# Population ecology and lifetime reproductive success of dippers *Cinclus cinclus*

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Doctor of Philosophy

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## Abstract

Acidified catchments are known to hold significantly reduced dipper *Cinclus cinclus* populations throughout the year relative to circum-neutral rivers, although the processes leading to these declines remain unclear. This study considered the population ecology of dippers within the circum-neutral River Devon catchment, Central Scotland, and focused primarily on determining the factors influencing survival, breeding probabilities and reproductive success. It aimed to examine the role of spatial variation in 'habitat quality' on the population (and meta-population) dynamics of dippers, based on measures of seasonal and lifetime reproductive success, and the balance between survival and reproduction; in particular, to assess if the reduced reproductive success of dippers on acid rivers is likely to lead to population declines.

Within the Devon catchment, approximately 81% of all adults survived from spring (March/April) to autumn (September/October), with 65% of these birds surviving from autumn to the following breeding season. Overall, these estimates predicted annual adult survival rates of c.53%, with no significant differences between years. Population density had no detectable effect on adult mortality rates, although juvenile over-winter survival was significantly lower than the adult rate at between 40 and 58%, and negatively related to the total size of the autumn population. There was no evidence of sex differences in juvenile over-winter survival, or any significant influence of weather or river flows on the rates for adults or juveniles. The local post-fledging survival of females was significantly lower than for males, however, apparently reflecting sex differences in post-natal dispersal. On average, less than 6.5% of all eggs laid, or 10.4-14.5% of male and 6.3-9.2% of female fledglings raised within the Devon catchment survived locally to breeding age. Juvenile, although not adult, recapture rates in spring were significantly lower than for birds known to have bred previously and negatively related to spring river flows. This suggested that with recapture dependent on a breeding attempt that was successful at least until laying, either more first year birds failed during the initial stages of nesting or that full breeding was not achieved at age one.

The birds fledging the most young, both within a season and over a lifetime, all bred at 'prime' lowland sites characterised by wide, shallow rivers of intermediate gradient, although with less than 10% of all birds attempting to raise a second brood each year, no significant habitat differences were identified in any component of reproductive output measured until fledging. River width, altitude and gradient were all significantly inter-correlated and related to laying date, however, and post-fledging survival was significantly reduced for late fledged young. On average, lowland birds laid earlier than upland breeders, and were significantly more likely to produce autumn 'recruits' due to the enhanced post-fledging survival prospects of their young. This suggested that broad measures of river structure can provide a biologically appropriate classification of habitat quality.

The size of the breeding population of dippers within the Devon catchment appeared to be related to the availability of critical resources, most likely food, roost sites and ultimately breeding territories through density-dependent changes in over-winter mortality and recruitment. The relative importance of resource abundance and recruitment levels in determining autumn population densities on acid streams still remained unclear, although reference to published relationships between acidity and reproductive success suggested that with adult survival at the rate estimated for the Devon catchment, many dipper populations are unlikely to produce sufficient recruits to match all adult losses, and may only persist with continued immigration from more productive (circum-neutral) catchments elsewhere.

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Before a trip to Paris, I asked Dave Bryant if he could get hold of some computer software, so that I could look at it, and when I arrived, I wouldn't seem an like idiot. In true professorial style, he replied 'Idiot? Hmmmmm... I don't think there's any easy way round it!'. What follows is a 200 page testament to that, but I think, Dave, we just about got a way with it, and now seems an appropriate time to name all those responsible for getting me where I am today.

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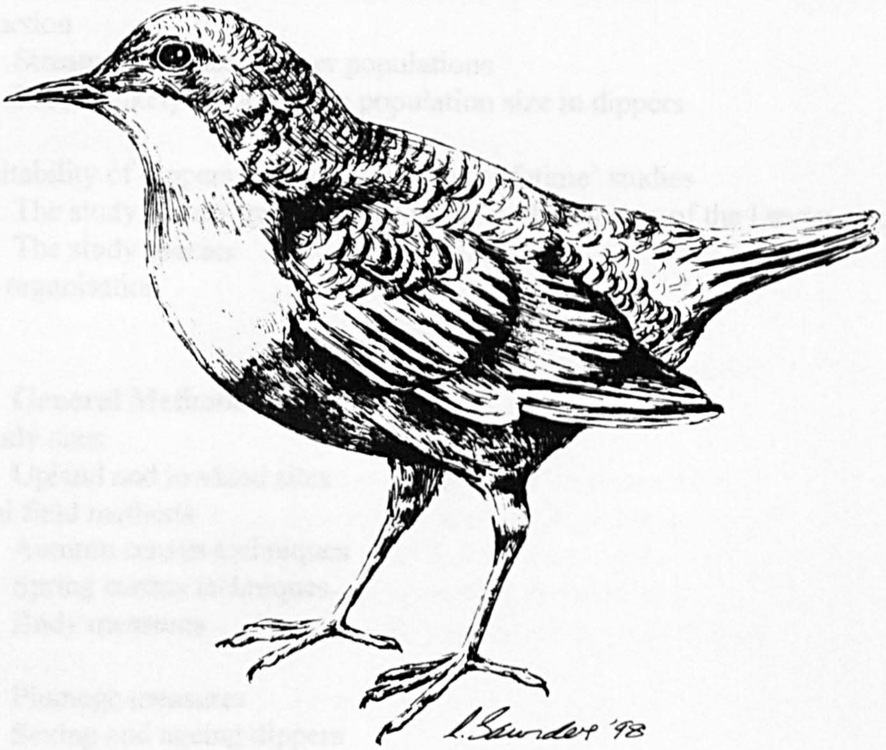


*He is a singularly joyous and loveable little fellow. He is the mountain streams' own darling, the humming bird of the blooming waters, loving rocky ripple slopes and sheets of foam as a bee loves flowers, as a lark loves sunshine and meadows. Among all the mountain birds, none has cheered me so much in my lonely wanderings, none so unfailingly. For both in winter and summer he sings, sweetly, cheerily, independent alike of sunshine and of love, requiring no other inspiration than the stream on which he dwells. While water sings, so must he, in heat or cold, calm or storm, ever attuning his voice in sure accord; low in the drought of summer and the drought of winter, but never silent.*

John Muir (1894).

# Contents

# Chapter 1

# Introduction

## 1.1 Introduction

There has been much controversy over the relative importance of the factors influencing the size of populations (Andrewartha and Birch 1954; Brown 1969; Chitty 1967; Lack 1954, 1966; Newton 1980; Nicholson 1933, 1954; Patterson 1980; Moss and Watson 1985; Wynne-Edwards 1962; See Sinclair 1989 for review). Andrewartha and Birch (1954) proposed that environmental factors, principally weather, determined population size, and although numbers could be limited by resources, they rarely were because external influences acted on survival or reproduction before resources were depleted. Nicholson (1933), however, suggested that although extrinsic (density-independent) processes were important components determining birth and death rates, the stability, and ultimately the persistence, in populations could only arise from density-dependence on production, mortality and/or dispersal rates, acting most strongly on the 'average individual' when population densities were high. In agreement with Nicholson's views, Lack (1954, 1966) noted that the size of bird populations tended to fluctuate within rather small limits relative to what was theoretically possible, and argued that in many species, external factors such as food, nest-sites, predators or parasites, acted to limit populations. Importantly, he proposed that density-dependent influences on mortality outwith the breeding season, rather than on reproduction, and primarily tied to food availability were critical, stating that for the great tits *Parus major* of Wytham wood, 'the average number of young produced per pair varied inversely with population density, but it probably had no influence in population regulation, as this variation was swamped by the much greater variations in juvenile mortality after the young fledged, which were not density-dependent. The critical density-dependent mortality was not brought about by disease, predation or territorial activities; very possibly the winter numbers in relation to food supply were important'.

Although some studies have shown that populations could be regulated by external influences such as predation, parasites or disease before the constraints of resource availability are imposed (Arcese and Smith 1988; Hudson and Dobson 1991; Lindstrom *et al.* 1994; Marcstrom *et al.* 1988; Martin 1988; McCleery and Perrins 1991; Potts and Aebischer 1991; van Riper *et al.* 1986). Lack's (1966) views have found much support in the field (e.g. Arcese *et al*, 1992; Brown 1969; Dhondt *et al.* 1990; Klomp 1972; Krebs 1970; Lack 1954, 1966; McCleery and Perrins, 1985; Newton 1980, 1991, 1992 for reviews; Nilsson, 1987; Southern 1970; Tinbergen *et al.* 1985; Village 1983). In his review, Sinclair (1989) noted that 74% of avian population studies (n=19) reported density-dependent juvenile mortality over the period from fledging to their first winter.

Important density-dependent influences on breeding success have been identified in some studies with changes in the clutch size, brood size, fledging success and/or the incidence of second broods being related to population size (e.g. Alatalo and Lundberg 1984; Arcese and Smith 1988; Ekman 1984; Krebs 1970; Lack 1966; Nilsson 1987; Sinclair 1989 for review; Stenning *et al.* 1988; Tinbergen *et al.* 1985), and some authors have suggested that density-dependent changes in fecundity may play an important role in regulating passerine populations (e.g. Ekman 1984; Klomp 1980). On the island of Vlieland, for example, a five-fold increase in the population size of great tits was accompanied by only a doubling in the number of young fledged (Tinbergen *et al.* 1985), and Arcese *et al.* (1992) noted that the fledgling success of female song sparrows *Melospiza melodia* fell from 5 to 1 young per female as female density increased from 4 to 72 birds. The insular nature of both these study sites probably inhibited (or prohibited) population expansion spatially and the increased population size lead to a direct increase in local densities. More often, variations in reproductive success have seemed insufficient to regulate populations since although per capita breeding success may decline, total fledging success continues to increase with total population size. These results suggest instead that regulatory effects may be more likely to be apparent by way of differences in mortality and recruitment rather than fecundity (Alatalo and Lundberg 1984; Dhondt 1971, 1977; Ekman 1984; Kluyver 1951; Krebs 1970; Lack 1966; Nilsson 1987; Perrins 1965; Stenning *et al.* 1988).

The remarkable stability in the size of the dipper population of the River Devon catchment (Newton 1989a) relative to other studied passerine species (Arcese *et al.* 1992, 1996; Ekman 1984; McCallum 1989; Nilsson 1987; Perrins 1979; Tinbergen *et al.* 1985; Van Balen 1980) and noted by

Newton (1989a), appears to be a feature of dipper populations in general (Carter 1989; Dobinson and Richards 1964; Marchant *et al.* 1990; Ormerod and Tyler 1994; Wilson 1996; Williams *et al.* 1988). This stability, coupled with evidence from this population and dippers elsewhere, that pre-breeding survival and entry to the breeding population apparently involve competitive processes, that birds physiologically capable of breeding may fail to do so through the behaviour of others, and that breeding pairs are often regularly spaced throughout suitable habitats (Clobert *et al.* 1990; Marzolin in prep.; Price and Bock 1983; Newton 1989a) suggest that, at least in circum-neutral catchments, populations do not fluctuate at random and that breeding density is limited.

It is now widely accepted that stability and persistence within populations normally requires density-dependence (Royama 1977 and Sinclair 1990 for reviews). In some populations, intrinsic processes may be dominant in their effects (e.g. Clutton-Brock *et al.* 1991; Grenfell 1992; Krebs *et al.* 1995; Newton 1991; Southern 1970), and many studies of passerines have identified important regulatory processes, both within (Dhondt 1971; Kluyver 1951; Krebs 1970; Krebs and Perrins 1977) and between breeding seasons (Ekman 1984; Kluyver 1971; Lack 1966; Nilsson 1987; Sinclair 1989 for review; Tinbergen *et al.* 1985). Yet, even where important regulatory influences are involved, the strength of density-dependence may often vary substantially between years, depending on food availability and/or the severity of the prevailing weather conditions with, in some cases, environmental influences being more pronounced than those related to intrinsic population processes (Arcese *et al.* 1992, 1996; Ekman 1984;McCallum 1989; McCleery and Perrins 1985; Nilsson 1987; Perrins 1966; Van Balen 1980; Tinbergen *et al.* 1985). Moreover, some density-dependent responses, such as those on avian breeding success may be insufficient to stabilise populations (e.g. Alatalo and Lundberg 1984; Arcese and Smith 1988; Ekman 1984; Krebs 1970; Lack 1966; McCleery and Perrins 1991; Nilsson 1987; Stenning *et al.* 1988; Tinbergen *et al.* 1985), whilst others may be ‘over-compensatory’, where mortality more than offsets changes in density (e.g. juvenile survival in the Sparrowhawk *Accipiter nisus,* Newton 1988), and leads to pronounced, and persistent, cycles of population growth and decline (e.g. winter mortality in Soay sheep *Ovis aries*, Clutton-Brock *et al.* 1991, Grenfell *et al.* 1992). The stability in dipper numbers in many catchments suggest that population size may be ‘tightly’ regulated by intrinsic population processes, although Price and Bock (1983), Clobert *et al.* (1990), Marzolin (in prep), Tyler and Ormerod (1994) and Wilson (1996) have all highlighted environmental influences on the survival of adult dippers or their young. Perhaps the most appropriate questions when examining the factors determining population size are to consider the relative importance of density-dependent and density-independent processes within populations and to establish how, and when within the annual cycle, any regulation is achieved.

By following populations over several seasons and recording the patterns of mortality or breeding success, or by comparing breeders from contrasting habitats, the influence of current conditions can often be inferred (e.g. Dhondt *et al.* 1990; Enoksson 1990; Kluyver 1951; Ormerod *et al.* 1985, 1988; Perrins and McCleery 1989; Swann and Etheridge 1995; Van Noordwijk *et al.* 1995; Vickery 1991). Factors known to be play a critical role in regulating (or limiting) populations or determining survival and reproductive rates include food availability (Lack 1966; Martin 1987 for review; Nilsson 1987; Ormerod *et al.* 1985; Van Balen 1980; Vickery 1991), competitive behaviour (Arcese *et al.* 1991, Newton 1980, 1991, 1992 for reviews; Southern 1970; Village 1983; Watson and Jenkins 1968; Watson and Moss 1970; Watson *et al.* 1994) weather conditions (Arcese *et al.* 1992, 1996; Ekman 1984;McCallum 1989; McCleery and Perrins 1985; Nilsson 1987; Perrins 1966; Van Balen 1980; Tinbergen *et al.* 1985), predation (Ligon and Ligon 1990; McCleery and Perrins 1991) and/or parasites and disease (Hudson *et al.* 1992; Woolfenden and Fitzpatrick 1991; van Riper *et al.* 1986). In some cases, the importance of these factors is supported by findings from corresponding experimental manipulations (e.g. Boutin 1990; Hudson *et al.* 1992; Jansson *et al.* 1981; Kallander 1981; Kluyver 1971; Newton 1991, 1992; Patterson 1980; Van Balen 1980), although often the evidence is correlational, and fails to highlight the particular processes involved.

