Female	Attending	0.27, *P*<0.001	x	0.13, *P*<0.05
	Brooding	-	x	0.03, n.s.
	Incubation		-	-0.10, n.s.

The positive association between anti-predator behaviour (defence) and the attendance of young by female Lapwings, resulted from the tendency for females to frequently associate with their chicks after disturbance from a predator (pers. obs.).

The following section investigates the constraints on feeding resulting from the allocation of time to reproductive behaviour. Both sexes exhibited a significant negative association between the proportion of time allocated to reproductive behaviour (mating and parental) and feeding (Table 4.3.5), which appears particularly strong for males. However, separate examination of mating and parental behaviour shows that mating behaviour did not constrain the time allocated to feeding by males, whereas parental behaviour did (Table 4.3.5). Interestingly, females showed a significant positive association between time allocated to mating behaviour and feeding and a negative association between parental behaviour and feeding (Table 4.3.5). This reflects the increased proportion of time allocated by females to both feeding and mating behaviour during the pre-laying period of the breeding cycle (Table 4.3.1). This suggests that for both sexes mating behaviour did not constrain the allocation of time to feeding.

Table 4.3.5. Spearman correlation coefficients for the proportion of time spent feeding and in reproductive behaviour, for male and female Lapwings, 1995. Absent=absent from the territory.

		Behaviour				
Sex	Behaviour	Reproductive behaviour	Mating	Parental	Vigilant	Absent
Male	Feeding	-0.76, *P*<0.001	-0.08, n.s.	-0.49, *P*<0.001	-0.05, n.s.	-0.26, *P*<0.001
Female	Feeding	-0.52, *P*<0.001	0.34, *P*<0.001	-0.58, *P*<0.001	0.29, *P*<0.001	-0.34, *P*<0.001

The time spent feeding was also not constrained by vigilant behaviour for male Lapwings, and females again showed a positive association between these two behaviours (Table 4.3.5). Not surprisingly, there was a negative association between the time spent away from the territory and feeding for both sexes (Table 4.3.5). This is probably misleading as it is likely that individuals off of the territory were feeding in nearby fields (Galbraith 1989a, pers. obs.).

Evidence of alloparental care in the Lapwing

One case of alloparental care was recorded, for a single female Lapwing, during 1995. This form of care occurs when an individual tends young that are not its own (Wilson 1975). The case in point concerns an unringed female (A) who was paired with a bigamous individually-ringed male. Female A's clutch of four eggs hatched on 5 May and three of the chicks were ringed (the fourth was still emerging from the egg). In an attempt to capture and ring the fourth chick on 12 May, female A was flushed whilst brooding an unknown number of chicks and as another, unringed chick was seen walking towards her. In total, five chicks were found at the spot from where the female was flushed, only two of whom were ringed.

The two ringed chicks and two of the unringed chicks had been brooded by the female, whilst the final unringed chick had been walking towards her, apparently responding to her calls. Thus, at least one chick produced by another female was being cared for by female A (one of the unringed chicks being brooded), probably two, and perhaps even three (if none of the unringed chicks were hers and if the chick walking towards her was being cared for). Rings were fitted to the remaining unringed chicks but the association was not seen again, and only one chick was known to reach fledging age. The parents of the other chicks cared for by female A were not known. It is possible that they were produced by her mate and his second female (B).

4.4 DISCUSSION

Mating behaviour

The investment in mating effort by male Lapwings (as measured by the proportion of time allocated to mating behaviour) peaked during the "pre-egg" stages of the breeding cycle. This would be particularly evident when including the heavy investment in territorial establishment and defence made by males before their mates joined them. Female mating effort also peaked during this time but, during all periods, male mating effort significantly exceeded that of females, with differences between the sexes in the median proportion of time allocated to mating behaviour of between 0% and 19%. The repertoire of mating behaviour also differed between the sexes, with males exclusively performing the flight display, as found by Dabelsteen (1978), and females not performing various behavioural acts at different stages throughout the breeding cycle (e.g. ground displays were not performed by females during egg-laying and both incubation periods, and nest displays were not performed during chick-rearing). In contrast, the only exception to the ubiquitous performance of the full repertoire of mating behaviour by males was the absence of the ground display during early incubation.

But why should males maintain a relatively high level of mating effort throughout the breeding cycle, even during chick-rearing? This could be of benefit to males if such behaviour facilitated the reclaiming of a territory in the following season. For example, males may acquire valuable experience of the territory and/or neighbours, as suggested for new recruits in the Red-winged

Blackbird *Agelaius phoeniceus* (Yasukawa 1979), or perhaps by maintaining their advertisement of residency they lower the likelihood of facing competitors in the following year: potential competitors being neighbours looking to expand their territory or new recruits (assuming some reconnaissance of potential breeding sites by recruits, e.g. Michael Reed & Lewis Oring pers. comm.). Also, males would benefit from continuing to indulge in mating behaviour if they could gain additional copulations with new females, either by attracting another female to the territory or by gaining extra-pair fertilisations (as suggested in the Corn Bunting *Miliaria calandra*, Møller 1983). In the event of loss of their mate this behaviour may even facilitate the acquisition of a new female. This would be feasible as individuals were known to arrive and settle in the area until very late in the season (Chapters 1 & 2) and the demonstration of sequential polyandry (Chapter 2) also suggests a benefit of continued mating effort. However, it does seem unlikely that conditions later in the season will be as favourable for breeding (Thompson *et al.* 1994) and relatively few instances of late-settling females breeding with established males have been recorded (pers. obs.). This raises the question of whether new pair bonds formed late in one season (perhaps without an associated breeding attempt) would re-form in the following season. Alternatively, Møller (1991a,b) suggested that post-mating displays by male birds could be a form of mate guarding: individual males would display during their mate's fertile period in order to deter potential cuckolders. Nonetheless, even if the potential benefits of prolonged mating effort are assumed to be small, the lesser role of the male in parental care (see below) suggests the associated time-costs would be small too (Maynard Smith 1977).

The proportion of time spent away from the territory was minimal for both sexes, although females spent more time off the territory during incubation than males. This indicates that although foraging does take place away from the territory (Galbraith 1989a; pers. obs.) the bulk occurs within the territory boundary, and that off-territory feeding was probably of greater importance to females.

Parental behaviour

Although biparental care of offspring is the predominant form of parental care among shorebirds, and was probably the ancestral state, this group exhibits the greatest diversity of care systems of any similarly-aged taxon (Székely & Reynolds 1995). For example, in many waders parental care by the male exceeds that of the female (Least Sandpiper *Calidris minutilla*, Miller 1985; Kentish Plover *Charadrius alexandrinus*, Lessels 1984; Paton 1995; Fraga & Amat (1996); Killdeer *Charadrius vociferus*, Mundahl 1982; Brunton 1988; Semipalmated Sandpipers *Calidris pusilla*, Gratto-Trevor 1991; Knot *Calidris canutus*, Whitfield & Brade 1991), mainly as the result of brood desertion by the female. This apparently contradicts predictions based on sexual selection (Bateman 1948; Trivers 1972; Clutton-Brock 1991; Arnold & Duvall 1994). However, among birds, females invest considerably more than males in their gametes (King 1973), leading to the suggestion that up to hatching, female waders will have incurred greater energetic costs than males and so, particularly in food-stressed environments, increase their fitness by departing to better feeding grounds (Ashkenazie & Safriel 1979). Uniparental care of offspring was also reported in 30% of 28 Lapwing broods by Blomqvist & Johansson (1994), but males were just as likely to desert as females.

In this study, parental effort was greatest among female Lapwings. Females spent up to 82% more time incubating than males, and up to 11% more time attending and brooding chicks. Although this estimate does not include energy expenditure, it is unlikely that this would reverse the above conclusion as it is generally accepted that females invest more energy in their gametes than males (King 1973). Indeed, the energetic cost of production for a single egg in shorebirds has been estimated at more than twice the female's basal metabolic rate: that is, each egg requires energy expenditure at more than twice the rate of normal maintenance requirements (Maxson & Oring 1980; Brunton 1988). It could be argued that the contribution of male Lapwings to parental effort was greater than suggested above due to the superior male effort devoted to vigilance during incubation. The maximum difference between the sexes with regards to time allocated to vigilance, however, was just 5%, clearly insufficient to compensate the extra expenditure of time by females in incubation (which was a more energetically-demanding task).

There were no differences in nest attendance by male and female Lapwings through the incubation periods or with time during daylight hours. However, it is not known whether males incubated more often than females at night as in some other waders (Willets *Catoptrophorus semipalmatus*, Howe

1982; Wilson's Plover *Charadrius wilsonia*, Bergstrom 1986; Thibault & McNeil 1995; Killdeer, Mundahl 1982; Brunton 1988; Kentish Plover, Warringer *et al.* 1986; Fraga & Amat 1996). If so, this could considerably alter the relative investment of the sexes in parental effort, particularly as incubating during low night-time temperatures may be more energetically demanding than during the daytime (Mundahl 1982).

The behaviour of male and female Lapwings during the incubation and chick-rearing periods illustrates quite distinct roles. Females take a more direct role in the care of the offspring, carrying-out the bulk of incubation (by day), brooding and tending of the young, whilst males were more actively involved with vigilant behaviour: the "tending" and "off-duty" roles described by Walters (1982, 1984). This was reflected by the spatial relations between the adults and chicks, with females most often found closest to the chicks (pers. obs.). However, unlike the situation reported by Walters (1982, 1984), in this study there was no evidence for the cycling of parental roles, for example, between the members of a breeding pair.

From the preceding section (and Chapter 2) it is clear that Lapwings conform to the general contention that investment by males in reproduction is biased towards mating effort, with female investment tending towards parental effort (Bateman 1948; Trivers 1972; Clutton-Brock 1991; Arnold & Duvall 1994).

Time constraints and associated trade-offs

Individuals have a fixed amount of time each day during which they must carry out all behaviour pertaining to maintenance, survival and reproduction. Under such conditions there are likely to be conflicts in the allocation of limited time to different, essential behaviour. In the Lapwing, reproductive behaviour clearly constrained feeding time (that spent searching for, handling and consuming prey) in both sexes, as indicated by the negative correlation between the proportion of time allocated to each behaviour. This was due to a negative association between the parental component of reproductive behaviour and feeding, as no evidence of a constraint on feeding time caused by mating behaviour was found for either sex. Given the greater role of female Lapwings in parental behaviour, this relationship would probably have a greater impact on females than males, and may be one reason why females were more likely to leave the territory than males: they may have used this time to feed in areas with greater prey abundance in order to improve their feeding efficiency.

Parental care in birds with precocial young is often regarded as less demanding than for altricial species because of the general absence of the need to feed chicks (Lack 1968; Emlen & Oring 1977; Oring 1982; Erckmann 1983). Where the investment of these species in reproduction has been quantified, however, parental behaviour has often resulted in less time available for feeding (Ashkenazie & Safriel 1979; Maxon & Oring 1980; Walters 1982, 1984; Brunton 1988), suggesting a significant cost. Indeed, the costs of parental care in the Southern Lapwing *Vanellus chilensis* are thought to have led to co-operative breeding (trigyny) in order to share parental duties and allow more maintenance time per individual (Walters & Walters 1980; Walters 1982). Data from the current study support the notion that parental behaviour in shorebirds should not be regarded as trivial without justification. No differences were found, however, in the parental behaviour of monogamous or polygamous individuals (see Chapter 2). This may have been due to the specialisation of parental care roles maintained by the sexes, as previously mentioned: the "off-duty" care provided by male Lapwings is a form of non-depreciable care (Clutton-Brock 1991), meaning that its value per individual offspring does not decline with increasing brood size. Thus males could provide sufficient care for offspring from two or three females without adjusting their activity budget. Also, as males adopt a less active role in the direct care of young (i.e. in depreciable forms of care), females were unlikely to need to adjust their activity budget when paired with an already-mated male.