The influence of resource availability in determining population size is often detected most readily (see Boutin 1990, Martin 1987, Newton 1992 for reviews), yet the size and distribution of any population, and the trends within it rely on the relative balance between births, deaths, immigration and emigration, all of which may, or may not, be resource dependent. For example, the national declines of peregrine *Falco peregrinus* and sparrowhawk *Accipiter nisus* numbers, associated with pesticide impacts appeared to reflect sub-lethal effects on egg formation, embryo survival and breeding failure in many areas of North America, with the number of recruits failing to match adult losses (Cade *et al.* 1986). In much of Europe, numbers fell so rapidly that declines had to be due to increased adult mortality, primarily attributable to more toxic compounds, such as aldrin and dieldrin (Newton 1986, 1991 and 1995 for reviews; Ratcliffe 1980). Recent research has confirmed the importance of early breeding success, rather than losses on migration or in its African wintering grounds, in the decline in corncrake *Crex crex* numbers over the last century (Green and Stowe 1993; Green 1997). These impacts were largely independent of resource abundance.

Newton (1991) states that 'while we study populations by demography alone, we will never understand what ultimately determines their average level, and why this level varies greatly between areas. To understand the differences in population mean densities in a species requires study of the external factors'. While this is certainly true and, in many cases, a knowledge of resource abundance may seem sufficient to explain population size, the examples above illustrate that for effective conservation a thorough knowledge of species' ecology and demography are required at all stages of the life cycle, particularly in disturbed, degraded or marginal habitats. Although correlations between population distributions or densities and environmental conditions may highlight some features of habitat suitability, alone a knowledge of the conditions for individual survival or successful breeding is often insufficient to reveal the status (in terms or growth or decline) or 'health' of populations. In this respect, the relative balance between recruitment and mortality is paramount, and populations must, on average, be able to raise sufficient young to match all adult losses.

### 1.1.1. Stream acidity and dipper populations

Intensive studies of both Eurasian *Cinclus cinclus aquaticus* and American dippers *Cinclus mexicanus* have considered many aspects of the species' ecology (Clobert *et al.* 1990; Marzolin in prep.; Price and Bock 1983). In North-eastern France, Marzolin and others have provided valuable descriptions of age-specific survival and breeding probabilities at the population level, and have highlighted the importance of river flows, habitat structure, first-year breeding status and site fidelity in determining these rates (Clobert *et al.* 1990; Marzolin in prep.). In a comprehensive although short-term study, Price and Bock (1983) considered many of elements likely to determine population densities, territory quality and the breeding success of American dippers in the Colorado Mountains. In particular, they emphasised the importance of territory size, food availability, polygyny, nest site quality, and both temperature and river flows in determining breeding success. The age of the breeders was an important influence on the quality of the occupied territory and hence the importance of many of these attributes mentioned above. The measures of habitat quality listed, together with the availability of roosts were also important in determining population densities throughout the year, although significant seasonal movements of birds also occurred reflecting additional site requirements at some stages in the annual cycle (e.g. refuges for moulting birds and ice-free winter foraging sites).

In the UK, evidence highlighting declines in dipper populations on many acidified rivers (Gibbons *et al.* 1993) and concerns over the susceptibility of some upland catchments to acidification effects (Battarbee 1992, 1993; Ormerod *et al.* 1989, 1993; Rundle *et al.* 1992), have focused interest on the role of habitat quality in the population ecology of dippers, and in particular, the relationships between water quality, habitat structure, population densities and seasonal reproductive success (Ormerod *et al.*; 1985a, 1986a,b; Vickery 1991, 1992; Logie 1995; Logie *et al.* 1996). The densities of the invertebrate prey taken by dippers, and of dippers themselves, are known to be significantly reduced on acid relative to circum-neutral streams (Logie 1995; Ormerod *et al.* 1985, 1988; Vickery 1991). Long-term data for some sites have also shown significant declines in dipper densities with concurrent reductions in pH (Ormerod *et al.* 1985), and although these patterns appear strong and consistent in both time and space (Logie 1995, Logie *et al.* 1996; Ormerod *et al.* 1985, 1988; Vickery 1991, 1992), the mechanisms linking population declines to stream acidification still remain unclear.

### 1.1.2. Factors likely to determine population size in dippers

Since territoriality generally centres on some critical resources, and territory size is often related to the abundance of these resources (Enoksson and Nilsson 1983; Gill and Wolf 1975; Ormerod *et al.* 1985; Vickery 1991), territorial behaviour can provide a mechanism by which population size is tied to resource availability (Lack 1966; Martin 1987; Patterson 1980). Dippers are known to be strongly territorial during breeding and to defend larger territories on acid streams (Ormerod and Tyler 1987; Vickery 1991), and the reduced population densities in acidified catchments may simply reflect low prey abundance. Yet, dippers on acid streams consistently lay smaller clutches, fledge fewer chicks and have a lower probability of double-brooding than those on circum-neutral rivers (Ormerod *et al.* 1985a, 1986b, 1986; Vickery 1991, 1992). Work in Wales has suggested that the reduced brood sizes and fledging success of birds on acid streams could be accounted for solely by the smaller clutches laid (Ormerod *et al.* 1991), and, since these small broods produce the most recruits, the reduced clutch sizes may be explained in terms of some adaption to enhance post-fledging survival in relation to food availability (Ormerod and Tyler 1993). Vickery (1991, 1992), however, presents evidence that offspring survival from egg to fledging is reduced most severely with increasing acidity, suggesting some direct constraint, either energetic or nutritional, on the development and/or survival of young (see also Ormerod *et al.* 1991). In a study of dippers in the Rheingau region in Germany, Kaiser (1988) claimed that a population increase following the provision of 200 nest-boxes resulted from enhanced reproductive success at these safe nesting places, rather than from a previous absence of natural sites. Potentially, even in the absence of competitive effects, the low densities of dippers on acid streams may reflect the inability of breeders to produce sufficient recruits to replace all adult losses. The relative importance of these, or other mechanisms, remains unclear when considering the processes likely to determine the size of dipper populations. Indeed, Tyler and Ormerod (1994) stated that "in the case of change such as acidification, we are still some way from understanding which (processes) are most important in isolation or combination".

## 1.2. Aims

This study aimed to consider the factors and mechanisms likely to determine the number of breeding dippers within the circum-neutral River Devon catchment, central Scotland, and to examine the role of some elements of 'habitat quality' on the population (and meta-population) dynamics of dippers more generally; in particular, to assess if the reduced reproductive success of dippers on acid rivers is sufficient to lead to the population declines noted in many acidified catchments. At present, age-specific survival and breeding probabilities, estimated from long-term census records of known individuals, are lacking for dippers within the British Isles. Where these, and estimates of breeding success are available, and their relationships to external conditions are known, often it is possible to make predictions about remote sites, or the response and future status of populations following environmental change.

Central to making such assessments is gathering comparative demographic data from populations living under differing environmental conditions (Bernstein *et al.* 1991; Dhondt *et al.* 1990; Fretwell and Lucas 1970; Pulliam and Danielson 1991; Smith *et al.* 1996), yet few long-term studies of birds have considered spatial variation in population dynamics, tending instead to concentrate on single sites, often in optimal habitat (although see Dhondt *et al.* 1990; Kluyver and Tinbergen 1953; Smith *et al.* 1996; Watson *et al.* 1994). In most vertebrate populations, however, a proportion of individuals live and/or breed in marginal sites where they survive or reproduce poorly. Because of these patterns in distribution, identifying the processes determining where individuals settle and assessing the influence of habitat quality on production and mortality are central to understanding population regulation and dynamics, and explaining the patterns of lifetime reproductive success observed within populations (Bernstein *et al.* 1991; Pulliam and Danielson 1991; Newton 1989b).

If individuals settle optimally (and freely) within and between sites, going to where the rewards are highest, populations may differ greatly in densities depending on the abundance of resources, although the mean 'success' of all individuals may be equal (Fretwell and Lucas 1970). Moreover, since lifetime success represents the summed breeding performance over all ages, if the energy devoted to reproduction is not available for growth or somatic maintenance and current effort is traded-off against future success in terms of survival of reproductive performance (Bryant 1979, 1991; Linden and Moller 1989; McCleery *et al.* 1997; See Partridge 1989 for review), potentially, individuals occupying different sites could differ greatly in the number of young they raise each year, but not in the numbers of offspring they recruit over a lifetime. Thus, the quality of breeding habitat should not be judged merely on the density of the birds it contains or the seasonal success of the breeders, but by the average fitness of individuals, or by the extent to which reproduction can exceed mortality (Newton 1991; Pulliam 1996; Sutherland 1996). Within most populations, however, a precise measure of success, by which to compare individuals remains elusive. Natural selection will favour those animals that produce the greatest number of offspring surviving to breed in subsequent generations, although this measure is often unavailable given the incomplete knowledge of dispersal and post-natal survival inherent in most field studies. Typically, the total number of young raised to independence over a lifetime provides the most complete measure of individual variation in reproductive performance (Clutton-Brock 1988; Newton 1989b).

Populations are not homogeneous, but are comprised of individuals of varying abilities, and this will often translate into differences in fitness. Mean population rates fail to describe this variation or consider the differences between the individuals within populations, and only relatively recently have long-term studies of marked birds begun to reveal the full extent of individual variation, both within and between populations, or to consider the role of behavioural and morphological variability between individuals and their relationships to fitness (Clutton-Brock 1988; Lomnicki 1988; Sibly and Smith 1985; Newton 1989b; Sutherland 1996). For many species, age, experience, status, phenotype or 'body condition' in terms of fat or protein reserves, or parasite burdens for example, as well as the habitat an individual occupies, may all be important elements influencing an individuals ability to survive and reproduce (e.g. Bryant and Westerterp 1982; Coulson and Thomas 1985; Daan *et al.* 1990; Hogstedt 1981; Perrins 1965; Price and Bock 1983; see Clutton-Brock 1988, McNamara and Houston 1996, Newton 1989b and Saether 1990 for reviews). In most bird species, just a small minority of eggs laid may ever lead to individuals of reproductive age (Clutton-Brock 1988 and Newton 1989b for reviews), and there is evidence for many that, even from the earliest stages of development, individual traits may play an important role in the probabilities of survival and/or establishment within breeding populations (e.g. Daan *et al.* 1990; Green and Rothstein 1993; Magrath 1991 for review, 1993; Tinbergen and Boerlijst 1990). Identifying the attributes or circumstances influencing individual lifetime reproductive success is not only central to determining qualitative differences between individuals, but the study of individual differences in LRS allows assessments of 'fitness' and hence habitat quality to be made, and provides insight into the processes by which individual differences in phenotype and/or behaviour influence population dynamics. Thus, a further aim of this work was to assess the extent, causes and components of individual variation in lifetime reproductive success.

## 1.3 The suitability of dippers for population and 'lifetime' studies

To date, the majority of long-term studies of European passerines have considered forest species, principally tits *Paridae* and flycatchers *Muscicapidae*, mainly due to their willingness to accept artificial nest sites (Alatalo and Lundberg 1984; Dhondt *et al.* 1990; Ekman 1984a,b; Haartman 1990; Kluyver 1951; Krebs 1970, 1971; Krebs and Perrins 1977; Lack 1966; Perrins 1966; McCleery and Perrins 1989; Nilsson 1982, 1987; Sternberg 1989; Stenning *et al.* 1988; Tinbergen *et al.* 1985; Van Balen 1973, 1980). However, the comparability of such studies with populations under natural conditions has been questioned (Moller 1989; Nilsson 1987). Nest boxes generally provide sites of equal and high quality compared to natural cavities, possibly with 'unnatural' parasite populations or predation levels (Moller 1989; Oppliger *et al.* 1994). Moreover, the provision of excess nesting sites may not only influence breeding densities, but also breeding parameters such as laying dates, clutch size and breeding success (East and Perrins 1988; Karlsson and Nilsson 1977; Van Balen 1984). There is thus a need to consider populations under wholly natural conditions.

By definition, 'lifetime' studies require that the fate of known individuals should ideally be followed from fertilisation until death. Within the confines of field studies, even for the most sedentary or philopatric species, complete histories are usually only available for a small sample of locally raised young, and the fate or previous histories of birds moving to or from study sites remain unknown. Mortality and permanent emigration can rarely be separated, and where breeders are liable to leave the study areas, both survival rates and individual LRS are likely to be underestimated. Acknowledging some of these problems and requirements, Price and Bock (1983) first recognised the suitability of dippers *Cinclidae* (in their case the American dipper *Cinclus mexicanus*) for large scale population studies.

Dippers rarely alight more than a few metres from rivers and, since the river-banks themselves provide clearly de-lineated habitat boundaries, in many situations, all suitable habitat can be identified and studied. They are resident, sedentary, conspicuous in their habits and show strong fidelity to both nest and roost sites. On capture, juveniles can easily be distinguished from adults, and immigrants can be captured and ringed in the months immediately following post-natal dispersal (Newton 1989a; Tyler *et al.* 1990). Nest sites are invariably located directly above flowing waters (Shaw 1978), and apart from some difficulties in site accessibility, most can be located early in the breeding season, allowing breeding success to be monitored. Together, these features mean populations can be followed and reliably censused throughout much of the year, allowing the full lifetime reproductive histories of individual birds to be recorded.

### 1.3.1. The study history and previous work on the dippers of the Devon catchment

Dippers have been individually marked within the Devon catchment since the 1972, when Geoff Shaw began ringing in Glendevon (Shaw 1979). Shaw's initial work within the catchment considered the likely function of dipper roosts (Shaw 1979), and formed part of a wider description of the breeding biology of dippers, including an analysis of BTO nest records (Shaw 1978). The breeding population has been continuously followed since 1980, when David Bryant, together with Paul Tatner, began monitoring the River Devon between Glendevon reservoir and Crook O'Devon (Figure 2.1b). At this time, a single marked individual of 6 years old survived from the Shaw's earlier studies. In the early 1980's, studies focused on the energetics of the annual cycle of dippers (Bryant *et al.* 1985, 1988), a topic that continued to receive much attention throughout the following years, particularly during moult (Brown and Bryant 1996) and incubation (Bryan 1996, Ward 1992). Johnstone (1994) considered the energetics of some aspects of space use and territoriality.

In 1985, the study was extended by Steve Newton to consider all suitable habitat within the catchment (Newton 1989a). In this year, some sites within the adjacent Teith and Allan catchments, assumed to be the most likely rivers for the exchange of dispersing juveniles, were also added to the study area. Newton's work continued from the spring of 1985 to the autumn of 1987, and focused on the recruitment dynamics of dippers within the catchment (Newton 1989a, 1993). The detailed records of survival and reproductive success he collected, form the foundations on which much of the later population data are based. David Bryant maintained the project throughout 1988, although only partial surveys were undertaken in both the spring and autumn of that year. In the coming chapters, 1988 is distinguished as a 'low effort' year, when fewer birds than usual were ringed in the nest or recaptured as independent juveniles or adults. Complete monitoring of the population was resumed in 1989 by David Bryant and Anne Newton who, extending some of Newton's earlier studies (Newton 1989a), assessed the determinants and costs of dominance within this population, in terms of energy expenditure and survival. After 1992, all fieldwork was conducted by John Logie, who undertook complete surveys of breeding and autumn populations until the autumn 1996. The data collected between 1972 and 1996, spanning more than 24 years, form the basis of this thesis, although most of the work presented is based only on the period from 1985 to 1996, when the complete population was monitored. Between 1985 and 1996, 2326 dippers were ringed within the catchment, including 1496 nestlings, 522 juveniles and 203 adult birds. During this time, more than 850 breeding attempts were recorded, with the size of the breeding population ranging between 35 and 66 pairs (Figure 8.3).