In conclusion, therefore, although significant activity-budget costs of parental care were identified for both sexes in the form of constraints on the time available for feeding, the specific parental roles of the sexes permit the occurrence of polygyny without the need to adjust behaviour.

During this study, one female was recorded caring for at least one chick, and probably three, produced by another female. Similar behaviour was reported in a related species, the Southern Lapwing by Walters and Walters (1980). Three of the four cases they described bear a remarkable resemblance to the bigynous mating system described here for *V. vanellus*, the exception being that in *V. chilensis* the females co-operated with nest and territory defence, incubation and chick rearing (Walters & Walters 1980). The female in this study found caring for another's young was mated with a polygamous male, raising the possibility that this may occur regularly among polygamous individuals. It is feasible that such occurrences have been previously overlooked, particularly where some chicks were lost so that the total number cared for by an individual may appear normal (i.e. 1-4). This type of co-operation may provide a benefit of polygamous associations (Altmann *et al.* 1977).

GENERAL DISCUSSION

I believe that some of the main points noted in this thesis may illustrate the interplay between habitat, population demography and behaviour, although at this time it is not possible to prove the connection. Suitable breeding habitat for Lapwings is limited in Upper Teesdale: habitat quality within the study site is variable (as reflected by varying breeding densities in different fields and reproductive consequences to individuals; Baines 1988, 1989, 1990), and the habitat surrounding the study site (extensive heather moors around the head of the valley and intensively-managed hay fields lower down) would appear to be largely unsuitable for breeding Lapwings (Shrubb & Lack 1991). This has resulted in a limited area for breeding and a still smaller area (i.e. unimproved fields; Baines 1989) offering high breeding success. Along with the relatively high and stable number of breeding Lapwing in Upper Teesdale (Thompson *et al.* 1994), these factors may be linked with at least two major attributes noted in this thesis: 1) high rates of non-breeding, and 2) a high frequency of polygyny. High rates of non-breeding were reported in Chapter 3, particularly among yearling males, together with an associated tendency for older males to maintain the same breeding status in consecutive years, even where this meant persistent non-breeding. These factors are symptomatic of intense competition among males for limited breeding territories. As discussed in Chapter 3, it is unlikely that such high frequencies of non-breeding were the result of breeding restraint, primarily because of the high mortality rate in this species (Peach *et al.* 1994). Chapters 2 and 3 showed that a male's success at establishing a territory and his mating success increased with age, suggesting that the older males (three years plus) were the more successful at monopolising territories and mates. The prevention of some male birds from breeding due to territoriality was discussed at length by Brown (1969) and has been demonstrated in a number of species (e.g. by Orians 1961; Watson & Jenkins 1968; Krebs 1971; Crook & Shields 1985; Arcese 1987; Robertson & Stutchbury 1988; Martin 1989; Meek & Robertson 1991; Gori *et al.* 1996). The prevention of males from breeding, via territoriality, has been suggested in only four species of waders: Dunlin *Calidris alpina* (Holmes 1966), Oystercatcher *Haematopus ostralegus* (Harris 1970), Temminck's Stint *Calidris temminckii* (Hildén 1979) and the Lapwing (Galbraith 1988c). The mechanism by which this process may operate in the Lapwing was discussed in Chapter 3. Briefly, it seems likely that most yearling males were competitively inferior to older males and as such could not obtain a territory, and that once established in a territory, site-faithful residents had a competitive advantage over non-territorial males.

In this study, there was little evidence of female Lapwings being prevented from breeding, as most of the ringed-females that were seen also bred and many paired with already-mated males. That females were not prevented from breeding suggests that territoriality is unlikely to result in the density-dependent regulation of Lapwings in Upper Teesdale (assuming only a minimal reduction in productivity per female due to polygyny, see Chapter 2) (Brown 1969). This contrasts with the views of Galbraith (1988c) and Hudson *et al.* (1994) regarding the regulation of Lapwing populations, although the frequency of polygyny was assumed to be "restricted to a minority of males" by the former author and not considered at all by the latter authors. The extent to which potential productivity was lost, however, by those individuals breeding in marginal habitats (e.g. improved fields; Baines 1989) is not known as the fields comprising the intensive site were largely of high quality. This could potentially provide a mechanism for density-dependent regulation if sufficient individuals were "forced" into such areas and productivity within them was sufficiently low to prevent an increase in numbers. In a review of the population dynamics of wading birds, Evans and Pienkowski (1984) concluded that territoriality on the breeding grounds was unlikely to lead to the regulation of numbers of breeding females due to the availability of ample breeding sites for most species. However, this conclusion was couched in terms of the species' entire range. It seems reasonable to suggest that on a local scale breeding density (at least of males) would ultimately be limited by the availability of suitable habitat, assuming that individuals require a certain area for successful reproduction.

The high frequency of polygyny found in this study may be another consequence of the limited availability of suitable breeding habitat in Upper Teesdale. As first postulated by Emlen and Oring (1977), the occurrence of polygyny is determined largely by the distribution of available resources and the ability of males to monopolise them and females. In this study, some males were deterred from breeding (by territorial exclusion), which resulted in a female-biased operational sex ratio (the ratio of fertilisable females to sexually active males), increasing the likelihood of polygyny (Emlen & Oring 1977). Changes in the frequency of polygyny induced by manipulations of the operational sex ratio have been reported in other bird species, e.g. Red Grouse *Lagopus lagopus scoticus* (Watson & Jenkins 1968; Hannon 1984) and Song Sparrow *Melospiza melodia* (Smith *et al.* 1982), and the link from resources (e.g. breeding habitat) via female dispersion to mating systems, has also been demonstrated in insects, fish, amphibians, reptiles and mammals (reviewed by Davies 1991). This is not to say, however, that female Lapwings in Upper Teesdale were forced into mating polygynously due to a lack of unmated males. In all years of this study, unmated, territory-holding males were present for large periods of the breeding season, certainly at the time around female settlement.

If polygyny in the Lapwing is closely associated with the availability of suitable breeding habitat, this raises the possibility that the frequency of polygyny was recorded as low in many previous studies because it was indeed rare, due to ample breeding habitat able to accommodate all males. However, as stated in Chapter 2, it is also possible that high frequencies of polygyny, as found in this study, were overlooked by previous workers where unmarked birds were studied. Assuming a link between habitat availability and the frequency of polygyny, it would follow that recent declines in the suitability of agricultural habitats for breeding Lapwings (see General Introduction) may be increasing the frequency of polygyny in this species. That, on average, productivity per female was not significantly decreased when females mated polygynously, suggests that an induced increase in the frequency of polygyny would have little impact on population dynamics, at the frequencies of polygyny found in this study.

A significant relationship between age and some components of Lapwing breeding biology was found here for both males and females (Chapters 2 & 3). It was concluded that this pattern resulted from constraints (ecological and developmental) which limited breeding success; i.e. factors beyond the control of the individual which impaired reproductive performance. Patterns of age-specific reproductive success are common among birds (see Chapter 3 and refs. therein) and appear to be nearly ubiquitous in vertebrate breeding systems (Clutton-Brock 1988b). Some examples are used here to illustrate the effects of age on breeding biology in the non-bird taxa.

In fish, amphibians and reptiles, most species continue to grow (perhaps at a decreasing rate) throughout life, whereas mammals and birds cease growing (in mammals this is at about the age of sexual maturity, whilst in birds cessation of growth occurs sometime during their first year of life) (Lagler *et al.* 1962; Bellairs 1969; Pough *et al.* 1989; Duellman & Trueb 1994). The continued growth throughout life of the "lower" vertebrates complicates the investigation of age-related fecundity due to the positive correlation between age and body size, and the general increase in fecundity (particularly of females) with increasing size (Lagler *et al.* 1962; Bellairs 1969; Pough *et al.* 1989; Duellman & Trueb 1994). For example, in both Bullfrogs *Rana catesbeiana* and Woodfrogs *Rana sylvatica*, there is a close relationship between age and body size for both sexes (Howard 1988). In both species, older (larger) males had greater mating success, which resulted mainly from their ability to monopolise prime oviposition sites (Howard 1983; Howard & Kluge 1985; Howard 1988). In contrast, older females were more fecund than their younger congeners, with both species producing more eggs as they aged and older female Woodfrogs also producing larger eggs (Howard 1983; Howard & Kluge 1985; Howard 1988). Evidence for the exclusion of some males from breeding was also found: in one year out of three, a year of high male-density, the hatching success of male Bullfrogs was strongly skewed in favour of the few individuals able to secure oviposition sites (Howard 1983). Therefore, in years with a high density of males, young males were prevented from breeding by the older, despotic males (ecological constraint). No evidence for such constraints on the breeding of females was found.

Among mammals, many examples of age-related reproductive variation have been documented. In the Northern Elephant Seal *Mirounga angustirostris*, the number of females inseminated, and the number of pups sired, by males increased between the ages of six and 11 years, although the number of pups produced declined again after this point (Le Boeuf & Reiter 1988). Likewise, more females weaned pups after six years-of-age, despite more younger females successfully giving birth, but here there was no decline in fecundity in later life (Reiter *et al.* 1981; Le Boeuf & Reiter 1988). Again, the age-specific pattern of breeding success probably resulted from different causes in males and females. Among males, breeding success increased with age up to the prime age of about 11, due to increased size and social dominance (Le Boeuf & Reiter 1988). At 11 years-of-age, males were most successful at excluding other males from a particular area of the beach and so gained exclusive access to a large number of females. This suggests that subordinate males were prevented from breeding by social constraints, presumably ultimately determined by the limited breeding habitat (island beaches). The breeding success of old territorial males was greater than that of younger territorial males, because the former were better able to monopolise more females by way of their larger body size. Some subordinate individuals will approach females when not deterred by dominant males (Le Boeuf & Reiter 1988), suggesting that they were not showing reproductive restraint. Reiter *et al.* (1981) suggested that female Elephant Seals would not be expected to show reproductive restraint as mortality rates increased throughout life, a situation also true of males. Increasing mortality rates with age increase the cost to benefit ratio for breeding restraint, as any individual is increasingly less likely to return in successive breeding seasons. Thus, selection in this situation should favour breeding at the earliest opportunity. Instead, female fecundity appeared to be constrained by their own size and experience (Reiter *et al.* 1981).

A similar breeding system, involving social dominance hierarchies, occurs in many polygynous mammals. For example, in the European Rabbit *Oryctolagus cuniculus* older individuals are usually dominant over those that are younger, in both sexes, such that only dominant individuals breed in any year, or subordinate individuals are forced to breed at the periphery of the warren in less desirable sites (Thompson & Worden 1956; Lockley 1961). Likewise, only the older, dominant Red Deer *Cervus elephus* breed successfully in any year (Clutton-Brock *et al.* 1986, 1988). Among group-living Red Foxes *Vulpes vulpes*, however, such a hierarchy seems to prevail among the females only, as usually only one male is present in any group who has exclusive access to the breeding, dominant female(s) (MacDonald 1989). Age-related breeding performance, via dominance hierarchies, occurs frequently among primates (Cowlishaw & Dunbar 1991), having been demonstrated in, for example, the Rhesus Monkey *Macaca mulatta* (Smith 1980), Chimpanzee *Pan troglodytes* (Goodall 1990), Red Howler Monkey *Alouatta seniculus* (Pope 1990) and Barbary Macaque *Macaca sylvanus* (Kuester & Paul 1992; Kuester *et al.* 1995). For instance, in the Savannah Baboon *Papio cynocephalus*, males were prevented from mating until 7-8 years-of-age, despite being capable of reproducing when 6-years-old, by socially higher-ranking (older) individuals (Altmann *et al.* 1988). Among females, the ability to reproduce was also attained when about 6-years-old, although this was modified by the mothers rank within the group: daughters of high-ranking mothers (at the time of conception) themselves conceived about seven months earlier than daughters of low-ranking mothers. After their first conception (the litter size for Baboons is one), females produced young at a relatively constant rate until the age of 10-12 years. After this age, illness often resulted in decreased breeding success. In the absence of pathologies, however, females could keep producing young until death (Altmann *et al.* 1988). Among female Baboons, therefore, reproduction did not appear to be influenced by any form of constraint after maturation, except that caused by illness in later life, although it could be argued that the age of reproductive maturation was constrained by their mothers dominance rank. The modifying influence of the mothers dominance rank has also been found to affect males in other primates. Sons of high-ranking mothers in the Rhesus Monkey *Macaca mulatta* often rise to a high social rank themselves after spending less time at lower ranks (Koford 1963), and may live longer with a higher lifetime reproductive success, than sons of low-ranking mothers (Meikle *et al.* 1984; Meikle & Vessey 1988). A similar modification of the linear dominance relationships sometimes occurs in primates due to the formation of coalitions between two or more individuals as, for example, in the Chimpanzee (Goodall 1990), Red Howler Monkey (Pope 1990) and Barbary Macaque (Kuester & Paul 1992; Kuester *et al.* 1995). Indeed, the high reproductive success of the oldest males in the latter species (Kuester *et al.* 1995) was maintained largely by way of teamwork between such individuals. This behaviour effectively limited the mating opportunities open to the younger males, despite their superiority over older males in one-on-one confrontations (Kuester & Paul 1992; Kuester *et al.* 1995).

The above examples of age-related reproduction share some striking points of similarity and generally concur with the situation found in birds (see Chapter 3 and refs. therein). Constraints preventing breeding in younger individuals were evident in at least one sex for all species. Among males, these constraints took the form of the exclusion of subordinate (younger) individuals by the older despotic males, which appeared to be linked to limited breeding habitat (oviposition sites in the Frogs and beaches in the Seals), although this was less clear in the Savannah Baboons. The social organisation of the latter species, however, is known to be related to habitat, and in particular, the distribution (clumped or dispersed) of food (e.g. Barton *et al.* 1996). Likewise, Goodall (1990) suggested that suitable habitat for the Chimpanzees at Gombe, Tanzania may have been limited. Thus ecological constraints appear to be relatively common. Among the females, the main constraints evident (if any) were physiological, associated with the process of reproductive maturation, although in some group-living species, like the Rabbit and Fox, young females may be prevented from breeding by older, dominant females too (Thompson & Worden 1956; MacDonald 1989). None of the species provided a clear example of reproductive restraint. That is, none refrained from breeding despite having reached sexual maturity and despite the absence of any constraints. Indeed, I am not aware of any study able to demonstrate a pattern of age-specific breeding performance resulting from reproductive restraint (as defined here), lending support to the notion that this is probably relatively rare in the animal kingdom (Clutton-Brock 1988b; Chapter 3 and refs. therein).

SUGGESTIONS FOR FURTHER STUDY

I believe this thesis has highlighted several areas that would benefit from further study, all of which have been briefly mentioned in the relevant sections. Here I wish to discuss in more detail a few of these topics, which I feel are important in furthering our understanding of Lapwing biology, but also have broader applications too. The topics are 1) the occurrence of polygyny, 2) age-specific reproductive performance and 3) the heritability of laying dates and egg size. The proposals below are based on further studies of the Lapwings in Upper Teesdale, as they provide an excellent system in which to examine these points. Firstly, the high site-fidelity and philopatry of this species offers good returns on investment in the individual ringing of birds (which is essential for the following discussion) and allows individuals and their offspring to be monitored in successive years. Also, in detailed studies it is possible to estimate with relative confidence the breeding success to fledging of Lapwings, and if this were associated with a more extensive, long-term approach, a good indication of success up to the recruitment of offspring would be possible. The site used in this study (and by previous workers) offers good access to all areas and current relations with land owners and workers are good.

The variable mating system demonstrated for the Lapwings in Upper Teesdale provides a good opportunity to investigate the factors determining the occurrence of different facets of this behaviour. In particular, the high frequency of polygyny among territorial males is ripe for exploitation in this way. The occurrence of polygyny has been of considerable interest for some time, with most attention focusing on the predictions of the polygyny threshold model (see Vehrencamp & Bradbury 1984; Searcy & Yasukawa 1989). Some points of interest were noted in this study: for example, males were shown to benefit from polygyny by producing more offspring, and the occurrence of polygyny was probably facilitated by a female-biased operational sex ratio. The question remains, however, as to why females mated polygynously. Were they doing so because there were no unmated males available? - apparently not, as some unmated males were present in all years. Were females choosing to breed on territories where their fitness was maximised, or did they settle at random? These questions were raised in Chapter 2. To answer them thoroughly, I believe an investigation into the habitat parameters determining the breeding success of Lapwings is necessary. If key factors could be identified, and their effects quantified, then predictions following the polygyny threshold model (and other hypotheses) could be made regarding male and female settlement and male mating success, and correlations confirmed via experimental manipulations (where possible). This approach has been adopted in relatively few studies (Vehrencamp & Bradbury 1984) due to practical complexities (but see Pleszczynska 1978 and Evans & Burn 1996). The accessibility of breeding Lapwings in Upper Teesdale, and the simplicity of the habitat, would facilitate such a study without serious complications.

If habitat quality could be homogenised across several territories (either by random selection of territories, habitat manipulations or statistical control), a corollary to the above investigation would be one into the influence of male characteristics on female settlement. There was some evidence in this study to tentatively suggest that male flight displays played some role in mate attraction and pair formation, although, other than in terms of activity budgets, this behaviour was not quantified (e.g. number of twists and dives, etc.). Such quantification would be difficult without the aid of video equipment allowing the repeat examination of such flights at reduced speed. A simple way of superseding this approach would be to reduce the ability of individual males to perform this display. Such an approach has been used successfully by Anders Møller and co-workers during studies on the Skylark *Alauda arvensis* and the Black Wheatear *Oenanthe leucura* (Møller 1991a; Møller *et al.* 1995): the removal of some primary feathers of males impaired their ability to display in both studies (Skylark: flight display; Black Wheatear: stone carrying [a post-mating display, Soler *et al.* 1996]). Likewise, I would expect the removal of one or two primaries from each wing of male Lapwings to impair their ability to perform flight displays, either by forcing them to perform simpler displays (i.e. comprising fewer units) or for shorter periods. The mating success of experimental and control males could then be compared. Ringing efforts have previously demonstrated the practicality of catching adult Lapwings.

The second point for further study was the investigation of age-specific breeding performance. This phenomenon has been found in many species of birds (see Chapter 3) and other vertebrates (see General Discussion). In the Lapwing, however, relatively little effect of age was found in relation to breeding success, although this conclusion may have been compromised by the small sample sizes in some analyses. This is surprising as even short-lived passerines have been shown to exhibit significant age-specific reproductive effects (e.g. Blackbird *Turdus merula*, Desrochers & Magrath 1993). Here again I feel it would be important to confirm this pattern of apparent indifference of breeding success to age, given the unexpected nature of the result. Greater effort devoted to the location and monitoring of clutches laid by yearling females would be necessary, followed by similar comparisons with older females as made in this thesis.

One difference in fecundity found between yearling and older female Lapwings was egg size (see Chapter 3). In a cross-sectional analysis, egg size was 5% smaller in yearling females than adults, a result confirmed by a longitudinal analysis of individuals present in more than one year. It was proposed that this was the result of a constraint on the ability of yearling females to produce larger eggs, with one possibility being inefficient foraging. I suggest that one way of testing this relationship would be to manipulate food availability on a sample of territories, by providing supplemental food to both yearling and adult females. Such an approach was employed in a study of Blackbirds by Desrochers (1992). If yearling females were constrained by a lower foraging efficiency relative to adults, the provision of extra food should compensate for this and allow them to produce larger eggs. Alternatively, this action may have no effect, or it may increase egg size in both yearlings and adults. The former result would suggest that neither yearlings nor adults were constrained by food availability and that some other factor caused the difference in egg size between them (perhaps morphological differences), and the latter would suggest that egg size in both yearling and adult females was limited by food availability, with the relative increase in egg size in both groups indicating whether yearlings also suffered from lower foraging efficiency. Preliminary trials conducted in 1995, suggest that the provision of supplementary food may be problematic, unless Lapwings became accustomed to feeding from an artificial feeder. An alternative approach may be to chemically remove potential prey items from experimental territories, perhaps by treatment with formaldehyde to remove worms and/or a general insecticide for other invertebrate groups.

Finally, I believe that the high rates of philopatry and site-fidelity exhibited by Lapwings in Upper Teesdale, provide the perfect opportunity to investigate the degree of heritability of laying dates and egg size. A high degree of heritability has been suggested for these traits in other waders (see Chapter 3), but Galbraith (1988b) suggested that low variation in egg size within clutches laid by the same female may reflect maternal condition, and Leblanc (1989) suggested between year consistencies may result from little temporal variation in environmental conditions. One of the strongest ways to investigate the role of heredity in determining laying dates and egg size would be to compare these traits in mother-daughter correlations. In the Lapwing, the fact that young birds recruit into areas close to where they had previously hatched allows the control of within-year environmental variation, and it should be possible to compare some mothers and their daughters breeding in the same year. Effort targeted at catching these females during the pre-laying period (by tried and tested methods used to catch Lapwings for ringing) would also facilitate the consideration of body condition (i.e. body weight scaled for size). Multivariate statistical methods could then be used to separate, and at least rank, the effects of different variables on egg size.

SUMMARY

1. Between 1993 and 1995, the behavioural ecology of uniquely colour-ringed Lapwings *Vanellus vanellus* was studied in Upper Teesdale, Co. Durham. The aims of the study were to describe the mechanisms underlying group characteristics.

2. Male Lapwings arrived on the breeding grounds before females (by up to 8 days) and arrival dates (of both sexes) varied with age. Among males, arrival dates became progressively earlier with advancing age, up to at least four years-of-age. Among females, however, arrival dates were earlier for 2-year-olds than for younger and older females, and the relationship could be described by a quadratic equation. Further study was recommended to confirm the different relationships in the two sexes.

3. Arrival dates at the breeding grounds in 1993 were, on average, six days later than during 1994. It was shown that this was caused in part by both harsh weather during early 1993 and by the late recording of early-arriving individuals by field workers in the same year.

4. Differences in arrival dates were not correlated with the type of field chosen in which to breed, nor with eventual breeding status. However, the date of egg laying for the first clutch was found to advance by one day for every three-day advancement in the arrival of individual females.