Although Newton (1989a) considers some aspects of the breeding biology and demography of this population, the extended data-sets that are now available mean that many of these parameters can be considered with greater precision, as well as allowing inter-annual variation to be considered. Recent statistical advances (Lebreton *et al.* 1992) make it possible to consider some parameters, such as age-specific survival and breeding probabilities, for the first time or by using more appropriate statistical methods.

Within this population, the relationships between phenotype and some elements of 'fitness' have already been examined at a number of stages within the life cycle (Bryant and Newton 1994, 1996; Newton 1989a, 1993). Newton (1989a), in an investigation of the recruitment dynamics of dippers suggested that juveniles in better 'condition' (as judged from pectoral muscle thickness) were more likely to survive over-winter, although few measures of body size were able to predict juvenile survival for either sex, and importantly, some measures enhancing survival apparently lead to low breeding success. Bryant and Newton (1996) found that the annual survival of juvenile males was negatively related to their dominance status the previous autumn, even though it seems likely that, for dominants, priority access to basic resources would confer some net fitness benefits over subordinates. The phenotypic components or individual attributes conferring 'quality' to dippers, therefore, remain unclear. In a study in Southern Germany, Schmid and Spitznagel (1985) suggested that large males paired with small females may have the highest seasonal breeding success, although as yet, individual variation in lifetime reproductive performance has not been considered in this species.

### 1.3.2. The study species

The Eurasian or white-throated dipper *Cinclus cinclus* (hereafter referred to as the dipper) is unique amongst European passerines in its association with the stream habitat. Dippers are obligate riverine predators, feeding almost exclusively on aquatic invertebrates and small fish (Ormerod 1985; Ormerod *et al.* 1987). As such, densities have been closely linked to the availability of these prey items (Da Prato and Langslow 1976; Price and Bock 1983) and to the shallow, fast-flowing riffles preferred for foraging (Logie and Bryant 1994; Shooter 1970).

With their reliance on the stream system, nest and roost sites are invariably located directly above flowing waters, traditionally on cliffs, below river banks, behind waterfalls or on bankside trees, although many birds now choose to nest on artificial structures such as bridges, culverts, weirs or retaining walls (Shaw 1978). Dippers maintain home-ranges throughout the year and during breeding defend exclusive territories (Cramp 1988).

On circum-neutral rivers in central Scotland, nest-building generally begins in March with the first eggs being laid during April and May or exceptionally the last days of March (Shaw 1978; Newton 1989a). Nests are large, enclosed domes of moss, lined with dry grasses, Wood rush

*Luzula sylvatica* and leaves. Typically, clutches hold from 3 to 6 eggs, although both mean clutch and brood sizes may be smaller on acid then circum-neutral streams (Shaw 1978; Tyler and Ormerod 1985; Vickery 1992). One egg is normally laid each day following clutch initiation, with incubation (only by the female) commencing when the clutch is complete and generally lasting c.16 days (range 12-18 days, Shaw 1978). Chicks are fed in the nest by both parents for between 18-24 days and for up to two weeks post-fledging. Nestlings are strong swimmers with well-developed wings and tarsi by c.12 days and, if threatened, will often fledge prematurely (Feltham 1987; Shaw 1978). Should this happen, extended parental care may continue outwith the nest (Balat 1964). Comprehensive descriptions of the biology and taxonomy of dippers are given in Cramp (1988), Shaw (1978) and Tyler and Ormerod (1994).

### 1.4. Thesis organisation

The work in this thesis is divided into seven main sections. Chapter 2 provides a brief description of the study sites and the general field methods, although were appropriate, more complete methods are given in later chapters. Generally, these refer to data handling and analytical techniques, although some field methods may also be described.

Chapter 3 presents the results of a national survey of non-breeding dippers within Scotland. This work was undertaken primarily as a test of the biological relevance of UK critical load exceedance estimates (Battarbee 1992, 1993) and the discussion focuses mainly on the management potential of these models. The survey provides an introduction to the habitat requirements of dippers and the status of Scottish populations, as well as placing the dippers of the Devon catchment within the context of populations elsewhere. Much of the work already undertaken on the ecology of dippers has focused on breeding birds (Ormerod *et al.* 1985a 1986b, 1986; Vickery 1991), and this work also extends these habitat studies to non-breeding populations. This work has recently been published in association with David Bryant, Juliet Vickery and David Howell (Logie *et al.* 1996).

Chapters 4 and 5 consider the population ecology of dippers within the Devon catchment. Estimates of local survival, recruitment and breeding probabilities are given in Chapter 4 and the importance of some environmental influences are described. Chapter 5 gives an account of the population breeding biology of dippers within the Ochil Hills.

Individual variation in lifetime reproductive success in considered in Chapter 6. The proportions of young failing to breed are estimated, before considering the LRS of breeders in relation to a number of morphological traits and ecological factors. The validity of fledgling production as an appropriate measure of lifetime reproductive success is considered in Chapter 7. The final chapter (Chapter 8) considers how the findings from the Devon catchment might apply to dipper populations more generally, specifically to those in acidified catchments and considers if the reduction in reproductive success on these rivers are likely to have resulted in the recorded population declines. It also offers a general discussion and conclusions.

# Chapter 2

# General Methods

## 2.1. The study sites

This study was conducted in the Ochil hills of central Scotland, focusing principally on the River Devon and its tributary streams, although including a number of sites within the adjacent Teith and Allan catchments (Figure 2.1a). The River Devon rises on Ben Cleuch in the western Ochil hills (NN 870 022) and flows east though Glendevon, towards Muckhart, before turning south and west along the southern edge of the Ochil escarpment, entering the Forth at Cambus (NS 849 937). The river thus flows along both the northern and southern edges of the Western Ochil hills and, unusually, all streams draining these hills enter the main River Devon (Figure 2.1b). These tributaries, together with the Devon itself, from its source to Dollar (NS 961 960), form the core study area. Downstream of Dollar the river generally becomes too deep and slow flowing for breeding dippers.

Within the catchment, land-use is primarily agricultural. The upper catchment consists mostly of open moorland used as rough-grazing for sheep, with some lower fields used for the production of root crops or as higher quality grazing for cattle. Recently, some small plots on the surrounding hill slopes have been afforested with Sitka *Picea sitchenis* and Norwegian *Picea abies* spruce. A thin corridor of deciduous trees, mostly oak *Quercus robur*, beech *Fagus sylvatica*, rowan *Sorbus aucuparia* and alder *Alnus glutinosa* line much of the lowland reaches of the River Devon to Dollar.

A more comprehensive description of the soils, geology and hydrology of the Ochils and the Devon catchment is given by Brown *et al.* (1993) and Grieve (1993) in Corbett *et al.* (1993), George and Smith (in Timms 1974) and Lennon (1988). Importantly, the catchment generally overlies base rich, well-buffered soils and geology and the mean long-term pH of the main River Devon is c. pH 7.07; (Scottish Environmental Protection Agency (SEPA), unpubl.). Although a number of sites within the Teith catchment have been identified as sensitive to acidification effects

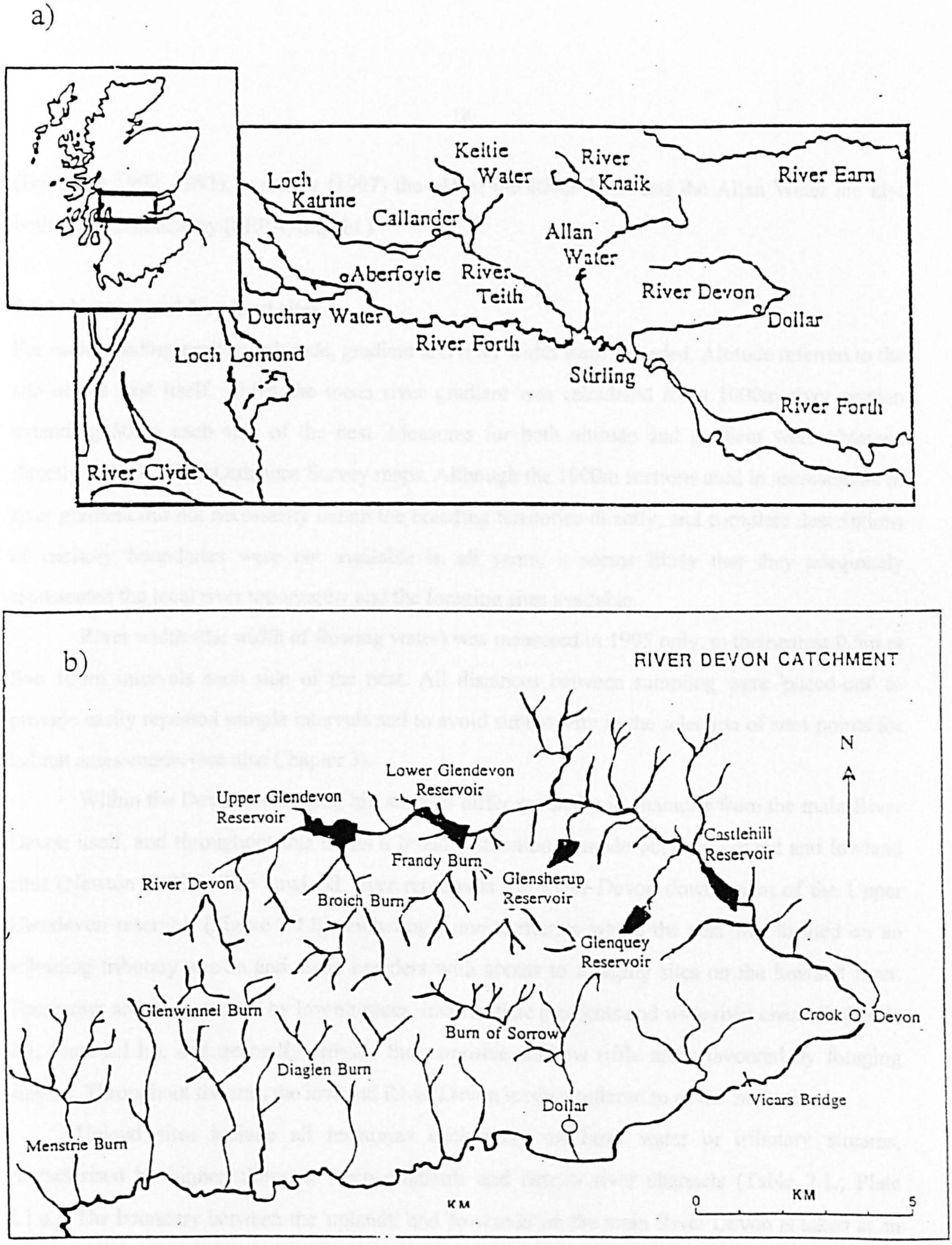


**Figure 2.1.** Location of the study rivers in central Scotland (a) and detail of the of the River Devon catchment (b).

(Battarbee 1992, 1993), currently (1997) the pH of the River Teith and the Allan Water are also both close to neutrality (SEPA, unpubl.).

### 2.1.1. Upland and Lowland sites

For each breeding territory, altitude, gradient and river width were recorded. Altitude referred to the site of the nest itself, whilst the mean river gradient was calculated for a 1000m river section extending 500m each side of the nest. Measures for both altitude and gradient were obtained directly from 1:25000 Ordnance Survey maps. Although the 1000m sections used in assessments of river gradient did not necessarily match the breeding territories directly, and complete descriptions of territory boundaries were not available in all years, it seems likely that they adequately represented the local river topography and the foraging sites available.

River width (the width of flowing water) was measured in 1995 only, to the nearest 0.5m at five 100m intervals each side of the nest. All distances between sampling were 'paced-out' to provide easily repeated sample intervals and to avoid subjectivity in the selection of sites points for habitat assessments (see also Chapter 3).

Within the Devon catchment, hill streams differ markedly in character from the main River Devon itself, and throughout this thesis a broad distinction is made between upland and lowland sites (Newton 1989a). The 'lowland' river represents the River Devon downstream of the Upper Glendevon reservoir (Figure 2.1.b), including some territories where the nest was located on an adjoining tributary stream and some breeders with access to foraging sites on the lowland river. These sites are characterised by low altitudes, intermediate gradients and wide river channels (Table 2.1, Plate 2.1.b.), and generally provide the extensive shallow riffle areas favoured by foraging dippers. Throughout the text, the lowland River Devon is often referred to as the 'main river'.

Upland sites include all territories exclusively on head water or tributary streams, characterised by higher altitudes, steep gradients and narrow river channels (Table 2.1.; Plate 2.1.a.). The boundary between the 'uplands' and 'lowlands' on the main River Devon is taken at an altitude of 250m, at the upper end of Glendevon. This coincides with the confluence of the River Devon and Frandy burn, directly below Glendevon Reservoir (GR NS940050). At this point, the impoundment of the Devon by two dams renders the river unsuitable for dipper for approximately 5200m upstream. Above the dams, the Devon is similar in character to upland streams elsewhere in the catchment.

**Table 2.1.** Mean habitat measures (±S.D.) for upland and lowland territories within the Devon catchment.

| Habitat | Mean Altitude (m.a.s.l.) | Mean Gradient (m $km^{-1}$) | Mean Width (m) |
|---|---|---|---|
| Upland | 305.75±97.56 | 95.43±51.50 | 3.22±1.48 |
| Lowland | 106.08±64.80 | 30.10±26.64 | 9.72±3.35 |

All differences are statistically significant (ANOVA $F_{3,140} \geq 99.02$, $p<0.001$ in all cases). Altitude and gradient were transformed ($\log_{10}$) prior to statistical analysis.

**Plate 2.1.** Examples of a) upland and b) lowland sites within the River Devon catchment

## 2.2. General field methods

Fundamental to these studies has been the ability to capture, measure and uniquely mark birds early in life, and follow their survival and reproductive histories.

### 2.2.1. Autumn census techniques

In autumn, birds were captured in mist-nets placed directly across the river channels during the day, or using hand-held nets at night-time roosts. At night, dippers are known to seek the shelter and security of river-side roosts, often choosing man-made structures such as bridges or culverts, where they can be captured with relative ease by approaching quietly, and placing a hand-net over the resting bird (Johnstone 1994; Newton 1989a; Shaw 1979; Tyler and Ormerod 1994). Birds that were missed or disturbed at roost could often be 'lured' back towards strong torch-light and captured in flight. The period after post-natal dispersal and moult, and prior to the peak in over-winter mortality (Galbraith *et al.* 1981; Newton 1989a), is known to be a stage of general population stability within this catchment and for dipper populations in general (Bryant *et al.* unpubl.; Shaw 1979). Few unringed birds were known to enter the population after the autumn census, and complete population censuses could be undertaken by roost catching and systematically netting all suitable stretches of river.

### 2.2.2. Spring census techniques

Dippers were generally conspicuous within their territories during breeding and their long unfeathered tarsi allowed colour ring combinations to be read easily (Price and Bock 1983). Consequently, birds marked in autumn could normally be identified without the need for physical capture, and spring 'recaptures' generally comprised sightings of colour ringed individuals. However, in all years some birds escaped capture in autumn or possibly entered the catchment late in the year, and thus remained unmarked at breeding. Where this occurred, normally, unringed females were taken from the nest during incubation, while males were captured using mist-nets within the breeding territory. It was considered that at least 95% of all breeding dippers within the Devon catchment were ringed and uniquely identifiable.

### 2.2.3. Body measures

On capture, all birds were marked with a metal British Trust for Ornithology (BTO) ring and given a unique combination of up to three celluloid colour rings. For each bird, body size and two measures of plumage coloration were taken. Body size measures were recorded as follows:

I) Body mass; measured to 0.1g using a 100g Pesola balance.

ii) Wing length; maximum chord for the flattened, straightened wing, measured to the nearest 1mm using a stopped rule (Spencer 1984; Svensson 1992).

iii) Keel length; measured to 0.1mm from the anterior notch to the posterior end of the sternum using vernier dial-reading callipers.

iv) Tarsus length; measured as the length of the tarso-metatarsus to 0.1mm using dial-reading callipers (Spencer 1984).

v) Head and bill length, maximum length from the back of the skull to the tip of the bill, measured to 0.1mm using dial-reading callipers.

vi) Bill length, from the bill tip to the edge of the feathering along the top surface of the upper mandible, measured to 0.1mm using dial-reading callipers.

vii) Bill depth, measured to 0.01mm at the anterior point of the nares, using dial reading callipers.

### 2.2.4. Plumage measures

It has been suggested that, in many species, appearance may be in important indicator of some elements of 'quality' such as social status, body condition or parasite burdens, and in turn. it may influence some components of fitness such as territory or mate quality and/or mating success (e.g. Gustafsson *et al.* 1995; Hamilton and Zuk 1982; Landmann and Kollinsky 1995; Lifjeld and Slagsvold 1988; Moller 1994a,b, 1997; Swaddel and Witter 1995). The 'breast' plumage of dippers can readily be divided into three distinct regions; a broad white throat patch, a rufous or chestnut-brown chest band extending over the lower breast and central belly, and a dark brown lower belly, and the extent and colour of the chest band is known to vary with age, sex and between individuals within each class (Cramp 1988; Newton 1989a). Following Newton (1989a), the 'area' and 'richness' of the rufous chest band plumage were recorded. Assessments of area were made on an arbitrary 10 point scale by considering the proportion of the rufous plumage covering the fore- and underparts below the white throat patch. With significant variation in body size between individuals, direct measurements of plumage area were not justified (Newton 1989a). Plumage 'richness' was scored on a 6 point scale from dull mid-brown or straw yellow-brown to a very rich rufous brown. More complete descriptions of scoring techniques are given in Newton (1989a).

### 2.2.5. Sexing and ageing dippers

Dippers were sexed based on known size criteria established from breeding birds (Galbraith and Broadly 1980; Ormerod *et al.* 1986; Svensson 1992). On average, males were heavier than females, with significantly longer wing, keel, tarsus and bill lengths. Although there was some overlap between the largest females and smallest males, most birds could be reliably sexed based on wing length alone. Generally, females had wing lengths less than 92mm, with males usually exceeding 94mm (Figure 2.2). Where wing length was inconclusive, birds were sexed considering mass and keel length. Males typically had masses and keel lengths greater than 65g and 30.0mm respectively.

First year birds were easily separable from adults by their white tipped primary and greater wing coverts (Galbraith *et al.* 1981; Svensson 1992). Throughout the text, all birds in their first-year, including breeders, are referred to as juveniles. Birds in their second year, or older, are considered as adults. The two censuses undertaken annually divided the year into two discrete periods, allowing the broad timing of mortality to be described. For adult birds, post-breeding refers to the period from breeding to the autumn census (September/October), whilst for first-year birds this is referred to as the post-fledging period. Over-winter refers to the period between the end of October and breeding (March/April).

Nestlings were sexed based on known relationships between body size, age and sex from chicks measured in the nest and subsequently recaptured and positively sexed as adults. Male dippers are known to be larger than females at fledging and discriminant analyses can allow many chicks to be sexed at 18 days of age (Feltham 1987). However, although correctly sexing all

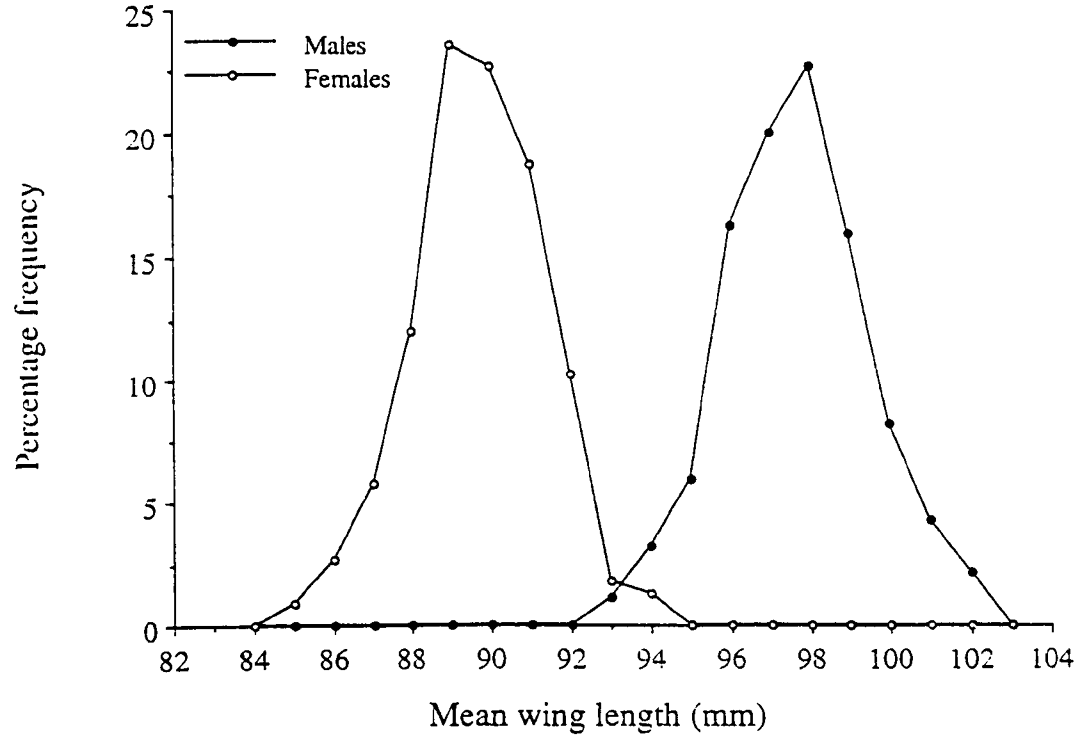


**Figure 2.2.** Percentage frequency distribution of mean wing length (maximum chord) for individual male and female dippers.

females, the discriminant function tends to classify some small males as female. A function constructed from data for all birds ringed at 18 days of age between 1993 and 1995 and subsequently recaptured and positively sexed, correctly sexed all females and 85% of male nestlings (n=34) ringed at a similar age and recaptured prior to 1993 (i.e. individuals not used in the calculation of the original function).

### 2.2.6. Breeding parameters

In all years, nests were located on both natural and man-made sites as early as possible in the breeding season, in many cases during the initial stages of construction. Once complete, nests were checked at least every four days until the final egg was laid. This allowed laying dates and final clutch sizes to be accurately determined with minimal disturbance, assuming that a single egg was laid each day following clutch initiation (Bryan 1996; Shaw 1978; Ward 1992). Nests were then visited on the expected day of hatching to record hatching success accurately. In all years, however, some nests were only located after clutch completion, and laying and hatching dates were calculated after Shaw (1978), or from growth rates based on nestling biometrics (Feltham 1987).

Nestlings were marked with a metal BTO ring, and tarsus length, wing length and chick mass were recorded at between 7 and 14 days. In the years from 1993-1995, final body measurements were also obtained for as many nestlings as possible at 18 days of age. Although some chicks were liable to 'explode' from the nest at this time, birds could be recaptured in a hand-net held directly below the nest and safely returned provide the nest entrance was temporarily blocked (for c.5-10 minutes), allowing the chicks time to resettle. All nests were revisited to confirm successful fledging and, in the following weeks, territories were checked for second or replacement breeding attempts.

# Chapter 3

# Biological significance of UK critical load exceedance estimates for flowing waters: assessments of Dipper *Cinclus cinclus* populations in Scotland.

### 3.1. Introduction

Critical loads are defined as 'the highest deposition of acidifying compounds that will not cause chemical changes leading to long term effects on ecosystem structure and function' (Battarbee 1992; Nilsson & Grennfelt 1988). By definition, therefore, exceedance of critical loads in fresh waters will have consequences for the biota, although the scale of any such effects is likely to differ between exceedance levels and organisms. Critical load models aim to predict the acidity status of freshwaters from source data on the acid neutralising capacity of the stream and lake catchments and acid deposition (Battarbee 1992; 1993). Models of this kind should be useful for predicting changes in the status of rivers and lochs following changes in sulphur deposition, as well as for remote assessments of current acid status. Yet, the biological implications of different exceedance levels remain unclear; in part because the relationship between water chemistry and biotic communities is not clearly defined for many species of conservation interest (Boon 1992). Equally, direct evaluations of the consequences of critical load exceedances have generally relied upon studies at single, sensitive (usually standing) waters, and may not, therefore, be typical of conditions across a wider area (Battarbee 1992). The biological consequences of critical load exceedances should be determined at an equivalent scale, in this case for 10km grid squares, if critical load estimates are to be used for evaluation of the impact of acidification or for anticipating some consequences of future changes in acid deposition.

It has been suggested that the population densities or breeding success of aquatic predators, especially birds, may provide a means by which the biotic status of flowing waters may be assessed indirectly and rapidly (Blancher & McAuley 1988; Meadows 1972; Ormerod & Tyler 1987, 1993; Vickery and Ormerod 1991). The dipper *Cinclus cinclus* is an ideal species for catchment scale studies since it is an obligate riverine predator, is widespread along Scotland's rivers (Gibbons *et al.* 1993), and its distribution and population densities have previously been closely linked to stream chemistry (Logie 1995; Ormerod *et al.* 1985, 1988; Vickery 1991).

Relationships between surface water chemistry, invertebrate abundance and dipper density have already been established for several parts of the British Isles. Mayflies, caddis flies, stoneflies and fish, the main prey of many small riverine predators, including dippers (Ormerod 1985; Ormerod *et al.* 1985; Ormerod and Perry 1986; Ormerod and Tyler 1986; Smith and Ormerod 1986; Vickery 1991, 1992), are all known to show reduced growth, reproductive success or densities in acidic waters (Bell 1971; Harriman and Morrison 1982; Maitland *et al.* 1987; Morrison 1989, 1994; Sutcliffe and Carrick 1973). Ormerod and co-workers in Wales (Ormerod *et al.* 1985, 1988) and Vickery (1991) in south-west Scotland documented reduced prey and dipper densities under elevated acidity levels whilst Da Prato and Langslow (1976) noted the absence of breeding dippers from river sections with low macroinvertebrate biomass in south-east Scotland. From these studies, and others in central Scotland (Lennon 1988; Logie 1995) and further afield (Kaiser 1985; Price and Bock 1983), it appears that dipper densities reflect the abundance and availability of prey species and, under normal conditions, a standardised census of dippers will allow useful inferences to be made about the comparative biotic status of running waters. When this applies, it would also allow the utility of the critical load exceedance models to be evaluated.

Assessing the utility of the CL models using the dipper as an indicator species is the principal aim of this study. However, since stream topography is known to be an important influence on dipper abundance (Ormerod *et al.* 1985, 1986; Vickery 1991) and because it remains possible that critical loads values have only limited explanatory or predictive powers (Battarbee, 1992), the utility of the exceedance estimates should be checked initially against explicit alternative hypotheses ($H_x$) for explaining variation in dipper density, of which the following will be considered here:

$H_{riv}$. Dipper density simply conforms to model predictions based on river gradient and altitude (Marchant and Hyde 1980) and area of riffle (Bryant *et al.* unpubl.). Riffle area is likely to be the more useful in the present context since sites have been standardised, as far as possible, with regard to gradient and altitude (see below).

$H_{pH}$. Dipper densities can be predicted more accurately using pH measurements or combinations of pH and habitat structure (Ormerod *et al.* 1985, 1986; Tyler and Ormerod 1985).

If $H_{pH}$, or a combination of $H_{pH}$ and $H_{riv}$ are supported, it suggests that an accurate critical loads exceedance model would describe variations in dipper densities with comparable precision, thereby allowing a third hypothesis to be evaluated :

$H_{CLE}$. Dipper density can be predicted from critical load exceedance estimates derived from the grid squares in which they occur.

### 3.1.1. Critical load models.

Two CL models are dealt with in this study: the 'Henriksen' and 'diatom' models. The 'Henriksen' or steady state water chemistry model calculates critical loads based on the assumption that in pristine, oligotrophic waters, the excess base cation production within a catchment should be greater than or equal to zero (Battarbee 1992, 1993). Assuming that inputs of atmospheric pollutants are in steady state with outputs, the sulphur load that maintains a preset acid neutralising capacity (ANC) for an appropriate target organism can then be calculated. The most commonly used Henriksen model, tested here, sets an ANC of zero, equivalent to a pH of approximately 5.3 in clear waters. This is known to be a critical point for many aquatic organisms and is intended to protect and conserve populations of brown trout *Salmo trutta* (Battarbee, 1992).

The 'diatom' model is an empirical model based on the dose-response relationship between sulphur deposition and changes in the composition of diatom assemblages within dated lake sediment cores (Battarbee 1990). The initial point of change in the diatom assemblages marks the time of initial acidification or critical load exceedance. Allowing for changes in the base cation concentrations of the water, the sulphur deposition received at this time, equivalent to the critical load, can then be derived from the dose response model (Battarbee 1990). As diatoms are amongst the most sensitive of aquatic organisms to acidity, and the diatom model is not linked to a preset ANC value (which may vary between sites, classifying naturally acid sites as showing exceedance, or excluding exceedance sites with positive alkalinity), this model can be seen to predict the site or baseline critical load.

From both models, exceedance estimates are derived by the comparison of critical loads ($keqH^{+}ha^{-1}y^{-1}$) with deposition levels. If the critical load is less than the actual measured load at any site, then the critical load is exceeded. The diatom model generally classifies squares into the same or a higher exceedance class than the Henriksen model, although both estimates of exceedance are highly correlated (Battarbee 1992, 1993). Both models however, rely on the determination of critical loads based on the single most sensitive site within a grid square. While catchment-specific models are now being developed, it clearly remains likely that current estimates do not account for the range of sensitivity conditions within a square. For these reasons initial evaluation of the biological consequences of 'exceedance' are only undertaken at a similarly coarse scale.