5. Among most age groups arrival dates did not influence subsequent survival rates. However, yearling males arriving before the median date of arrival for this group showed a 44% decrease in return rate the following year, when compared to those arriving after the median arrival date.

6. The Lapwings in this study exhibited a varied social mating system. On average, 30% of 136 territorial males mated with up to three females (despite the presence of unmated, territory-holding males); two polygynous males were polyterritorial (2% of 136 male-years); five females produced second clutches despite the successful hatching of their first clutch (4% of 104 female-years) and one female paired sequentially with two polygynous males (1% of 104 female-years), the second mate taken after the predation of her first clutch.

7. The number of females per territory-holding male was associated with male age, with males over 2-years-old having the highest frequency of polygyny (32%). In contrast, the majority of yearlings (67%) remained unmated and the majority of 2-year-olds (70%) were monogamous.

8. In a comparison of the number of mates per male in consecutive years, unmated males tended to gain at least one female, whilst mated males (monogamous and polygynous) usually remained unchanged.

9. Male Lapwings mated to more than one female raised an extra 1.0 chicks to fledging each year in comparison with monogamous males. No difference in between-year return rate was found among males in relation to the number of mates on their territory so, assuming similar rates of cuckoldry among males, and given the consistency in mating status between years, polygynous males would raise more young in their lifetime than monogamous males.

10. In a simple comparison of monogamous and polygynous females, no differences in seasonal reproductive success were found, tentatively suggesting little immediate impact of polygyny on female fitness.

11. Activity budgets of both males and females were similar when comparisons were made between monogamous and polygamous individuals, suggesting that neither sex had to make significant adjustments in behaviour in response to the mating system. However, polygynous females were more aggressive during the pre-laying period than monogamous females, mainly due to conflicts with their female territory-mates. It was suggested that this was due to female territoriality.

12. Territory size was found to be similar for unmated and monogamous males, whilst a linear increase in territory size occurred between monogamous and trigamous males. This suggested that a minimum area

of 2468 ±419m^2 was required by females before they settled with a male, probably to provide sufficient food for the female and/or her chicks.

13. As a stimulus for further study, it was suggested that polygyny in the Lapwing was facilitated by a female-biased operational sex ratio, resulting from the despotic exclusion of some males from limited breeding habitat. It also appeared that little or no choice of breeding situation occurred, suggesting random settlement of both sexes, or the repeated selection of an area based on a previous decision.

14. It was suggested that the establishment of an extra territory in 1995 by two male Lapwings, served either to prevent their first mates from hindering the attraction of a second mate, to improve their breeding success by reducing female-female aggression or to increase their territorial domain despite the restrictions imposed by neighbouring males around the original territory, and thus facilitate the attraction of a second mate.

15. Five females attempted to produce second clutches during this study, apparently in response to the reduction of the first brood to a single chick. This contrasts with the situation demonstrated in the only other record of double-brooding in the Lapwing, where this behaviour was apparently a genuine attempt to increase seasonal reproductive output.

16. Among males, the proportion of individuals which bred each year was dependent on age, with yearlings consistently having the lowest proportion of breeders (35%), although low proportions were also found for the oldest age group in each year (44% for 3-year-olds in 1993, 46% for 4-year-olds in 1994). No such patterns were discernible among females.

17. The proportion of breeding males within a cohort increased by 32% between the ages of one and two years. However, for age increases in the older cohorts the proportion of breeders (even when low) was remarkably constant between years. This was attributable to the maintenance of breeding status between years by individual older Lapwings, even where this meant consistent non-breeding. A similar effect was evident among females.

18. The pattern of non-breeding among males was probably the outcome of intense intermale competition for limited breeding space, which prevented some males from breeding. That some males in the older cohorts consistently failed to breed suggested inherent quality differences among individuals, or the effects of previous experiences, which influenced their competitive ability. Females were not influenced in the same manner as many were able to mate polygynously.

19. Overall, 20% more female Lapwings bred than males, with the majority of females in each age group breeding (the lowest proportion breeding was

63%). Non-breeding in female Lapwings may have been influenced by body condition rather than a lack of breeding vacancies.

20. Of 33 pairs in which both individuals were of known age, 39% were identical in age and 67% were of the same age, or differed by just one year. Where there was an age difference within pairs the male was usually 1-2 years older than the female, primarily the result of significantly more adult male-yearling female pairs than expected by chance (33% of pairs). This probably resulted from the higher proportion of females breeding as yearlings than males.

21. The location of 216 nests was recorded in relation to the distance from the field boundary (dry-stone wall or fence) between 1993-95, and 686 spot observations of individual Lapwings were made during 1994. Overall, only 25% of the nests, and 50% of the spot observations which were expected on the basis of chance, were found within 20m of the field boundary. For fields ranging in size between 4.1ha and 12.5ha, this suggests that between 22% and 66% of the total area of a field was avoided by Lapwings.

22. The avoidance of dry-stone walls was probably an anti-predator behaviour, either in response to raptor predation on adults and chicks and/or Mustelid predation on clutches. Alternatively, this could be an

inherited response to some previous form of selection pressure which is no longer acting (e.g. fox predation).

23. No consistent, detectable effect of female age on the date of laying or clutch size for first clutches was found. Over the three-year study period, about 70% of 100 first clutches were laid within a 12-day period centred around 8 April, and 86% of 106 first clutches contained four eggs.

24. On average, eggs laid by yearling female Lapwings (n=33 clutches) were 11% narrower than those of adults (n=110 clutches), which resulted in a 5% discrepancy in egg volume. The change in egg volume within 7 individuals between one- and two-years-of-age reflected the pattern predicted from within year differences between age groups.

25. It is suggested that the age-specific pattern of egg size resulted from the reproductive maturation of individuals (i.e. constraint hypothesis). Specifically, an increase in feeding efficiency was regarded as the most likely cause of increases in egg size with age.

26. Variation in egg volume was greater between clutches laid by different females than within. Similarly, mean egg volume for clutches laid in consecutive years showed a high index of repeatability (0.72), probably due to a high degree of heritability of egg size. Likewise, the date of laying

for the first clutch was also probably heritable, as repeatabilities were again high (0.50).

27. An important assumption of the Mayfield method for estimating hatching success, that clutch mortality rates are constant across space and time, was found to be invalid for the Lapwing clutches in Upper Teesdale. Significant variation in hatching success of first clutches was found both between and within fields, throughout the breeding season and between years. This emphasises the need to justify the pooling of clutches in calculations of hatching success.

28. Overall, hatching success of first clutches was around 20% lower in 1995 than the previous two years, and during 1995 hatching success was also found to be about 25% lower within 25m of the field boundary. Variation in clutch mortality appeared to result from differences in activity of Stoats *Mustela erminea* between years and fields, within fields and throughout the breeding season. This was also accompanied by differences in farming practices between fields and through the season.

29. No differences in the hatching success of first clutches were found among females of different ages and overall 63% of 104 first clutches hatched at least one chick.

30. The proportion of hatched-chicks which subsequently fledged per successful first clutch, and the number of chicks fledging from each first clutch laid, did not differ among females of different ages.

31. That no effect of age on breeding performance was found contradicts many previous studies on age-specific reproductive success in birds. This may have been an artificial result based on small sample sizes, although this is regarded as unlikely. Alternatively, age effects may have been masked due to good, or bad, environmental conditions (e.g. food abundance or predation respectively). Further study is recommended.

32. Of 39 females who lost their first clutches, 61% of them laid a replacement clutch. The frequency of relaying was found to be independent of female age, the date of loss of the first clutch and the "age" of the first clutch. The average period between the failure of the first clutch and laying of the replacement was 7.8 days (S.D.=4.6 days, n=18). There was no relationship between the "age" of the first clutch at failure, and the period between failure of the first clutch and laying of the replacement.

33. Biometrics were recorded from first and replacement clutches of 19 females. Clutch size was the same (four eggs) for 13 females (68%). Egg volume was 4% smaller in replacement clutches than in first clutches, the result of a significant decrease in egg length (1.8%) and breadth (1.1%) in replacement clutches. Thus, indices of repeatability were low between first

and replacement clutches, probably reflecting environmental influences on egg size.

34. The hatching success of replacement clutches (32%) was 37% lower than for first clutches in 1993 and 1994, but not significantly different from that of first clutches in 1995. The success of replacement clutches did not vary with differences in female age.

35. The median number of chicks raised per female on the intensive site from first clutches, between 1993-95 (64 individually-recognisable females, 92 female-years) was 0.5, inter-quartile range=0.0-2.0 (mean=1.0). Productivity at this level would be more than sufficient to maintain the local population. However, this may not be ubiquitous, so should not be taken as an indicator of productivity for Lapwings in all of Upper Teesdale.

36. The mode of investment by each sex in reproduction was investigated in 1995 via activity-budget analyses.

37. The allocation of time to somatic behaviour (mainly feeding) peaked for both sexes during the pre-laying period (median proportion of time: 60% and 74% for males and females respectively). Thereafter the allocation of time to somatic behaviour by males declined to between 30-40%. Among females, however, this fell to zero during incubation and increased again to 42% during chick-rearing.

38. The allocation of time to somatic behaviour by females exceeded that of males during the pre-laying period (by 14%), but that of males exceeded females during incubation (by 28-45%).

39. The proportion of time allocated to mating behaviour peaked during pre-laying and egg-laying for male Lapwings (22% and 14% respectively) and declined to 0-6% thereafter. For females, the peak also occurred during pre-laying (3%) but declined to zero thereafter.

40. At all stages throughout the breeding cycle the allocation of time to mating behaviour by males exceeded that of females by up to 19%.

41. The proportion of time allocated to parental behaviour peaked in both sexes during incubation, although median values for males were zero throughout the breeding cycle. The allocation of time by females during this period varied between 65-82%, dropping to 11% during the chick-rearing period.

42. The allocation of time to parental behaviour by females exceeded that of males during the latter half of incubation and chick-rearing (by 82% and 11% respectively). No other periods were significantly different.

43. For both sexes, the frequency of incubation did not vary between the early and late incubation stages, nor between morning and afternoon. At

any time, females were more likely to be incubating than males: males were found at the nest in just 35% of 133 observation sessions of incubating adults.

44. The allocation of time to vigilant behaviour peaked in both sexes during the chick-rearing period of the breeding cycle (23% and 13% of activity budget for males and females respectively), and was lowest during incubation (max. of 5% for males and zero for females).

45. The allocation of time to vigilant behaviour was similar for both sexes, except during incubation, when that by males exceeded females by up to 5%.

46. The proportion of time spent away from the territory was low for both sexes: all median values were zero throughout the breeding cycle. However, females spent significantly more time away during incubation when they presumably left to feed in fields offering greater food availability. The high rate of territorial attendance illustrates the importance of the territory in providing most of the resources needed by breeding Lapwings.

47. Correlations between the components of mating behaviour indicated that male Lapwings employed a suite of tactics in mate attraction and pairing. Such associations also implicated the use of flight displays during both mate attraction and territorial defence.

48. The proportion of time allocated to mating behaviour by both sexes did not constrain that allocated to feeding. However, the proportion of time allocated to parental behaviour did significantly constrain the time spent feeding for both male and female Lapwings.

49. That parental behaviour reduced the amount of time available for feeding demonstrates a cost of parental behaviour in the Lapwing.

50. Male and female Lapwings clearly adopted different parental-care roles: females played the greater part in forms of "depreciable" care (incubation, brooding and tending), whilst males were concerned mainly with "non-depreciable" forms (vigilance). The division of labour between the sexes in this way also facilitated the occurrence of polygyny: males could provide care to offspring from two or three clutches without significantly altering their activity budget. Likewise, females would not need to make significant behavioural alterations in a polygynous association because they performed the majority of parental care of their clutches in monogamous associations too.

51. The activity budgets of male and female Lapwings indicate that, in concordance with sexual selection theory, males invest more time (and probably energy) in mating behaviour than parental care of offspring, whilst females show the opposite pattern of investment.

52. During the three years of study, one female was found brooding and tending at least one, and probably three chicks that were not her own, along with two of her offspring. The true parents of the “adopted” young were not known. The association was only seen on one occasion.

REFERENCES

Alatalo, R.V., Carlson, A., Lundberg, A. & Ulfstrand, S. 1981. The conflict between male polygamy and female monogamy: the case of the Pied Flycatcher *Ficedula hypoleuca*. Am. Nat. 117: 738-753.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49: 227-267.

Altmann, J., Hausfater, G. & Altmann, S.A. 1988. Determinants of reproductive success in Savannah Baboons, *Papio cynocephalus*. In: Reproductive Success (Clutton-Brock, T.H. ed.). Chicago: University of Chicago Press; pp. 403-418.

Altmann, S.A., Wagner, S.S. & Lenington, S. 1977. On the evolution of polygyny. Behav. Ecol. Sociobiol. 2: 397-410.

Arcese, P. 1987. Age, intrusion pressure and defence against floaters by territorial male Song Sparrows. Anim. Behav. 35: 773-784.

Arcese, P. 1989. Territory acquisition and loss in male Song Sparrows. Anim. Behav. 37: 45-55.

Arnold, S.J. & Duvall, D. 1994. Animal mating systems: a synthesis based on selection theory. Am. Nat. 143: 317-348.

Ashkenazie, S. & Safriel, U.N. 1979. Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. Ecology 60: 783-799.

Avise, J.C. 1996. Three fundamental contributions of molecular genetics to avian ecology and evolution. Ibis 138: 16-25.

Baines, D. 1988. The effects of improvement of upland, marginal grasslands on the distribution and density of breeding wading birds (charadriiformes) in northern England. Biological Conservation 45: 221-236.

Baines, D. 1989. The effects of improvement of upland, marginal grasslands on the breeding success of Lapwings *Vanellus vanellus* and other waders. Ibis 131: 497-506.

Baines, D. 1990. The roles of predation, food and agricultural practice in determining the breeding success of the Lapwing (*Vanellus vanellus*) on upland grasslands. J. Anim. Ecol. 59: 915-929.

Baker, R.R. 1978. The evolutionary ecology of animal migration. New York: Holmes & Meier Publishers Inc.

Barba, E., Gil-Degado, J.A. & Monrós, J.S. 1995. The costs of being late: consequences of delaying Great Tit *Parus major* first clutches. J. Anim. Ecol. 64: 642-651.

Barnard, C.J. & Thompson, D.B.A. 1985. Gulls and Plovers: the ecology and behaviour of mixed species feeding groups. London: Croom Helm.

Barton, R.A., Byrne, R.W. & Whiten, A. 1996. Ecology, feeding competition and social structure in Baboons. Behav. Ecol. Sociobiol. 38: 321-329.

Bateman, A.J. 1948. Intrasexual selection in *Drosophila*. Heredity 2: 349-368.

Beintema, A.J. 1991. Breeding ecology of meadow birds (charadriiformes); implications for conservation and management. Ph.D. thesis, Rijksuniversiteit Groningen, Netherlands. (ISBN: 90-9004083-8).

Beintema, A.J. & Müskens, G.J.D.M. 1987. Nesting success of birds breeding in Dutch agricultural grasslands. J. Appl. Ecol. 24: 743-758.

Bellairs, A. 1969. The life of reptiles (Vol. 2). London: Weidenfeld & Nicolson.

Berg, Å. 1993. Habitat selection by monogamous and polygamous Lapwings on farmland - the importance of foraging habitats and suitable nest sites. Ardea 81: 99-105.

Berg, Å., Lindberg, T. & Kallebrink, K.G. 1992. Hatching success of Lapwings on farmland: differences between habitats and colonies of different sizes. J. Anim. Ecol. 61: 469-476.

Bergstrom, P.W. 1986. Daylight incubation sex roles in Wilson's Plover. Condor 88: 113-115.

Birkhead, T.R. 1991. The Magpies: the ecology and behaviour of Black-billed and Yellow-billed Magpies. London: T. and A. D. Poyser.

Birkhead, T.R. & Møller, A.P. 1992. Sperm competition in birds. Evolutionary causes and consequences. London: Academic Press.

Black, J.M. & Owen, M. 1995. Reproductive performance and assortative pairing in relation to age in Barnacle Geese. J. Anim. Ecol. 64: 234-244.

Blomqvist, D. & Johansson, O.C. 1994. Double clutches and uniparental care in Lapwing *Vanellus vanellus*, with a comment on the evolution of double-clutching. J. Avian Biology 25: 77-79.

Blomqvist, D. & Johansson, O.C. 1995. Trade-offs in nest site selection in coastal populations of Lapwings *Vanellus vanellus*. Ibis 137: 550-558.

Breiehagen, T. 1989. Nesting biology and mating system in an alpine population of Temminck's Stint *Calidris temminckii*. Ibis 131: 389-402.

Breiehagen, T. & Slagsvold, T. 1988. Male polyterritoriality and female-female aggression in Pied Flycatchers *Ficedula hypoleuca.* Anim. Behav. 36: 604-605.

Brown, J.L. 1969. Territorial behaviour and population regulation in birds. Wilson Bull. 81: 293-329.

Brunton, D.H. 1988. Sexual differences in reproductive effort: time-activity budgets of monogamous Killdeer *Charadrius vociferus.* Anim. Behav. 36: 705-717.

Burger, J. 1988. Effects of age on foraging in birds. Proc. Int. Ornith. Cong. XIX: 1127-1140.

Byrkjedal, I. 1980. Nest predation in relation to snow cover - a possible factor influencing the start of breeding in shorebirds. Ornis Scand. 11: 249-252.

Byrkjedal, I., Grønstøl, G.B., Pedersen, K.M., Sandvik, H. & Stalheim, S. 1997. Mating system and territorial quality in Lapwings *Vanellus vanellus.* Ibis 139: In press.

Cézilly, F. & Nager, R.G. 1996. Age and breeding performance in monogamous birds: the influence of pair stability. Trends Ecol. Evol. 11: 27.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge: Cambridge University Press.

Charlesworth, B. & León, J.A. 1976. The relation of reproductive effort to age. Am. Nat. 110: 449-459.

Chastel, O., Weimerskirch, H. & Jouventin, P. 1995. Influence of body condition on reproductive decision and reproductive success in the Blue Petrel. Auk 112: 964-972.

Clutton-Brock, T.H. (ed.) 1988a. Reproductive success. Chicago: University of Chicago Press.

Clutton-Brock, T.H. 1988b. Reproductive success. In: Reproductive success (Clutton-Brock, T.H. ed.). Chicago: University of Chicago Press; pp. 472-485.

Clutton-Brock, T.H. 1991. The evolution of parental care. Princeton: Princeton University Press.

Clutton-Brock, T.H., Albon, S.D. & Guiness, F.E. 1986. Great expectations: dominance, breeding success and offspring sex ratios in Red Deer. Anim. Behav. 34: 460-471.

Clutton-Brock, T.H., Albon, S.D. & Guiness, F.E. 1988. Reproductive success in male and female Red Deer. In: Reproductive success (Clutton-Brock, T.H. ed.). Chicago: Chicago University Press; pp. 325-343.

Corbet, G.B. & Southern, H.N. (eds.) 1977. The handbook of British mammals (second edition). London: Blackwell Scientific Publications.

Coulson, J.C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. J. Anim. Ecol. 35: 269-279.

Coulson, J.C. & Horobin, J. 1976. The influence of age on the breeding biology and survival of the Arctic Tern *Sterna paradisaea*. J. Zool. Lond. 178: 247-260.

Coulson, J.C., Potts, G.R. & Horobin, J. 1969. Variation in the eggs of the Shag (*Phalacrocorax aristotelis*). Auk 86: 232-245.

Coulson, J.C. & White, E. 1958. The effect of age on the breeding biology of the Kittiwake *Rissa tridactyla*. Ibis 100: 4-51.

Cowlishaw, G. & Dunbar, R.I.M. 1991. Dominance rank and mating success in male primates. Anim. Behav. 41: 1045-1056.

Cramp, S. & Simmons, K.E.L. 1983. The birds of the western palearctic, vol. 3. Oxford: Oxford University press.

Crawford, R.D. 1980. Effects of age on reproduction in American Coots. J. Wildl. Manage. 44: 183-189.

Cristol, D.A. 1995. Early arrival, initiation of nesting, and social status: an experimental study of breeding female Red-winged Blackbirds. Behav. Ecol. 6: 87-93.

Crook, J.R. & Shields, W.M. 1985. Sexually selected infanticide by adult male Barn Swallows. Anim. Behav. 33: 754-761.

Curio, E. 1983. Why do young birds reproduce less well? Ibis: 125: 400-404.

Dabelsteen, T. 1978. An analysis of the song-flight of the Lapwing (*Vanellus vanellus* L.) with respect to causation, evolution and adaptations to signal function. Behaviour 66: 136-178.

Davies, N.B. 1985. Co-operation and conflict among Dunnocks, *Prunella medularis*, in a variable mating system. Anim. Behav. 33: 628-648.

Davies, N.B. 1989. Sexual conflict and the polygamy threshold. Anim. Behav. 38: 226-234.

Davies, N.B. 1991. Mating systems. In: Behavioural ecology: an evolutionary approach (third edition) (Krebs, J.R. & Davies, N.B. eds.). Oxford: Blackwell Scientific Publications; 263-294.

Davis, J.W.F. 1975. Age, egg-size and breeding success in the Herring Gull *Larus argentatus.* Ibis 117: 460-473.

Desrochers, A. 1992. Age-related differences in reproduction by European Blackbirds: restraint or constraint. Ecology 73: 1128-1131.

Desrochers, A. & Magrath, R.D. 1993. Age-specific fecundity in European Blackbirds (*Turdus merula*): individual and population trends. Auk 110: 255-263.

Duellman, W.E. & Trueb, L. 1994. Biology of Amphibians. London: Johns Hopkins University Press.

Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215-223.

Ens, B.J., Kersten, M. Brenninkmeijer, A. & Hulscher, J.B. 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). J. Anim. Ecol. 61: 703-715.

Ens, B.J., Weissing, F.J. & Drent, R.H. 1995. The despotic distribution and deferred maturity: two sides of the same coin. Am. Nat. 146: 625-650.

Erckmann, W.J. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. In: Social behaviour of female vertebrates (Wasser, S.K. ed.). London: Academic Press; 113-168.

Evans, A. 1995. Forgotten farmland birds. BTO News 199: 10-11.

Evans, M.R. & Burn, J.L. 1996. An experimental analysis of mate choice in the wren: a monomorphic, polygynous passerine. Behav. Ecol. 7: 101-108.