## 3.2. Methods

### 3.2.1. General methods and field protocol.

Streams in twenty-seven 10km grid squares were censused for dippers during October and early November 1993 (Figure 3.1). At this time of year the following conditions allow the abundance of dippers to be rapidly and reliably assessed:

i) Populations are close to their highest annual levels (Ormerod *et al.* 1985, 1988) giving the greatest chance of encountering birds even where they are scarce, and hence identifying differences between sites.

ii) Birds have mostly deserted tributary streams by this time. Earlier in the year, during breeding, dippers use these extensively, and may be overlooked except in the most intensive studies ( Newton 1989a).

iii) Territory occupation related to breeding sites is flexible and largely absent at this time of year and so effects of nest site availability on local distribution and hence density estimates are minimal ( Newton 1989a).

iv) All birds have completed moult, a period of general inactivity and inconspicuousness, and bankside vegetation has died back, together enhancing dipper 'visibility' (Galbraith *et al.* 1981; Newton 1989a).

v) Late autumn is a period of general population stability, hence only limited population changes would be expected between the first and last sites to be censused ( Newton 1989a; Shaw 1979).

These points, together with evidence highlighting the persistence of acidity effects throughout the year (Ormerod *et al.* 1985, 1988), suggest that for single census visits, autumn population estimates are the least likely to be biased by local topography, by phenology or behaviour.

### 3.2.2. Site selection

Census squares were selected from three areas; north-west, west-central and south-west Scotland, with three grid squares from each class of nil (<0.1 $keqH^{+}ha^{-1}y^{-1}$), medium (0.1-0.5) and high (>0.5) exceedance (Battarbee 1993), initially being surveyed in each region. Following the calculation of updated exceedance estimates (UKCLAG *unpubl.*) however, a single grid square from the south-west region was reclassified later from the nil to medium exceedance class.

All squares were chosen as containing river habitat physically suitable for foraging dippers to minimise variation related to topography (usually 10-25m $km^{-1}$ gradient, <400m altitude (Ormerod and Tyler 1985; Ormerod *et al.* 1985, 1986; Bryant *et al.* unpubl.). Additionally, catchments with blanket coniferous forests were not sampled to minimise confounding influences on water quality (Harriman and Morrison 1982; Ormerod *et al.* 1989) and, where possible, squares in the same CLE category under both the diatom and the Henriksen models (Battarbee 1992) were selected. Adjacent grid squares also were avoided to maintain site independence, although this was not always possible due to the clumping of the relatively small number of medium and high exceedance sites (Battarbee 1992, 1993) and the additional constraints of within-square stream length, afforestation and site accessibility.

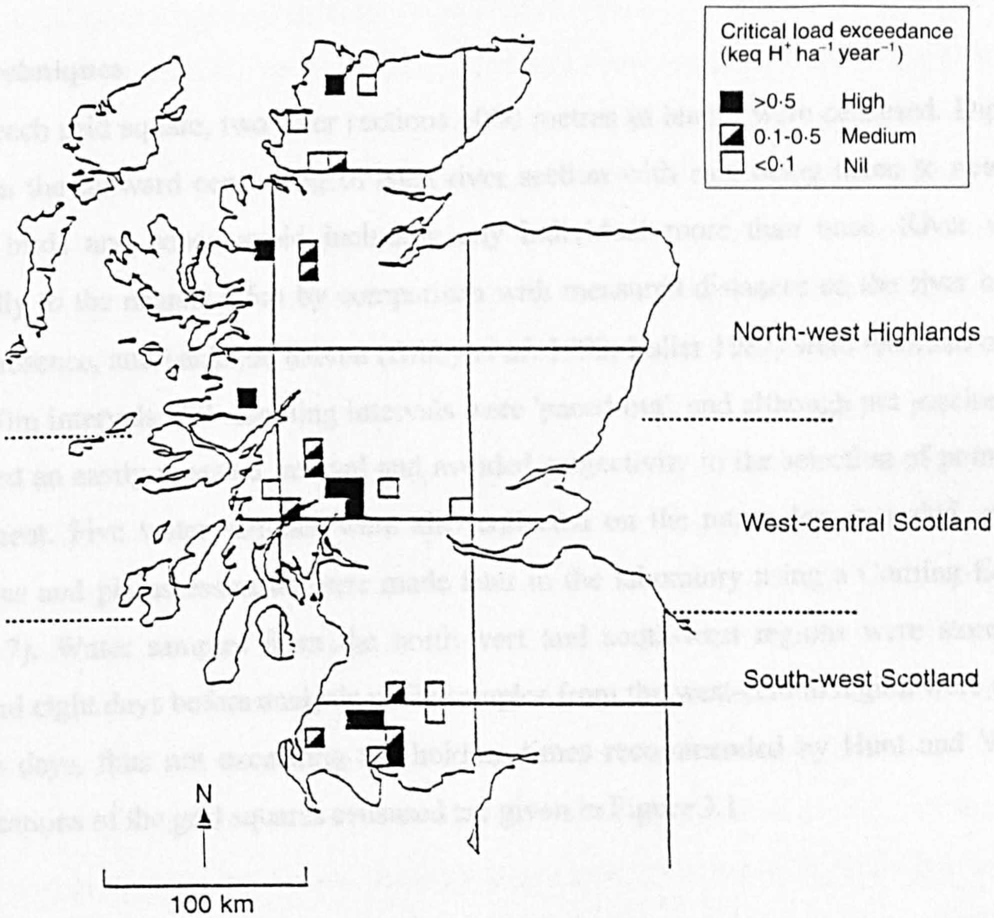


**Figure 3.1.** Locations of the grid squares censused for dippers, autumn 1993.

### 3.2.3. Census techniques

Within each grid square, two river sections 4000 metres in length were censused. Dippers were counted on the outward census leg of each river section with care being taken to note the movements of birds and hence avoid including any individual more than once. River width (assessed visually to the nearest 0.5m by comparison with measured distances on the river bank), riffle presence-absence, and bankside habitat (Bibby *et al.* 1992; Fuller 1982) were recorded on the return leg at 100m intervals. All sampling intervals were 'paced-out', and although not precise, this method provided an easily repeated interval and avoided subjectivity in the selection of points for habitat assessment. Five water samples were also collected on the return leg in sealed, sterile, polythene bottles and pH assessments were made later in the laboratory using a Corning Eel pH meter (Model 7). Water samples from the north-west and south-west regions were stored for between one and eight days before analysis while samples from the west-central region were stored less than three days, thus not exceeding the holding times recommended by Hunt and Wilson (1986). The locations of the grid squares censused are given in Figure 3.1.

### 3.2.4. Statistical analyses.

Previous studies of dippers have shown strong relationships between breeding densities and stream topography (Marchant and Hyde 1980; Ormerod *et al.* 1985, 1986). As similar factors are known to be important in determining dipper densities throughout the year (Ormerod *et al.* 1985, 1988), observed densities were initially compared with predicted densities based on two least squares regression models derived from the breeding data of Marchant and Hyde (1980). Predictions based on gradient ($mkm^{-1}$) were made from the quadratic equation: Territories $10km^{-1}$ of river = $2.5631 + 0.5178*gradient + 1.5192*gradient^2*10^{-2}$ ($r^2=0.893$, $p<0.001$). Predictions based on altitude (m a.s.l.) were made from the linear model: Territories $10km^{-1}$ of river = $1.9867 + 2.1927*altitude*10^{-2}$ ($r^2=0.953$, $p<0.001$) with the additional effects of riffle habitat area, known to hold the greatest invertebrate diversities and biomass, and to provide the shallow waters favoured by foraging dippers (Price and Bock 1983) considered by testing all model predictions against both the raw density counts and densities expressed as 'birds per unit riffle area'.

To confirm the applicability of dipper/acidity relationships established elsewhere (Vickery and Ormerod 1991) and assess the importance of stream topography, the combined data set incorporating all habitat and density data was examined using linear regression and stepwise multiple regression with natural log transformations applied for normality where appropriate. Differences between regions and exceedance categories were investigated using analysis of variance and covariance with exceedance classes entered as factors and habitat variables as covariates.

Analyses have been undertaken first by grid square, with data points derived from the mean of two 4000m sections and expressed as dippers $10km^{-1}$ of river. Secondly, a number of analyses were carried out to utilise the more extensive river section data set, although using only data specific to each river section i.e. density and habitat variables, and including only river sections from different catchments to maintain independence. Accordingly, where both censuses were undertaken on a single river the mean value of these two sections has been used, resulting in 44 of a possible 54 sections (82%) being included in these analyses. As critical load exceedance data were only available at a grid square resolution these have not been included in any analysis by river section. Statistical analyses have been undertaken using the SPSSx computer package (SPSSx inc. 1988), with all data being checked for intercolinearity prior to analysis.

## 3.3. Results

### 3.3.1. Regional dipper densities.

Dippers were absent from 3 of 27 (11%) grid squares (one in each region) and from 12 of the 54 river sections censused (22%). Their presence was confirmed on all rivers of pH$^3$6.44 (n=31) while below this level dippers were recorded on only 11 of 23 river sections (48%). Although a random sampling technique would be required to test rigorously for inter-regional differences, no significant differences between regions were identified within this study (ANOVA $F_{2,26}$=0.768,

$p=0.447$ by squares; $F_{2,43}=0.142$, $p=0.868$ by catchments), allowing all data to be combined for analysis purposes. However, stream pH and dipper densities (Table 3.1) cannot be taken as representative of each region since some high CLE squares were specifically selected, and are over-represented relative to a random sample within the data sets, thereby reducing mean dipper densities.

### 3.3.2. Dipper densities and model predictions ($H_{riv}$)

No significant relationships were evident between the observed densities of non-breeding dippers, either expressed as birds per unit river length or birds per unit riffle area, and the density predictions based on the altitude data of Marchant and Hyde ($r^2<0.044$, $p>0.743$ in all cases, n=27 grid squares, n=44 river sections). Although the gradient predictions approached significance in the grid square analysis by river length ($r^2=0.127$, $p=0.067$, n=27), this result was due almost entirely to a single outlying point and no relationship was evident after accounting for this outlier by correcting for differences in riffle area ($r^2<0.039$, $p>0.05$, n=27 grid squares, n=44 river sections). Using linear regression, site altitude, gradient and riffle area were all insufficient to describe the dipper densities observed ($r^2<0.068$, $p>0.128$ in all cases, n=27 grid squares, n=44 river sections), whilst gradient also remained non-significant when quadratic regression techniques similar to those used to construct the predictive gradient model were employed ($r^2=0.141$ by square, $r^2=0.101$ by section with densities expressed as birds $10km^{-1}$; $r^2=0.062$ by square, $r^2=0.053$ by section with densities as birds $10000m^{-2}$ of riffles; $p>0.05$ in all cases). Considered alone or in combination, no measure of stream topography was able to account for the observed variation in dipper densities.

### 3.3.3. Dipper densities, pH and habitat structure ($H_{pH}$)

Dipper density was found to be significantly related to stream pH ($r^2=0.703$, $p<0.001$, n=27 grid squares; $r^2=0.625$, $p<0.001$, n=44 river sections, Figure 3.2) and bankside deciduous cover ($r^2=0.343$, $p<0.001$, n=27 grid squares; $r^2=0.325$, $p<0.001$, n=44 river sections) for both river sections and grid squares. Deciduous cover was also significantly correlated with pH (Pearson's

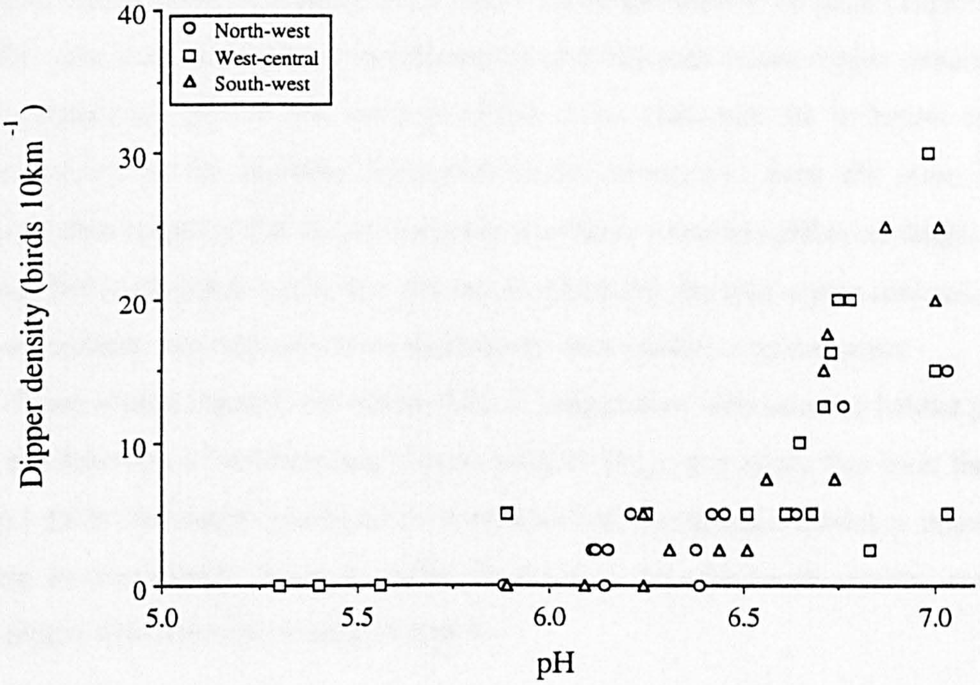


**Figure 3.2.** Non-breeding dipper density in three regions of Scotland in relation to winter stream pH. $r^2=0.703$, $p<0.001$, n=27 grid squares; $r^2=0.625$, $p<0.001$, n=44 river sections.

correlation coefficient=0.50, p=0.004, n=27 grid squares; 0.47, $p<0.001$, n=44 river sections), however, and its importance in determining dipper densities initially appeared unclear.

Stepwise multiple regression showed both riffle area and altitude also to have a significant partial influence on dipper density considering only river sections, with these factors together with pH and deciduous cover explaining more than 81% of the density variance (Table 3.3b). Only pH and riffle area were included as significant (at $p<0.05$) with mean dipper densities within grid squares, explaining 75% of the variance (Table 3.3a). Although the inclusion of both pH and deciduous cover in the multiple regression model constructed from the more extensive river catchments data suggests that deciduous cover may have a positive effect on dipper densities, over and above that attributable to pH, this was not confirmed by the grid square analyses. No significant effects of gradient were apparent from analyses by river section or grid squares.

These results suggest that stream pH, in conjunction with selected habitat parameters, can predict the densities of non-breeding dippers reliably ($H_{riv}$), and imply that were the surface water chemistry to be accurately predicted by a critical load exceedance model, a regression equation including an exceedance parameter rather than pH to describe water quality, could be used to predict dipper densities with similar precision.

**Table 3.1.** The pH and non-breeding dipper densities for three Scottish regions analysed by grid square (densities expressed as birds $10km^{-1}$ of river).

| | | Density | | | pH | |
|---|---|---|---|---|---|---|
| Region | Mean±se | Min | Max | Mean±se | Min | Max |
| North-west (n=9) | 4.44±1.12 | 0.00 | 12.50 | 6.33±0.08 | 5.88 | 6.84 |
| West-central (n=9) | 9.58±2.01 | 0.00 | 22.50 | 6.46±0.13 | 5.40 | 7.00 |
| South-west (n=9) | 8.20±2.02 | 0.00 | 25.00 | 6.49±0.08 | 5.89 | 6.94 |

**Table 3.2a.** Stepwise multiple regression analysis for the abundance of non-breeding dippers by grid square (mean of two river sections) in relation to selected variables ($y= a + bx_1 + bx_n$). Dipper density is expressed as birds 10km$^{-1}$ of river. Density (*y*+1), and riffle area (m 10km$^{-1}$), gradient (m$^2$km$^{-1}$) and altitude (m a.s.l.) were transformed (ln *x*) prior to analysis, deciduous cover (%) was arcsine transformed. n=27 grid squares in all cases.

| Variables in Equation | b±s.e. | Beta±s.e. | Cum $r^2$ | F (Eqn) | p |
|---|---|---|---|---|---|
| 1. pH | 1.438±0.173 | 0.854±0.103 | 0.703 | 59.098 | 0.001 |
| 2. Riffle area | 0.345±0.168 | 0.212±0.102 | 0.747 | 35.498 | 0.001 |
| Constant (a) | -9.594±1.676 | | | | |

Deciduous cover, gradient and altitude not included as significant (p>0.05).

**Table 3.2b.** Stepwise multiple regression analysis for the abundance of non-breeding dippers by river section in relation to selected habitat variables ($y= a + bx_1 + bx_n$). Dipper density is expressed as birds 10km$^{-1}$ of river. Density (*y*+1), and riffle area (m$^2$10km$^{-1}$), gradient (m$^2$km$^{-1}$) and altitude (m a.s.l.) data were transformed (ln *x*), deciduous cover (%) was arcsine transformed. n=44 river sections in all cases.

| Variables in Equation | b±s.e. | Beta±s.e. | Cum $r^2$ | F (Eqn) | p |
|---|---|---|---|---|---|
| 1. pH | 1.257±0.152 | 0.673±0.081 | 0.613 | 64.958 | 0.001 |
| 2. Riffle Area | 0.572±0.116 | 0.356±0.072 | 0.694 | 45.469 | 0.001 |
| 3. Decid Cover | 0.009±0.002 | 0.394±0.089 | 0.741 | 37.253 | 0.001 |
| 4. Altitude | 0.350±0.090 | 0.316±0.082 | 0.814 | 41.690 | 0.004 |
| Constant (a) | -11.996±1.425 | | | | |

Gradient not included as significant (p>0.05).

### 3.3.4. Dipper densities and critical load exceedance categories ($H_{CLE}$)

Since the explanatory or predictive powers of the critical loads models remain uncertain, for reasons outlined by Battarbee (1992), initial assessments of the models were undertaken, testing only for differences in dipper densities between the broad classes of nil, medium and high exceedance (Table 3.3, see methods for category definitions).

Significant differences were identified between exceedance categories in all analyses indicating that, at a very general level, the biological effects predicted by the critical load models are indeed evident on the ground (Table 3.4). Although the importance of riffle area, suggested by previous workers (Robson 1956; Shooter 1970), was not confirmed when entering this variable as a covariate, this probably simply reflects the overriding influence of stream pH on dipper densities. However, the inclusion of riffle area in the multiple regression equations for both river sections and grid squares and its significant positive relationship with dipper density when considering only circum-neutral river sections ($r^2=0.315$, $p=0.007$, $n=22$; circum-neutral based on the 'acidic/non-acidic' threshold pH of 6.5 adopted by the Scottish River Purification Boards) have been taken to justify the further use of densities expressed as birds per unit riffle area. Applying this correction, differences between exceedance classes were of greater statistical significance (Table 3.4). Although the inclusion of deciduous cover as a covariate further confirmed the between class differences, the validity of this result remains questionable in view of the significant correlation between deciduous cover and pH noted earlier.

The mean density of dippers in nil-exceedance squares was more than 2.6 times that recorded for either of the exceedances categories, whereas 'high' exceedance squares held only 11% fewer dippers than 'medium' squares, equivalent to a density reduction of only one bird per 10km of river. This suggests that differences in dipper densities may be most pronounced between exceedance and non-exceedance squares rather than within the exceedance classes of medium and high (Table 3.3). Indeed, the greatest density of dippers recorded for any exceedance square in this study was on the River Fyne, Argyll, in a square from the highest exceedance category.

**Table 3.3.** Non-breeding dipper density and pH within critical load exceedance categories. Dipper densities expressed as birds 10km$^{-1}$ of river.

| Exceedance Category | | Density | | | pH | | |
|---|---|---|---|---|---|---|---|
| | | Mean±s.e. | Min | Max | Mean±se | Min | Max |
| Nil | (n=8) | 13.44±2.94 | 1.25 | 25.00 | 6.68±0.11 | 6.16 | 7.00 |
| Medium | (n=10) | 5.13±1.14 | 0.00 | 12.50 | 6.49±0.10 | 5.89 | 6.93 |
| High | (n=9) | 4.58±1.77 | 0.00 | 16.25 | 6.15±0.15 | 5.40 | 6.73 |
| Overall | (n=27) | 7.40±1.33 | 0.00 | 25.00 | 6.43±0.08 | 5.40 | 7.00 |

**Table 3.4.** Statistical comparisons (ANOVA) of non-breeding dipper densities in relation to critical load exceedance categories (see text and Table 3.3) and selected habitat parameters.

| Dependent Variable | Main Effects (Exceedance class) | Covariates | Significance of Covariates |
|---|---|---|---|
| Dipper density 10km$^{-1}$ | $F_{2,24}$=3.867, p=0.035 | ----- | ----- |
| Dipper density 10km$^{-1}$ | $F_{2,22}$=4.115, p=0.030 | Riffle area<br>Altitude | $F_{1,22}$=0.175, p=0.857<br>$F_{1,22}$=0.053, p=0.820 |
| Dipper density 10km$^{-1}$ | $F_{2,21}$=4.854, p=0.018 | Decid Cover<br>Riffle area<br>Altitude | $F_{1,21}$=20.056 p=0.001<br>$F_{1,21}$=1.236, p=0.279<br>$F_{1,21}$=3.492, p=0.076 |
| (Dippers/Riffle Area) | $F_{2,24}$=4.316, p=0.025 | ----- | ------ |
| (Dippers/Riffle Area) | $F_{2,22}$=4.264, p=0.027 | Decid Cover<br>Altitude | $F_{1,22}$=20.239, p=0.001<br>$F_{1,22}$= 3.453, p=0.077 |

### 3.3.5. Critical load exceedance (CLE) values and dipper density.

With the identification of significant differences between broad measures of exceedance, further analyses were undertaken to establish how much precision was evident within the CLE estimates. Stepwise multiple regression techniques, similar to those used to determine the relationships between pH, habitat parameters and dipper density, were applied with exceedance estimates replacing pH to represent water quality. All analyses were repeated with and without the inclusion of deciduous cover for reasons outlined earlier.

Dipper density was found to be significantly related to both critical loads models, with the Henriksen and diatom estimates explaining 37% and 34% of the variance in density respectively (Figures 3.3a and b, Table 3.5). In all analyses, deciduous cover (when entered) was included as the only significant habitat variable, accounting for approximately an additional 13% of the variance in all cases. Again all relationships with exceedance estimates were strengthened by expressing dipper density as birds per unit riffle area rather than simply river length, with an additional 4% and 3% of the variance explained for the Henriksen and diatom model values, respectively (Figures 3.4a and b, Table 3.5).

## 3.4. Discussion

While the dipper is still widely distributed over much of northern and western Britain, there is evidence of a recent decline (Gibbons *et al.* Chapman 1993), with many of the areas of population reduction generally coincident with 'centres' of CLE (Battarbee 1993). The Trossachs in west-central Scotland and Galloway, for example, are both regions highlighted by the CL models, where dippers are known from recent studies to be scarce or absent on acidified streams (Logie 1995; Vickery 1991). This suggests that declines of dippers between 1968/72 and 1988/91 were, at least in part, related to the exceedance of catchment critical loads, and that closer consideration of the relationship between dipper abundance and CLE would allow the biological implications of exceedance estimates to be evaluated. Indeed, the results of studies involving both the breeding and non-breeding seasons support the value of dippers as indicators of water chemistry, and hence their utility in assessments of the critical load models (Ormerod *et al.* 1985, 1988; Vickery 1991).

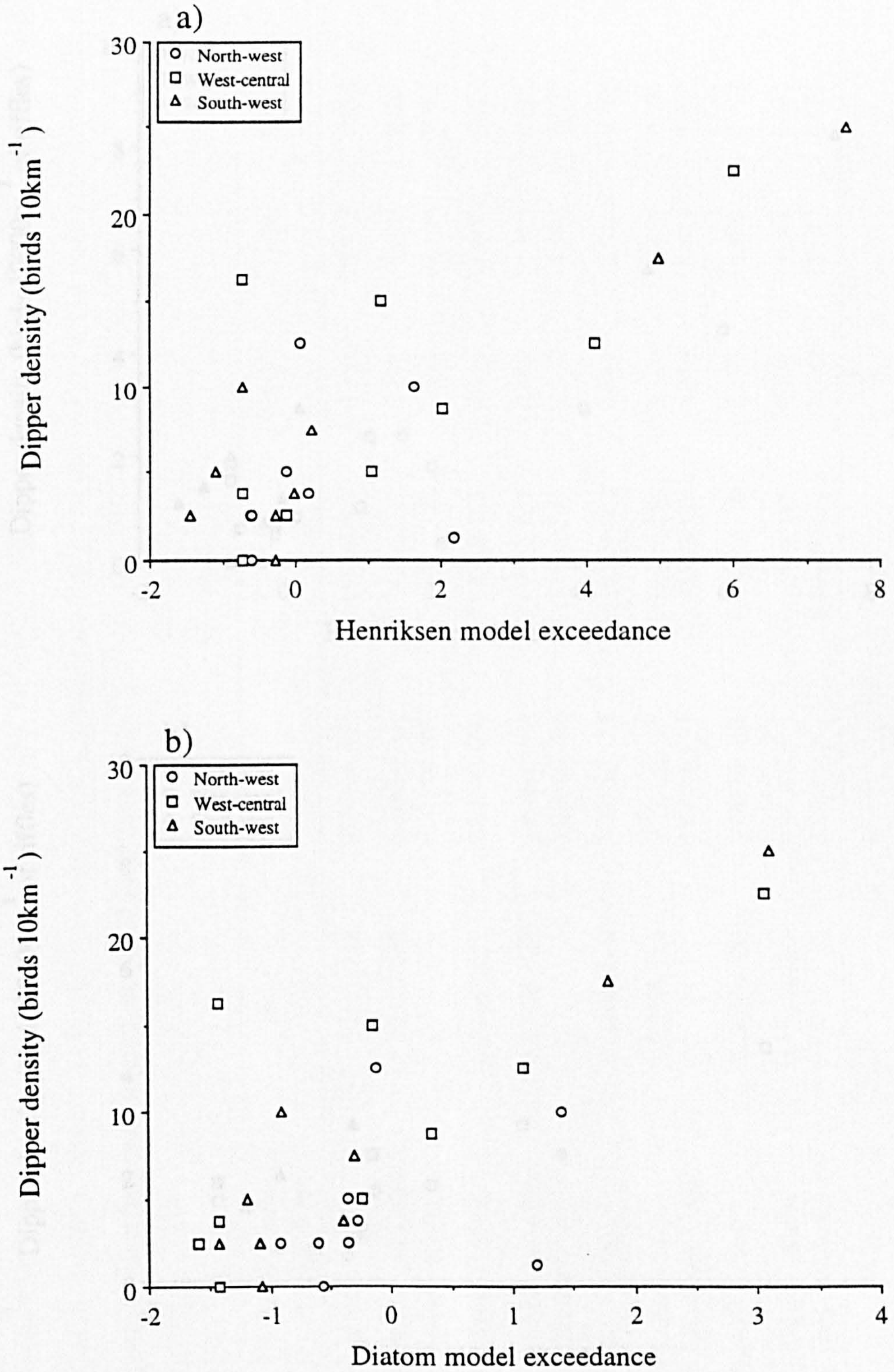


**Figure 3.3.** Density of non-breeding dippers in three regions of Scotland in relation to a) 'Henriksen' model critical load exceedance values (UKCLAG, *unpubl.*), $r^2$=0.372, p=0.001, n=27 grid squares, and b) 'diatom' model critical load exceedance (UKCLAG, *unpubl.*). $r^2$=0.339, p=0.001, n=27 grid squares. Negative values denote exceedance (see Table 3.5).