Evans, P.R. & Davidson, N.C. 1990. Migration strategies and tactics of waders breeding in arctic and north temperate latitudes. In: Bird migration: physiology and ecophysiology (Gwinner, E. ed.). Berlin: Springer-Verlag; 387-398.

Ezaki, Y. 1990. Female choice and the causes and adaptiveness of polygyny in Great Reed Warblers. J. Anim. Ecol. 59: 103-119.

Falconer, D.S. 1981. Introduction to quantitative genetics (second edition). London: Longman.

Ford, N.L. 1996. Polyterritorial polygyny in North American passerines. J. Field Ornithol. 67: 10-16.

Forslund, P. & Larsson, K. 1992. Age-related reproductive success in the Barnacle Goose. J. Anim. Ecol. 61: 195-204.

Forslund, P. & Pärt, T. 1995. Age and reproduction in birds - hypotheses and tests. Trends Ecol. Evol. 10: 374-378.

Fowler, G.S. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. Amer. Zool. 35: 318-328.

Fowler, J. & Cohen, L. 1990. Practical statistics for field biology. Chichester: John Wiley and Sons Ltd.

Fraga, R.M. & Amat, J.A. 1996. Breeding biology of a Kentish Plover (*Charadrius alexandrinus*) population in an inland saline lake. Ardeola 43: 69-85.

Galbraith, H. 1987. Marking and visiting Lapwing *Vanellus vanellus* nests does not affect clutch survival. Bird Study 34: 137-138.

Galbraith, H. 1988a. Effects of agriculture on the breeding ecology of Lapwings *Vanellus vanellus*. J. Appl. Ecol. 25: 487-503.

Galbraith, H. 1988b. Effects of egg size and composition on the size, quality and survival of Lapwing *Vanellus vanellus* chicks. J. Zool., Lond. 214: 383-398.

Galbraith, H. 1988c. The effects of territorial behaviour on Lapwing populations. Ornis Scand. 19: 134-138.

Galbraith, H. 1988d. Adaptation and constraint in the growth pattern of Lapwing *Vanellus vanellus* chicks. J. Zool. Lond. 215: 537-548.

Galbraith, H. 1989a. Arrival and habitat use by Lapwings *Vanellus vanellus* in the early breeding season. Ibis 131: 377-388.

Galbraith, H. 1989b. The diet of Lapwing *Vanellus vanellus* chicks on Scottish farmland. Ibis 131: 80-84.

Gauthreaux, S.A.Jr. 1982. The ecology and evolution of avian migration systems. In: Avian biology (vol. 6) (Farner, D.S., King, J.R. & Parkes, K.C. eds.). London: Academic Press; 93-168.

Gibbons, D.W., Reid, J.B. & Chapman, R.A. (eds.) 1993. The new atlas of breeding birds in Britain and Ireland: 1988-91. London: T. & A.D. Poyser.

Gibbs, H.L., Weatherhead, P.J., Boag, P.T., White, B.N., Tabak, L.M. & Hoysak, D.J. 1990. Realised reproductive success of polygynous Red-winged Blackbirds revealed by DNA markers. Science 250: 1394-1397.

Goodall, J. 1990. Through a window. My thirty years with the Chimpanzees of Gombe. Boston: Houghton Mifflin Company.

Gori, D.F., Rohwer, S. & Caselle, J. 1996. Accepting unrelated broods helps replacement male Yellow-headed Blackbirds attract mates. Behav. Ecol. 7: 49-54.

Grant, M. C. 1991. Relationships between egg size, chick size at hatching, and chick survival in the Whimbrel *Numenius phaeopus*. Ibis 133: 127-133.

Gratto, C.L., Cooke, F. & Morrison, R.I.G. 1983. Nesting success of yearling and older breeders in the semipalmated sandpiper, *Calidris pusilla*. Can. J. Zool. 61: 1133-1137.

Gratto-Trevor, C.L. 1991. Parental care in Semipalmated Sandpipers *Calidris pusilla*: brood desertion by females. Ibis 133: 394-399.

Graul, W.D. 1976. Food fluctuations and multiple clutches in the Mountain Plover. Auk 93: 166-167.

Green, G.H., Greenwood, J.J.D. & Lloyd, C.S. 1977. The influence of snow conditions on the date of breeding of wading birds in north-east Greenland. J. Zoology 183: 311-328.

Greenhalgh, M.E. 1968. The sex ratio of migrant Ruffs. Bird Study 15: 210-212.

Gregory, R.D. 1987. Comparative winter feeding ecology of Lapwings *Vanellus vanellus* and Golden Plovers *Pluvialis apricaria* on cereals and grasslands in the lower Derwent valley, North Yorkshire. Bird Study 34: 244-250.

Gustafsson, L. & Pärt, T. 1990. Acceleration of senescence in the Collared Flycatcher *Ficedula albicolis* by reproductive costs. Nature 347: 279-281.

Gwinner, E. (ed.) 1990a. Bird migration: physiology and ecophysiology. Berlin: Springer-Verlag.

Gwinner, E. 1990b. Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod. In: Bird migration: physiology and ecophysiology (Gwinner, E. ed.). Berlin: Springer-Verlag; 257-268.

Hamer, K.C & Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in Great Skuas *Catharacta skua*. J. Anim. Ecol. 60: 693-704.

Hamman, J. & Cooke, F. 1987. Age effects on clutch size and laying dates of individual female Lesser Snow Geese *Anser caerulescens*. Ibis 129: 527-532.

Hannon, S.J. 1984. Factors limiting polygyny in the Willow Ptarmigan. Anim. Behav. 32: 153-161.

Harris, M.P. 1966. Breeding biology of the Manx Shearwater, *Puffinus puffinus*. Ibis 108: 17-33.

Harris, M.P. 1967. The biology of Oystercatchers *Haematopus ostralegus* on Skokholm island, south Wales. Ibis 109: 180-193.

Harris, M.P. 1970. Territory limiting the size of the breeding population of the Oystercatcher (Haematopus ostralegus) - a removal experiment. J. Anim. Ecol. 39: 707-713.

Harris, M.P. & Wanless, S. 1995. Survival and non-breeding of adult Common Guilemots *Uria aalgae*. Ibis 137: 192-197.

Hartley, I.R., Shepherd, M., Robson, T. & Burke, T. 1993. Reproductive success of polygynous male Corn Buntings (*Miliaria calandra*) as confirmed by DNA fingerprinting. Behav. Ecol. 4: 310-317.

Hasselquist, D., Bensch, S. & von Schantz, T. 1995. Low frequency of extrapair paternity in the polygynous Great Reed Warbler, *Acrocephalus arundinaceus*. Behav. Ecol. 6: 27-38.

Heim, J. 1974. Eiablage, gelegegroße und brutdauer beim Kiebitz. Orn. Beob. 71: 283-288.

Heitmeyer, M.E. 1995. Influences of age, body condition, and structural size on mate selection by dabbling ducks. Can. J. Zool. 73: 2251-2258.

Hensler, G.L. Nichols, J.D. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93: 42-53.

Hildén, O. 1975. Breeding system of Temminck's Stint *Calidris temminckii*. Ornis Fenn. 52: 117-146.

Hildén, O. 1979. Territoriality and site tenacity of Temminck's Stint (*Calidris temminckii*). Ornis Fenn. 56: 56-74.

Hildén, O. & Vuolanto, S. 1972. Breeding of the Red-necked Phalarope (*Phalaropus lobatus*) in Finland. Ornis Fenn. 49: 57-75.

Hinde, R.A. 1951. Further report on the inland migration of waders and terns. British Birds 44: 329-346.

Holmes, R.T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68: 3-46.

Holmes, R.T. 1971. Density, habitat and the mating system of the Western Sandpiper (*Calidris mauri*). Oecologia 7: 191-208.

Howard, R.D. 1983. Sexual selection and variation in reproductive success in a long-lived organism. Am. Nat. 122: 301-325.

Howard, R.D. 1988. Reproductive success in two species of anurans. In: Reproductive success (Clutton-Brock, T.H. ed.). Chicago: University of Chicago Press; pp. 99-113.

Howard, R.D. & Kluge, A.G. 1985. Proximate mechanisms of sexual selection in Woodfrogs. Evolution 39: 260-277.

Howe, M.A. 1982. Social organisation in a nesting population of eastern Willets (*Catoptrophorus semipalmatus*). Auk 99: 88-102.

Hudson, R., Tucker, G.M. & Fuller, R.J. 1994. Lapwing *Vanellus vanellus* populations in relation to agricultural changes: a review. In: The ecology and conservation of Lapwings *Vanellus vanellus* (Tucker, G.M., Davies, S.M. & Fuller, R.J. eds.). Peterborough: Joint Nature Conservation Committee (U.K. Nature Conservation No. 9); 1-33.

Hurly, T.A. & Robertson, R.J. 1984. Aggressive and territorial behaviour in female Red-winged Blackbirds. Can. J. Zool. 62: 148-153.

Hurly, T.A. & Robertson, R.J. 1985. Do female Red-winged Blackbirds limit harem size? Auk 102: 205-209.

Imboden, C. 1974. Zug, fremdansiedlung und brutperiode des Kiebitz *Vanellus vanellus* in Europa. Ornith. Beob. 71: 5-134.

Jackson, R. & Jackson, J. 1975. A study of breeding Lapwings in the New Forest, Hampshire 1971-74. Ring. and Migr. 1: 18-27.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96: 651-661.

King, J.R. 1973. Energetics of reproduction in birds. In: Breeding biology of birds (Farner, D.S. ed.). Washington, D.C.: Nat. Acad. of Sci.: 78-107.

Kirby, J.S. & Lack, P.C. 1993. Spatial dynamics of wintering Lapwings and Golden Plovers in Britain and Ireland, 1981/82 to 1983/84. Bird Study 40: 38-50.

Klett, A.T. & Johnson, D.H. 1982. Variability in nest survival rates and implications to nesting studies. Auk 99: 77-87.

Klomp, H. 1951. Over de achteruitgang van de Kievit in Nederland en gegevens over het legmechanisme en het eiproductievermogen. Ardea 39: 143-183.

Klomp, H. 1954. De terreinkus van de Kievit *Vanellus vanellus* (L.). Ardea 42: 1-139.

Koford, C.B. 1963. Rank of mothers and sons in bands of Rhesus Monkeys. Science 141: 356-357.

Krebs, J.R. 1971. Territory and breeding density in the Great Tit *Parus major* L. Ecology 52: 2-22.

Kuester, J. & Paul, A. 1992. Influence of male competition and female mate choice on male mating success in Barbary Macaques (*Macaca sylvanus*). Behaviour 120: 192-217.

Kuester, J., Paul, A. & Arnemann, J. 1995. Age-related and individual differences of reproductive success in male and female Barbary Macaques (*Macaca sylvanus*). Primates 36: 461-476.

Lack, D. 1954. The natural regulation of animal numbers. Oxford: Clarendon Press.

Lack, D. 1963. Migration across the southern North Sea studied by radar. Part 5. Movements in August, winter and spring, and conclusions. Ibis 105: 461-492.

Lack, D. 1968. Ecological adaptations for breeding in birds. London: Chapman & Hall.

Lack, P.C. (ed.) 1986. The atlas of wintering birds in Britain and Ireland. Calton: T. & A.D. Poyser.

Lagler, K.F., Bardach, J.E. & Miller, R.R. 1962. Ichthyology. New York: John Wiley & Sons Inc.

Langston, N.E., Freeman, S., Rohwer, S. & Gori, D. 1990. The evolution of female body size in Red-winged Blackbirds: the effect of timing of breeding, social competition and reproductive energetics. Evolution 4: 1764-1779.

LaPrade, H.R. & Graves, H.B. 1982. Polygyny and female-female aggression in Red-winged Blackbirds (*Agelaius phoeniceus*). Am. Nat. 120: 135-138.

Leblanc, Y. 1989. Variation in the size of eggs of captive and wild Canada Geese. Ornis Scand. 20: 93-98.

LeBoeuf, B.J. & Reiter, J. 1988. Lifetime reproductive success in Northern Elephant Seals. In: Reproductive success (Clutton-Brock, T.H. ed.). Chicago: University of Chicago Press; pp. 344-362.

Lessells, C.M. 1984. The mating system of Kentish Plovers *Charadrius alexandrinus*. Ibis 126: 474-483.

Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104: 116-121.

Lightbody, J.P. & Weatherhead, P.J. 1987. Polygyny in the Yellow-headed Blackbird: female choice versus male competition. Anim. Behav. 35: 1670-1684.

Lightbody, J.P. & Weatherhead, P.J. 1988. Female settling patterns and polygyny: tests of a neutral mate choice hypothesis. Am. Nat. 132: 20-33.

Ligon, J.D. 1993. The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems. In: Current ornithology vol. 10 (Power, D.M. ed.). New York: Plenum Press; 1-46.

Lister, M.D. 1964. The Lapwing habitat enquiry. Bird Study 11: 128-147.

Lockley, R.M. 1961. Social Structure and stress in the Rabbit warren. J. Anim. Ecol. 30: 385-423.

Lundberg, A. & Alatalo, R.V. 1992. The Pied Flycatcher. London: T. and A. D. Poyser.

MacDonald, D.W. 1989. Running with the Fox. London: Unwin Hymen.

Maclean, G.L. 1972. Clutch size and evolution in the charadrii. Auk 89: 299-324.

Marchetti, K. & Price, T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biol. Rev. 64: 51-70.

Martin, K. 1989. Pairing and adoption of offspring by replacement male Willow Ptarmigan: behaviour, costs and consequences. Anim. Behav. 37: 569-578.

Martin, K. 1995. Patterns and mechanisms for age-dependant reproduction and survival in birds. Amer. Zool. 35: 340-348.

Martin, P. & Bateson, P. 1993. Measuring behaviour: an introductory guide (second edition). Cambridge: Cambridge University Press.

Maxson, S.J. & Oring, L.W. 1980. Breeding season time and energy budgets of the polyandrous Spotted Sandpiper. Behaviour 74: 200-263.

Mayfield, H.F. 1961. Nesting success calculated from exposure. Wilson Bull. 73: 255-261.

Mayfield, H.F. 1975. Suggestions for calculating nest success. Wilson Bull. 87: 456-466.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. Anim. Behav. 25: 1-9.

Meek, S.B. & Robertson, R.J. 1991. How do floater male Eastern Bluebirds benefit by filling vacancies on territories where females already have young? Behav. Ecol. 3: 95-101.

Meikle, D.B., Tilford, B.L. & Vessey, S.H. 1984. Dominance rank, secondary sex ratio, and reproduction of offspring in polygynous primates. Am. Nat. 124: 173-188.

Meikle, D.B. & Vessey, S.H. 1988. Maternal dominance rank and lifetime survivorship of male and female Rhesus Monkeys. Behav. Ecol. Sociobiol. 22: 379-383.

Miller, E.H. 1985. Parental behaviour in the Least Sandpiper (*Calidris minutilla*). Can. J. Zool. 63: 1593-1601.

Milsom, T.P. 1984. Diurnal behaviour of Lapwings in relation to moon phase during winter. Bird Study 31: 117-120.

Milsom, T.P., Holditch, R.S. & Rochard, J.B.A. 1985. Diurnal use of an airfield and adjacent agricultural habitats by Lapwings *Vanellus vanellus*. J. Appl. Ecol. 22: 313-326.

Møller, A.P. 1983. Song activity and territory quality in the Corn Bunting Miliaria calandra; with comments on mate selection. Ornis Scand. 14: 81-89.

Møller, A.P. 1986. Mating systems among European passerines: a review. Ibis 128: 234-250.

Møller, A.P. 1991a. Influence of wing and tail morphology on the duration of song flight in Skylarks. Behav. Ecol. Sociobiol. 28: 309-314.

Møller, A.P. 1991b. Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. Am. Nat. 138: 994-1014.

Møller, A.P. 1994. Phenotype-dependant arrival time and its consequences in a migratory bird. Behav. Ecol. Sociobiol. 35: 115-122.

Møller, A.P., Lindén, M., Soler, J.J., Soler, M. & Moreno, J. 1995. Morphological adaptations to an extreme sexual display, stone-carrying in the Black Wheatear, *Oenanthe leucura*. Behav. Ecol. 6:368-375.

Mundahl, J.T. 1982. Role specialisation in the parental and territorial behaviour of the Killdeer. Wilson Bull. 94: 515-530.

Murray, B.G.Jr. 1984. A demographic theory on the evolution of mating systems as exemplified by birds. Evol. Biol. 18: 71-140.

Myers, J.P. 1981. A test of three hypotheses of latitudinal segregation of the sexes in wintering birds. Canadian Journal of Zoology 59: 1527-1534.

Nettleship, D.N. 1973. Breeding ecology of Turnstones *Arenaria interpres* at Hazen Camp, Ellesmere island, N.W.T. Ibis 115: 202-211.

Newton, I. 1986. The Sparrowhawk. London: T. & A.D. Poyser.

Newton, I. 1988. Age and reproduction in the Sparrowhawk. In: Reproductive success (Clutton-Brock, T.H. ed.). Chicago: University of Chicago Press; 201-219.

Newton, I. (ed.) 1989. Lifetime reproduction in birds. London: Academic Press.

Newton, I. 1989. Sparrowhawk. In: Lifetime reproduction in birds (Newton, I. ed.). London: Academic Press. 279-296.

Newton, I., Marquiss, M. & Moss, D. 1981. Age and breeding in Sparrowhawks. J. Anim. Ecol. 50: 839-853.

Newton, I., Wyllie, I. & Asher, A. 1991. Mortality causes in British Barn Owls *Tyto alba*, with a discussion of aldrin-dieldrin poisoning. Ibis 133: 162-169.

Norusis, M.J. 1993. SPSS for Windows base system user's guide, release 6.0. SPSS inc.

O'Connor, R.J. & Shrubb, M. 1986. Farming and birds. Cambridge: Cambridge University Press.

Orians, G.H. 1961. The ecology of Blackbird (*Agelaius*) social systems. Ecol. Monogr. 31: 285-312.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103: 589-603.

Oring, L.W. 1982. Avian mating systems. In: Avian biology vol. 6 (Farner, D.S., King, J.R. & Parkes, K.C. eds.). London: Academic Press; 1-92.

Oring, L.W. & Lank, D.B. 1986. Polyandry in Spotted Sandpipers: the impact of environment and experience. In: Ecological aspects of social evolution (Rubenstein, D.I. & Wrangham, R.W. eds.). Princeton: Princeton University Press; 21-42.

Oring, L.W., Reed, J.M., Colwell, M.A., Lank, D.B. & Maxson, S.J. 1991. Factors regulating annual mating success and reproductive success in Spotted Sandpipers (*Actitis macularia*). Behav. Ecol. Sociobiol. 28: 433-442.

Page, G. 1974. Moult of wintering Least Sandpipers. Bird Banding 45: 93-105.

Parmelee, D.F. & Payne, R.B. 1973. On multiple broods and the breeding strategy of Arctic Sanderlings. Ibis 115: 218-225.

Parsons, J. 1975. Seasonal variation in the breeding success of the Herring Gull: an experimental approach to pre-fledging success. J. Anim. Ecol. 44: 553-573.

Parsons, J., Chabrzyk, G. & Duncan, N. 1976. Effects of hatching date on post-fledging survival in Herring Gulls. J. Anim. Ecol. 45: 667-675.

Pärt, T. 1995. Does breeding experience explain increased reproductive success with age? An experiment. Proc. R. Soc. Lond. B 260: 113-117.

Paton, P.W.C. 1995. Breeding biology of Snowy Plovers at Great Salt Lake, Utah. Wilson Bull. 107: 275-288.

Patterson, I.J. 1982. The Shelduck: a study in behavioural ecology. Cambridge: Cambridge University press.

Peach, W.J., Thompson, P.S. & Coulson, J.C. 1994. Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. J. Anim. Ecol. 63: 60-70.

Pearson, D.J., Phillips, J.H. & Backhurst, G.C. 1970. Weights of some palearctic waders wintering in Kenya. Ibis 112: 199-208.

Perdeck, A.C. & Cavé, A.J. 1992. Laying date in the Coot: effects of age and mate choice. J. Anim. Ecol. 61: 13-19.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Picozzi, N. 1975. Crow predation on marked nests. J. Wildl. Manage. 39: 151-155.

Pienkowski, M.W. & Evans, P.R. 1984. Migratory behaviour in the western palearctic. In: Behaviour of marine animals, vol. 6. Shorebirds: migration and foraging behaviour (Burger, J. and Olla, B. eds.). New York: Plenum press; 73-123.

Pienkowski, M.W. & Evans, P.R. 1985. The role of migration in the population dynamics of birds. In: Behavioural ecology: ecological consequences of adaptive behaviour (Sibly, R.M. and Smith, R.H. eds.). Oxford: Blackwell scientific publications; 331-352.

Pleszczynska, W.K. 1978. Microgeographical prediction of polygyny in the Lark Bunting. Science 201: 935-937.

Pope, T.R. 1990. The reproductive consequences of male cooperation in the Red Howler Monkey: paternity exclusion in multi-male and single-male troops using genetic markers. Behav. Ecol. Sociobiol. 27: 439-446.

Pough, F.H., Heiser, J.B. & McFarland, W.N. 1989. Vertebrate life (third edition). New York: MacMillan.

Preston, F.W. 1966. The mathematical representation of migration. Ecology 47: 375-392.

Ramenofsky, M. 1990. Fat storage and fat metabolism in relation to migration. In: Bird migration: physiology and ecophysiology (Gwinner, E. ed.). Berlin: Springer-Verlag; 214-231.

Reid, W.V. 1988. Age correlations within pairs of breeding birds. Auk 105: 278-285.

Reiter, J., Panken, K.J. & LeBoeuf, B.J. 1981. Female competition and reproductive success in Northern Elephant Seals. Anim. Behav. 29: 670-687.

Reynolds, J.D. 1996. Animal breeding systems. Trends Ecol. Evol. 11: 68-72.

Richardson, W.J. 1978. Timing and amount of bird migration in relation to weather. Oikos 30: 224-272.

Richardson, W.J. 1990. Timing of bird migration in relation to weather: updated review. In: Bird migration: physiology and ecophysiology (Gwinner, E. ed.). Berlin: Springer-Verlag; 78-101.

Rinkel, G.L. 1940. Waarneminen over het gedrag van de Kievit (*Vanellus vanellus* (L.)) Gedurende de broedtijd. Ardea 29: 108-147.

Roberts, L.B. & Searcy, W.A. 1988. Dominance relationships in harems of female Red-winged Blackbirds. Auk 105: 89-96.