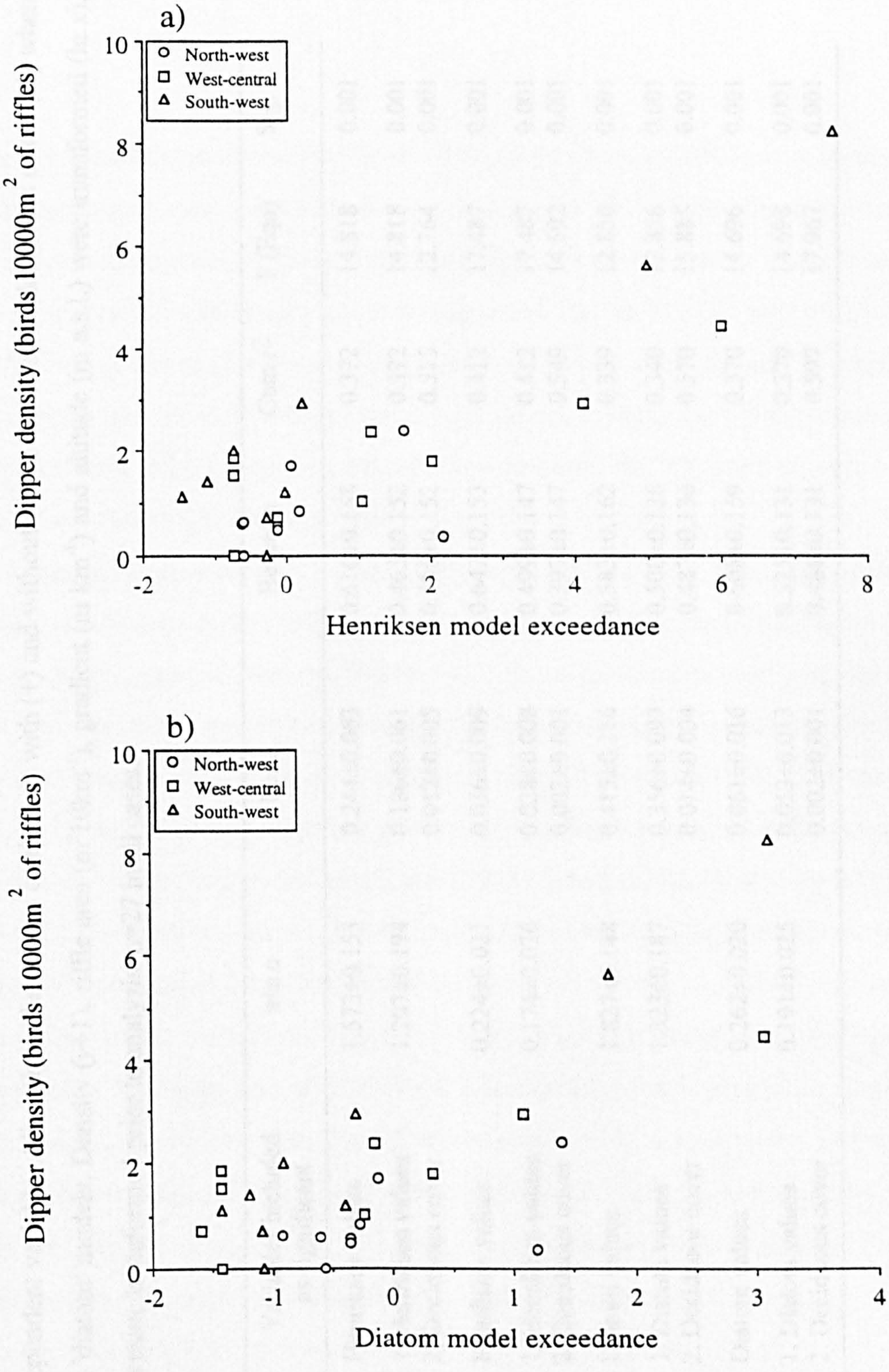


**Figure 3.4.** Density of non-breeding dippers in three regions of Scotland, adjusted for area of riffles, in relation to a) 'Henriksen' model critical load exceedance values (UKCLAG, *unpubl.*), $r^2$=0.412, p=0.001, n=27 grid squares, and b) 'diatom' model critical load exceedance values (UKCLAG, *unpubl.*), $r^2$=0.370, p=0.001, n=27 grid squares. Negative values denote exceedance (see Table 3.5).

**Table 3.5.** Stepwise multiple regression analyses for the abundance of non-breeding dippers by grid square (mean of two river sections) in relation to CLE estimates and selected habitat variables ($y= a + bx_1 + bx_n$). Dipper density is expressed as birds 10km$^{-1}$ of river (denoted '10km$^{-1}$') or birds 10000m$^{-2}$ of riffle (denoted '10$^4$m$^{-2}$'). Gradient (mkm$^{-1}$) and altitude (m a.s.l) entered into all analyses, riffle area (m$^2$10km$^{-1}$) entered into analyses with birds 10km$^{-1}$ as the dependent variable. All analyses have been carried out with (+) and without (-) the inclusion of deciduous cover (%) when testing the 'Henriksen' and 'diatom' models. Density ($y$+1), riffle area (m$^2$10km$^{-1}$), gradient (m km$^{-1}$) and altitude (m a.s.l.) were transformed (ln $x$), deciduous cover (%) was arcsine transformed prior to analysis. n=27 in all cases.

| Analysis | Variables included as significant | a±s.e | b±s.e. | Beta±s.e | Cum $r^2$ | F (Eqn) | Sig. F |
|---|---|---|---|---|---|---|---|
| Henriksen, 10km$^{-1}$, - | Henriksen values | 1.573±0.153 | 0.244±0.063 | 0.610±0.158 | 0.372 | 14.818 | 0.001 |
| Henriksen, 10km$^{-1}$, + | 1. Henriksen values | 1.207±0.194 | 0.186±0.061 | 0.465±0.152 | 0.372 | 14.818 | 0.001 |
| | 2. Deciduous cover | | 0.012±0.005 | 0.405±0.152 | 0.515 | 12.764 | 0.001 |
| Henriksen, 10$^4$m$^{-2}$, - | Henriksen values | 0.224±0.021 | 0.036±0.009 | 0.642±0.153 | 0.412 | 17.487 | 0.001 |
| Henriksen, 10$^4$m$^{-2}$, + | 1. Henriksen values | 0.174±0.026 | 0.028±0.008 | 0.499±0.147 | 0.412 | 17.487 | 0.001 |
| | 2. Deciduous cover | | 0.002±0.001 | 0.397±0.147 | 0.549 | 14.592 | 0.001 |
| Diatom, 10km$^{-1}$, - | Diatom values | 1.827±0.148 | 0.415±0.116 | 0.583±0.162 | 0.339 | 12.856 | 0.001 |
| Diatom, 10km$^{-1}$, + | 1. Diatom values | 1.323±0.187 | 0.356±0.097 | 0.500±0.136 | 0.340 | 12.856 | 0.001 |
| | 2. Deciduous cover | | 0.014±0.004 | 0.487±0.136 | 0.570 | 15.885 | 0.001 |
| Diatom, 10$^4$m$^{-2}$, - | Diatom values | 0.262±0.020 | 0.061±0.016 | 0.608±0.159 | 0.370 | 14.696 | 0.001 |
| Diatom, 10$^4$m$^{-2}$, + | 1. Diatom values | 0.191±0.025 | 0.053±0.013 | 0.525±0.131 | 0.370 | 14.698 | 0.001 |
| | 2. Deciduous cover | | 0.002±0.001 | 0.486±0.131 | 0.597 | 17.967 | 0.001 |

Variables not included as significant if $p>0.05$.

As in studies elsewhere (Ormerod *et al.* 1985, 1988; Vickery 1991), the principal factor controlling dipper density was stream pH, alone accounting for 70% of the grid square variance in abundance. By considering the additional effects of riffle area in a stepwise multiple regression, around 75% of the variation in density could be explained, and up to 81% with the river section data where the weaker effects of altitude and deciduous cover also were included as significant. In this context altitude was found to have a negative partial effect rather than the positive influence suggested by Marchant and Hyde (1980); a result consistent with findings from intensively studied catchments in central Scotland ( Newton 1989a).

The importance of deciduous cover, previously noted to have a positive influence on breeding densities (Ormerod *et al.* 1986), remains unclear because of its strong intercorrelation with pH. Studies noting elevated invertebrate densities in sites of increased coarse particulate organic matter input and retention suggest productivity may be enhanced in deciduously lined streams independently of stream acidity (Dobson and Hildrew 1992; Richardson 1991). The direct supply of terrestrial prey from broad-leaved trees may also be important for aquatic predators, particularly when other prey are scarce (Mason and MacDonald 1982). It seems likely that at least a proportion of this prey would be taken by dippers, known to accept soil invertebrates carried into the stream system (Ormerod *pers. comm.*) and the emerging adults of aquatic invertebrates (Shaw 1978). Although the basis of the correlation between pH and deciduous cover identified here remain uncertain, processes elevating prey availability in deciduously lined, acid streams will be of obvious importance to dipper densities. The apparent inability of deciduous cover (after accounting for pH) or any other measure of habitat structure to significantly predict dipper densities, however, probably reflects both the narrow range of variation considered and the overriding influences of water chemistry. Dipper density was significantly related to riffle area, for example, only when considering circum-neutral river sections.

The ability to predict dipper densities from a number of simple, measurable habitat parameters, principally pH, implies that if a critical loads model was to represent surface water chemistry accurately, then it should similarly account for the variation in observed dipper density, particularly if allowances are made for riffle area. A requirement for this arises in two contexts related to assessments of freshwater communities: when data on water chemistry are not available and, most importantly, when attempting to anticipate the biological impact of future changes in acid deposition (Battarbee 1992, 1993). Yet, the applicability of current models to both dippers and aquatic communities more generally has remained uncertain.

Within-catchment variation in water quality is still under study, although it is known already that critical load values may vary substantially within a 10km grid square depending on soils, geology and land-use (UKCLAG *pers comm*). Calculations of critical loads and exceedance estimates are also subject to problems associated with the temporal, as well as spatial, variability in water chemistry and uncertainties in estimates of sulphur deposition and the importance of nitrogen inputs in the acidification of individual sites (Battarbee 1992, 1993). Current models therefore aim only to predict the lowest within-square critical load or "worst case scenario" and for the reasons outlined above and by Battarbee (1992), some exceedance values, particularly for the north-west of Scotland, may still only be provisional (Battarbee 1992, 1993).

The significant differences in density identified between the broad exceedance classes defined in this study, indicate that at a general level, these simulated measures of water quality may be sufficient to draw useful biological inferences. Since the main differences in density were between nil-exceedance and exceedance squares, rather than between the mid and high exceedance classes, it appears that the anticipated negative consequences are evident even at low exceedance levels (Table 3.4). The strength of the correlations between dipper density and exceedance estimates relies on the high numbers of birds recorded at non-exceedance sites however, with model estimates for exceedance squares only poorly describing variation in dipper density. Clearly, for non-exceedance sites where the most sensitive waters are not expected to be acidified, no other streams within the square should hold reduced numbers of dippers. Within square variation in critical loads may be of greater importance at exceedance sites therefore, where the most sensitive waters may not represent conditions within the square as a whole. These uncertainties may help explain the limited precision of some exceedance estimates since recent studies of upland streams have suggested that site specific exceedance estimates may indeed represent the general status of invertebrate communities (Turnbull *et al.* 1995).

In view of the complexity of ecosystem processes there is often a requirement for biotic conditions to be assessed from a small range of indicator organisms which reflect the status of the wider environment (Ormerod 1993). As previous studies have found strong evidence linking dipper densities to prey availability (Da Prato and Langslow 1976; Logie 1995; Ormerod *et al.* 1985, 1986; Price and Bock 1983; Vickery 1991), it follows that if the CL models are able to predict dipper densities they will also describe the status of prey populations and general conditions within the wider ecosystem. A precise correspondence between exceedance estimates and aquatic biotas is unlikely to be universal, however, since responses to stream acidity will vary between species of both predators and prey (Battarbee 1992) and seasonally within single species. Indeed, the two models examined here are intended to predict critical loads for brown trout and a diatom community, not dippers. Many of the prey items important in the diet of dippers are known to be less acid-sensitive than, for example, some diatoms. Exceedance estimates based only on the diatom model will not be in complete agreement with dipper densities. Similarly, in contrast to the threshold ANC of $0meql^{-1}$ adopted for the Henriksen CL model, a critical value of $35meql^{-1}$ has been proposed as the point at which the densities and breeding performance of dippers may be affected (Ormerod 1993). Some Scottish waters with ANC values below $35meql^{-1}$ may be naturally acidic without CLE. Autumn also appears to be a period of minimal energetic demand for dippers (Bryant and Tatner 1988), with some rivers of low pH being occupied at this time but not during breeding (Ormerod *et al.* 1985, 1988). Acidity effects may have a greater impact when the energetic requirements for self-maintenance are coupled with the additional demands of chick-rearing (Bryant and Tatner 1988; Logie 1995) and the association between dippers and their prey populations may be tighter at this time. Under these conditions, or if exceedance estimates are calculated with dippers as the specific target organism, the predictive capacity of CL models may be improved, at least with regard to dipper densities.

The identification of significant relationships between the density of dippers, and both observed and predicted surface water chemistry, demonstrates that standardised dipper counts could allow the broad biotic and chemical status of flowing waters to be assessed quickly, at both river and catchment levels. Spatial correlations in acidity, as demonstrated here, may not necessarily translate directly into temporal trends of acidification with some Scottish waters being naturally acidic without CLE, and it remains impossible to show acidification in the absence of reliable historical data. Dipper densities however, provide a valuable and reliable means of assessing the current acidity status of flowing waters and thereby a means of identifying sites where acidification may have taken place. Although critical load models do not appear to capture all the details of effects on ecosystems within catchments, they provide a means of predicting the comparative biological status of surface waters at coarser resolutions and of anticipating the likely effects on fresh water communities of planned reductions in acid deposition.

This study represents the first independent biological validation of the current critical loads models. While the consistency of dipper/acidity relationships established throughout mainland Britain (Logie 1995; Ormerod *et al.* 1985, 1988; Vickery 1991; this study) suggests that the critical loads models may be similarly applicable, further work to confirm and refine the relationships identified here, and to test their general relevance, is required if the current models are to be accepted for management purposes.

# Chapter 4

# Local survival and the first year breeding probabilities of dippers in the River Devon catchment

## 4.1. Introduction

Within the UK, survival probabilities for dippers have been estimated using both return rates (Robson 1956) and ringing recoveries (Galbraith and Tyler 1982), although, to date, studies have considered only small numbers of individuals and average annual survival. Whilst these *ad hoc* estimates have been in general agreement, both within Britain (Hewson 1969; Galbraith and Tyler 1982) and with those determined from populations elsewhere (Clobert *et al.* 1990; Price and Bock 1983), mean estimates give no indication of annual variations in survival or the factors influencing rates.

National monitoring programs in the UK, such as the BTO waterways survey (Marchant *et al.* 1990), suggest a strong consistency in survival, with dippers appearing to have escaped the high mortality evident in many riparian species during recent severe winters (Dobinson and Richards 1964; Marchant *et al.* 1990). This consistency remains remarkable given the unique position occupied by dippers, with their restricted habitat requirements apparently imposing limits on possible responses at times of environmental stress. Some birds breeding on mountain streams move to lower altitudes in winter, or forage on loch and lake shores during severe flows, although unlike many northern European populations, British dippers are non-migratory and generally sedentary. They are thus forced to suffer unfavourable local conditions (Cramp 1988; Lundberg *et al.* 1981; Tyler and Ormerod 1986).

Studies of both Eurasian and American dippers have highlighted the importance of extremes of river flow, both floods and droughts, in influencing survival (Clobert *et al.* 1990; Price and Bock 1983). Similar effects have been suggested for local UK populations, albeit in the absence of formal analyses (George 1993; Tyler and Ormerod 1994; Wilson 1996). The elevated energetic costs of foraging under high river flows have been highlighted in a number of studies (Bryant *et al.* 1985; Bryant and Tatner 1988; O'Halloran *et al.* 1990) and Da Prato (1981) has shown that where foraging refuges are unavailable, many birds may be forced to forego foraging in spate conditions until flows subside. Floods may also wash prey downstream, whilst increased turbidity is known to kill many invertebrate species (Price and Bock 1983). In some cases, droughts or low flows may also reduce prey abundance by the silting of river channels or excessive growth of aquatic algae and macrophytes (Marzolin in prep.).

In this chapter, recent statistical developments for the handling of capture-recapture data sets are applied to estimate annual survival probabilities and to examine possible factors important in influencing these rates. Where birds are marked before the age of first breeding, and if recapture itself is dependent on the initiation of a breeding attempt, age-specific breeding probabilities can also be determined by a comparison of the recapture rates of first-year birds and individuals known to have bred previously (Clobert *et al.* 1990).