Robertson, G.J., Cooch, E.G., Lank, D.B., Rockwell, R.F. & Cooke, F. 1994. Female age and egg size in the Lesser Snow Goose. J. Avian Biology 25: 149-155.

Robertson, R.J. & Stutchbury, B.J. 1988. Experimental evidence for sexually selected infanticide in Tree Swallows. Anim. Behav. 36: 749-753.

Rockwell, R.F., Cooch, E.G., Thompson, C.B. & Cooke, F. 1993. Age and reproductive success in Lesser Snow Geese: experience, senescence and the cost of philopatry. J. Anim. Ecol. 62: 323-333.

Rockwell, R.F., Findlay, C.S. & Cooke, F. 1983. Life-history studies of the Lesser Snow Goose. I. The influence of age and time on fecundity. Oecologia 56: 318-322.

Sæther, B.E. 1990. Age-specific variation in reproductive performance in birds. In: Current Ornithology, Vol. 7. (Power, D.M. ed.). New York: Plenum Press; 251-283.

Safriel, U.N., Harris, M.P. Brooke, M.deL. & Britton, C.K. 1984. Survival of breeding Oystercatchers *Haematopus ostralegus*. J. Anim. Ecol. 53: 867-877.

Searcy, W.A. & Yasukawa, K. 1995. Polygyny and sexual selection in the Red-winged Blackbird. Princeton: Princeton University press.

Shaw, P. 1985. Age-differences within breeding pairs of Blue-eyed Shags *Phalacocorax atriceps*. Ibis 127: 537-543.

Shawyer, C.R. 1987. The Barn Owl in the British Isles: its past, present and future. London: The Hawk Trust.

Shrubb, M. 1988. The influence of crop rotations and field size on a wintering Lapwing *Vanellus vanellus* population in an area of mixed farmland in West Sussex. Bird Study 35: 123-131.

Shrubb, M. 1990. Effects of agricultural change on nesting Lapwings *Vanellus vanellus* in England and Wales. Bird Study 37: 115-127.

Shrubb, M. 1994. The effects of agriculture on the nesting of farmland Lapwings *Vanellus vanellus* in England and Wales. In: The ecology and conservation of Lapwings *Vanellus vanellus* (Tucker, G.M., Davies, S.M. & Fuller, R.J. eds.). Peterborough: Joint Nature Conservation Committee (U.K. Nature Conservation No. 9); 49-51.

Shrubb, M. & Lack, P.C. 1991. The numbers and distribution of Lapwings *Vanellus vanellus* nesting in England and Wales in 1987. Bird Study 38: 20-37.

Siegel, S. & Castellan, N.J.Jr. 1988. Nonparametric statistics for the behavioural sciences (second edition). London: McGraw-Hill.

Sinclair, A.R.E. 1983. The function of distance movements in vertebrates. In: The ecology of animal movement (Swingland, I.R. & Greenwood, P.J. eds.). Oxford: Clarendon Press.

Slagsvold, T. & Lifjeld, J.T. 1986. Mate retention and male polyterritoriality in the Pied Flycatcher *Ficedula hypoleuca*. Behav. Ecol. Sociobiol. 19: 25-30.

Slagsvold, T. & Lifjeld, J.T. 1994. Polygyny in birds: the role of competition between females for male parental care. Am. Nat. 143: 59-94.

Smith, D.G. 1980. Paternity exclusion in six captive groups of Rhesus Monkeys (*Macaca mulata*). Am. J. Phys. Anthropol. 53: 243-249.

Smith, H.G. 1993. Parental age and reproduction in the Marsh Tit *Parus palustris*. Ibis 135: 196-201.

Smith, J.N.M. 1988. Determinants of lifetime reproductive success in the Song Sparrow. In: Reproductive success (Clutton-Brock, T.H. ed.). Chicago: University of Chicago Press; 154-172.

Sokal, R.R. & Rohlf, F.J. 1995. Biometry (third edition). New York: W.F. Freeman.

Soler, M., Soler, J.J., Møller, A.P., Moreno, J. & Lindén, M. 1996. The functional significance of sexual display: stone carrying in the Black Wheatear. Anim. Behav. 51: 247-254.

Spencer, K.G. 1953. The Lapwing in Britain. London: A. Brown & Sons Ltd.

Sternberg, H. 1989. Pied Flycatcher. In: Lifetime reproduction in birds (Newton, I. ed.). London: Academic Press; 55-74.

Stutchbury, B.J. & Robertson, R.J. 1987. Do nest building and first-egg dates reflect settlement patterns in females? Condor 89: 587-593.

Sydeman, W.J., Penniman, J.F., Penniman, T.M., Pyle, P. & Ainley, D.G. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. J. Anim. Ecol. 60: 135-149.

Székely, T. & Reynolds, J.D. 1995. Evolutionary transitions in parental care in shorebirds. Proc. R. Soc. Lond. B 262: 57-64.

Teather, K.L., Muma, K.E. & Weatherhead, P.J. 1988. Estimating female settlement from nesting data. Auk 105: 196-200.

Temrin, H. & Tullberg, B.S. 1995. A phylogenetic analysis of the evolution of avian mating systems in relation to altricial and precocial young. Behav. Ecol. 6: 296-307.

Thibault, M. & McNeil, R. 1995. Day- and night-time parental investment by incubating Wilson's Plovers in a tropical environment. Can. J. Zool. 73: 879-886.

Thomas, C.S. & Coulson, J.C. 1988. Reproductive success of Kittiwake Gulls, Rissa tridactyla. In: Reproductive success (Clutton-Brock, T.H. ed.). Chicago: Chicago University Press; 251-262.

Thompson, D.B.A. & Barnard, C.J. 1983. Anti-predator responses in mixed species associations of Lapwings, Golden Plovers and Black-headed Gulls. Anim. Behav. 31: 585-593.

Thompson, D.B.A., Thompson, P.S. & Nethersole-Thompson, D. 1986. Timing of breeding and breeding performance in a population of Greenshanks (*Tringa nebularia*). J. Anim. Ecol. 55: 181-199.

Thompson, H.V. & Worden, A.N. 1956. The Rabbit. London: Collins.

Thompson, P.S., Baines, D., Coulson, J.C. & Longrigg, G. 1994. Age at first breeding, philopatry and breeding site fidelity in the Lapwing *Vanellus vanellus*. Ibis 136: 474-484.

Thompson, P.S. & Hale, W.G. 1991. Age-related reproductive variation in the Redshank *Tringa totanus*. Ornis Scand. 22: 353-359.

Trivers, R.L. Parental investment and sexual selection. In: Sexual selection and the descent of man (Campbell, B. ed.). Chicago: Aldine; 136-179.

Väisänen, R.A., Hildén, O., Soikkeli, M. & Vuolanto, S. 1972. Egg dimension variation in five wader species, the role of heredity. Ornis Fenn. 49: 25-44.

Van Rhijn, J.G. 1991. The Ruff. London: T. and A. D. Poyser.

Vehrencamp, S.L. & Bradbury, J.W. 1984. Mating systems and ecology. In: Behavioural ecology: an evolutionary approach (second edition) (Krebs, J.R. & Davies, N.B. eds.). Oxford: Blackwell Scientific Publications; 251-278.

Verhulst, S. & Tinbergen, J.M. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the Great Tit *Parus m. major*. J. Anim. Ecol. 60: 269-282.

Verner, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. Evolution 18: 252-261.

Verner, J. & Willson, M.F. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47: 143-147.

Village, A. & Westwood, N.J. 1994. The relationship of Lapwing *Vanellus vanellus* numbers and feeding rates to earthworm numbers in arable and pasture fields in autumn and winter. In: The ecology and conservation of Lapwings *Vanellus vanellus* (Tucker, G.M., Davies, S.M. & Fuller, R.J. eds.). Peterborough: Joint Nature Conservation Committee (U.K. Nature Conservation No. 9); 47-48.

Von Haartman, L. 1968. The evolution of resident versus migratory habit in birds, some considerations. Ornis Fenn. 45: 1-7.

Walters, J.R. 1982. Parental behaviour in Lapwings (charadriidae) and its relationships with clutch sizes and mating systems. Evolution 36: 1030-1040.

Walters, J.R. 1984. The evolution of parental behaviour and clutch size in shorebirds. In: Behaviour of marine animals (vol. 5): Shorebirds: breeding behaviour and populations (Burger, J. & Olla, B.L. eds.). London: Plenum Press; 243-287.

Walters, J. & Walters B.F. 1980. Co-operative breeding by Southern Lapwings *Vanellus chilensis*. Ibis 122: 505-509.

Warham, J. 1990. The Petrels. Their ecology and breeding systems. London: Academic Press.

Warringer, J.S., Warringer, J.C., Page, G.W. & Stenzel, L.E. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. Wilson Bull. 98: 15-37.

Watson, A. & Jenkins, D. 1968. Experiments on population control by territorial behaviour in Red Grouse. J. Anim. Ecol. 37: 595-614.

Webster, M.S. 1991. Male parental care and polygyny in birds. Am. Nat. 137: 274-280.

Westneat, D.F. 1993. Polygyny and extra-pair fertilisations in eastern Red-winged Blackbirds (*Agelaius phoeniceus*). Behav. Ecol. 4: 49-60.

Westneat, D.F., Sherman, P.W. & Morton, M.L. 1990. The ecology and evolution of extra-pair copulations in birds. In: Current ornithology vol.7 (Power, D.M. ed.). New York: Plenum Press; 331-369.

Wheelwright, N.T. & Schultz, C.B. 1994. Age and reproduction in Savannah Sparrows and Tree Swallows. J. Anim. Ecol. 63: 686-702.

Whitfield, D.P. & Brade, J.J. 1991. The breeding behaviour of the Knot *Calidris canutus*. Ibis 133: 246-255.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100: 687-690.

Williams, A.J. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biol. Rev. 69: 35-59.

Willis, E.O. 1981. Precautions in calculating nest success. Ibis 123: 204-207.

Wilson, E.O. 1975. Sociobiology. Boston, Massachusetts: Harvard University Press.

Wingfield, J.C., Schwabl, H. & Mattocks, P.W.Jr. 1990. Endocrine mechanisms of migration. In: Bird migration: physiology and ecophysiology (Gwinner, E. ed.). Berlin: Springer-Verlag; 232-256.

Winkel, W. & Winkel, D. 1984. Polygynie des Trauerschnäppers (*Ficedula hypoleuca*) am westrand seines areals in Mitteleuropa. J. Ornithol. 125: 1-14.

Wittenberger, J.F. 1976. The ecological factors selecting for polygyny in altricial birds. Am. Nat. 110: 779-799.

Wittenberger, J.F. 1979. The evolution of mating systems in birds and mammals. In: Handbook of behavioural neurobiology (vol. 3) (Marler, P. & Vandenbergh, J.G. eds.). London: Plenum Press; 271-349.

Wooller, R.D., Bradley, J.S., Skira, I.J. & Serventy, D.L. 1990. Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. J. Anim. Ecol. 59: 161-170.

Wootton, J.T., Bollinger, E.K. & Hibbard, C.J. 1986. Mating systems in homogeneous habitats: the effects of female uncertainty, knowledge costs, and random settlement. Am. Nat. 128: 499-512.

Yasukawa, K. 1979. Territory establishment in Red-winged Blackbirds: importance of aggressive behaviour and experience. Condor 81: 258-264.