## 4.2. Methods

### 4.2.1. Estimating Recapture and Survival rates

Until recently, determining survival probabilities for marked animals had mainly relied on *ad hoc* estimates of return rates; the proportion of a marked and released cohort which is recaptured or resighted at the following census period. This measure, in fact the product of survival ($\Phi$) by recapture probability (p), relies on the assumption that all animals alive at the start of a census period are subsequently caught. Then, $\Phi * p = \Phi * 1 = \Phi$, the true survival rate. In many field studies this assumption is not met, and a proportion of individuals escape capture on any occasion. The true survival is then underestimated since $p<1$ and hence $\Phi * p < \Phi$. However, recent developments from the methods of Cormack (1964) and Jolly-Seber (Seber 1973), now allow recapture and survival probabilities to be estimated separately. Recapture probabilities for all but the last occasion can be estimated from recapture histories, based on the probability of individuals escaping capture on any occasion, subsequently reappearing at a later time. Within these methods, parameter estimation relies on a number of implicit assumptions (Burnham *et al.* 1987; Lebreton *et al.* 1992):

i) Every animal (within a group), whether marked or not, has the same probability of survival between censuses, and of capture on any single census occasion.

ii) On a single census occasion, all samples are instantaneous.

iii) Once ringed, all animals retain their marks.

The assumptions that parameters are specific to sampling occasions and that the fate of an individual is independent of its previous capture history, can readily be tested using existing computer software. Goodness of fit tests and departures of the data from the Cormack-Jolly-Seber model (time dependence on survival and recapture probabilities) can be detected by Tests 2 and 3 of the program RELEASE (Burnham *et al.* 1987; 64). Within RELEASE, Test 1 allows a comparison of group (e.g. age or sex) estimates.

If the Cormack-Jolly-Seber (CJS) model adequately describes the data, it may then be possible to reduce the number of parameters considered by imposing equality constraints between groups or occasions, or by linking parameter estimation to in-built logistic regressions based on dummy and external variables (Lebreton *et al.* 1992). Model selection based on likelihood ratio testing (LRTs) aims to produce progressively refined (simplified) models. Where a simple model fits the data as well as a more complex alternative, the complexity of the initial models cannot be justified and the simple model is preferred (from the principle of parsimony). The resulting reduction in the number of parameters increases precision without creating bias in the model estimates (Lebreton *et al.* 1992), and selection continues to the most parsimonious model retaining all relevant biological information. A range of survival and recapture models can then be fitted to test specific biological questions within the package SURGE 4.2 (Pradel and Lebreton 1993). If many models appear equally suitable, or where several likelihood ratio tests are required to achieve parsimony (and the associated risk of Type 2 errors), model selection may be aided using Akaike's information criteria (Lebreton *et al.* 1992). This statistic (-2np*DEV) calculated from the number of model parameters estimated (np) and the deviation within the model (DEV, a measure of relative model fit) is known to emphasise parsimony and to be an appropriate function for model selection (Lebreton *et al.* 1992).

### 4.2.2. Estimation of age specific breeding probabilities

Estimation of age specific breeding probabilities are based on the methods of Clobert *et al.* (1990) and are given here only in outline. In principle, the procedure considers the situation where spring recapture is dependent on the breeding status of an individual. If the census effort is restricted to known breeding sites, the very presence of a bird indicates its status as a breeder. Breeding birds will thus be captured (with a probability equal to that of other known breeders), non-breeders will not. The overall recapture rate within a group of individuals having made no previous breeding attempt will then be lower than that of known breeders until the age of full breeding, assuming that:

i) individuals remain within the study area whether breeders or non-breeders, so the choice of breeding site is made at the first potential breeding occasion, whether an attempt to breed is subsequently made then or later.

ii) From the age to maturity, both breeding and non-breeding individuals have equal survival probabilities.

iii) Having bred once, each individual continues to breed in the study area every year until death.

iv) Capture rates are independent of the previous history of an individual i.e. independent of age and the number of previous breeding attempts (see above).

#### 4.2.2.1. Data preparation for the estimation of breeding probabilities

Within this analysis recapture histories are divided into 3 groups. Group 1 represents the histories of individuals marked before maturity until their first recapture (or sighting, see Chapter 2) as breeders. Under the assumption that the recapture rates of individuals should differ before and after first breeding, a two further groups (groups 2 and 3) are constructed including the same individuals as in group 1, but based on only the portion of the recapture histories following the first confirmed breeding attempt. At this time individuals are recorded as captured but unreleased birds in group 1, subsequently appearing as apparently independent, newly marked breeders in groups 2 or 3. Group

2 includes the recapture histories of all birds first breeding as juveniles, including birds marked before maturity and recaptured breeding in their first year and birds first marked as juvenile breeders. In a time-dependent model, estimating the proportion of breeders in the first year after ringing is only possible if data on the recapture rate of individuals first marked as breeders are available from the beginning of the study. This is obtained from group 3. Group 3 includes all birds first seen breeding as adults including birds marked before maturity but 'missing' their first breeding year, together with individuals first marked as adult breeders. In this study, a small number of birds first captured as adults in autumn are thus excluded until confirmed as breeders, then appearing within group 3.

Since the spring recapture rate of groups 2 and 3 is assumed to represent the rate at full breeding, the age by which all individuals enter the breeding population will be given where individuals of a given age remaining in group 1 have an equal recapture probability to groups 2 and 3. Within SURGE, the age of full breeding can thus be tested by a comparison of models where the age with equal recapture rates at breeding for group 1, and groups 2 and 3 is varied. The model (age of full breeding) that best describes the data is selected through likelihood ratio testing as in conventional SURGE analyses. Age specific breeding probabilities are then estimated by dividing the recapture probabilities from group 1, by that for groups 2 and 3, to account for the possibility of some known breeders escaping capture.

In this study, with spring 'captures' based on resighting records of colour ringed individuals rather than physical recapture, it remains possible that non-breeding birds may have been observed during the breeding season. Thus, 'recapture' is only confirmed if an individual or its mate is known to have initiated laying, since in some cases, individuals could not be positively assigned to nests before this stage. Confirmed sightings of unmated birds were rare, however, and usually only made very early in the breeding season when some territory boundaries are still flexible. The exclusion of these sightings is made to allow the calculation of age specific breeding probabilities using the methods outlined above (Clobert *et al.* 1990), and to satisfy the assumption of 'negligible' time within a single census period. In this context, the assumption is met by limiting recapture to a period of population stability that is short in comparison to the time between census intervals.

#### 4.2.2.2. Estimation of breeding probabilities with two censuses in a single year.

Conventionally, group 1 (birds marked before first breeding) has included only locally raised young and, to date, analyses of this kind have been confined to annual studies of individuals marked in the nest and followed to maturity (for passerines, ringing prior to fledging provides the only opportunity to mark individuals before maturity in annual studies). However, local recruitment rates for passerines may frequently be less than 20% and with important post-natal dispersal in many cases (e.g. Bulmer and Perrins 1973; Foppen and Reijnen 1994; Greenwood *et al.* 1979; Lack 1966; Von Haartman 1971), the pool of potential first time breeders may often include an important proportion of immigrant birds. Estimates of age specific breeding probabilities derived from locally raised young, may then be biased, based on small samples and a minority of potential first time breeders. Dippers, however, can readily be captured and aged in autumn (Bryant and Newton 1996; Ormerod *et al.* 1988; Chapter 2), and with two censuses within a single year, an opportunity exists to mark immigrant birds prior to maturity. Here, the methods of Clobert *et al.* (1990) are extended to include both nestlings and autumn captured juveniles within group 1. Breeding probabilities can then be estimated based on all (marked) juveniles, irrespective of natal origin.

## 4.3. RESULTS

### 4.3.1. Basic models (Cormack-Jolly-Seber model)

The CJS model (time dependence on survival and recapture rates) was fitted independently to each sex as the basic model for all breeders (groups 2 and 3 combined) and goodness of fit tests computed within the program RELEASE (Burnham *et al.* 1987).

#### 4.3.1.1. Goodness of fit of the CJS to known breeders

Although a number of the components of both Test 2 and Test 3 could not be calculated due to insufficient data (Burnham *et al.* 1987), results from RELEASE indicated that the basic assumptions of the CJS model were met; the fate of individuals was not dependent on the previous history of the birds released on any occasion and that parameters were specific to sampling occasions (Table 4.1). While Test 1, revealed no evidence of differences in capture or survival probabilities between sexes ($\chi^2_{36}$=35.4955, p=0.492), given the low power of this test (Burnham *et al.* 1987; Lebreton *et al.* 1990), initial models fitted within SURGE retained both sex and group effects for breeders.

**Table 4.1.** Goodness of fit tests of the Cormack-Jolly-Seber model (time dependence on survival and recapture probabilities) to the recapture histories of male and female dippers known to have bred previously (Test 2 and Test 3 combined, Burnham *et al.* 1987). Significant test results, should they arise, indicate departures from the model assumptions and suggest that the CJS model provides an inadequate description of the data.

| | $\chi^2$ | df | p |
|---|---|---|---|
| Males | 27.8404 | 29 | 0.5265 |
| Females | 41.4285 | 40 | 0.4082 |
| All birds | 69.2689 | 69 | 0.4683 |

### 4.3.2. Modelling recapture rates for known breeders.

With little information on annual variation in adult survival, initial attempts towards parsimony for groups 2 and 3 focused on recapture estimates, starting from the basic CJS model.

Initial testing reduced the time dependence in recapture to a measure of census effort (Model 1 *vs* 2, Table 4.2, $\chi^2_{56}$=64.84, p=0.225); constant across all years except 1988, when only partial censuses were conducted in each season (See Chapter 1 for explanation of 'effort'). Seasonal effects were retained to account for the different census methods employed in spring and autumn (Chapter 2).

Likelihood ratio testing (LRT) gave no indication of sex differences in autumn recapture (Model 2 *vs* 3, Table 4.2, $\chi^2_4$=6.39, p=0.172), although with the possibility that females may have been more conspicuous at the nest early in breeding (incubating females could be captured easily), and some males may not have been identified at nests failing early, sex differences in spring recapture were retained initially. In practice, later tests revealed no significant sex differences in recapture in either season (Model 4 *vs* 5, Table 4.2, $\chi^2_2$=1.27, p=0.265). Two further models with recapture rates constant across years (Model 6, Table 4.2), then across seasons (Model 7, Table 4.2), were both rejected. The recapture probabilities of known breeders were dependent on season and census effort only, with no sex or group differences.

### 4.3.3. Modelling survival for known breeders.

Testing within SURGE, confirmed the results of RELEASE, providing no evidence of sex (Model 1 *vs* 2, Table 4.3, $\chi^2_{38}$=44.90, p=0.205) or group differences (Model 2 *vs* 3, Table 4.3, $\chi^2_{19}$=14.88, p=0.730) in the survival rates of breeders. A model with constant post-breeding and over-winter survival rates (Model 4, Table 4.3) also fitted the data as well as more complex time dependent alternatives (Models 1, 2 and 3, Table 4.3; Figure 4.1). Adult over-winter survival was significantly lower than the post-breeding rate over all years, however, with a model including seasonal effects providing a significantly better fit to the data than one with survival held constant throughout the year (Model 4 *vs* 5, Table 4.3, $\chi^2_1$=5.54, p=0.019)

### 4.3.4. Modelling survival and recapture rates for immature birds (Group 1)

Having refined the model for known breeders, birds marked prior to maturity were then included in the analysis. An initial model for group 1 (Model 1, Table 4.4) assumed sex and time effects within 2 age classes for first year birds: post-fledging and juvenile over-winter survival; autumn and first-year breeding recapture probabilities; with all individuals sharing similar rates to known breeders thereafter (as Model 4, Table 4.3, see methods). Since only first year recapture rates at breeding are estimated separately from those of known breeders, initial models assume full breeding at age two.

**Table 4.2.** Comparison of recapture probabilities between group 2 (birds first breeding as juveniles) and group 3 (birds first breeding as adults). All models are fitted with group, sex and time effects on adult survival.

| Model[a] | Recapture rates | | Sex effects | Group effects | np[a] | Dev[a] | AIC[a] | Test between Models[b] | |
|---|---|---|---|---|---|---|---|---|---|
| | Spring | Autumn | | | | | | | |
| (1) | Variable | Variable | Both seasons | Both seasons | 148 | 1145.52 | 1441.52 | (1)vs(2) $\chi^2_{56}$=64.84, p=0.225 | Fits the data |
| (2)[c] | Effort | Effort | Both seasons | Both seasons | 92 | 1210.36 | 1394.36 | (3)vs(2) $\chi^2_4$= 6.39, p=0.172 | Accepted |
| (3) | Effort | Effort | Spring only | Both seasons | 88 | 1216.75 | 1392.75 | (4)vs(3) $\chi^2_6$= 2.88, p=0.824 | Accepted |
| (4) | Effort | Effort | Spring only | None | 82 | 1219.63 | 1383.63 | (5)vs(4) $\chi^2_2$= 1.27, p=0.265[d] | Accepted |
| (5) | Effort | Effort | None | None | 80 | 1220.90 | 1380.90 | (6)vs(5) $\chi^2_2$= 4.98, p=0.042[d] | Accepted |
| (6) | Constant | Constant | None | None | 78 | 1225.88 | 1381.88 | | Rejected |
| (7) | Effort, with equality between seasons | | None | None | 78 | 1230.21 | 1386.21 | (7)vs(5) $\chi^2_2$= 9.31, p=0.009[d] | Rejected |

[a] np: number of identifiable parameters; Dev: relative deviance; AIC: Akaikes' Information Criterion.

[b] Tests between models consider the relative fit of each model to the data. A significant result indicates that the more complex model provides a better description of the data and that the additional complexity of this model must be retained.

[c] Time effects reduced to a measure of effort, constant within seasons across all years except 1988 (See text).

[d] One-tailed test.

**Table 4.3.** Comparison of survival probabilities between group 2 (birds first breeding as juveniles) and group 3 (birds first breeding as adults). All are models fitted assuming adult recapture rates dependent on season and census effort, without sex and group effects.

| Model | Survival rates | | Sex effects | Group effects | np[a] | Dev[a] | AIC[a] | Test between Models | |
|---|---|---|---|---|---|---|---|---|---|
| | Post-breeding | Over-winter | | | | | | | |
| (1) | Variable | Variable | Both seasons | Both seasons | 80 | 1220.90 | 1380.90 | | Accepted |
| | | | | | | | | (1)vs(2) $\chi^2_{38}$=44.90, p=0.205 | |
| (2) | Variable | Variable | None | Both seasons | 42 | 1265.80 | 1349.80 | | Accepted |
| | | | | | | | | (3)vs(2) $\chi^2_{19}$=14.88, p=0.730 | |
| (3) | Variable | Variable | None | None | 23 | 1280.68 | 1326.68 | | Accepted |
| | | | | | | | | (4)vs(3) $\chi^2_{17}$= 7.56, p=0.975 | |
| (4) | Constant | Constant | None | None | 6 | 1288.24 | 1300.24 | | Accepted |
| | | | | | | | | (5)vs(4) $\chi^2_{1}$= 5.54, p=0.019 | |
| (5) | Constant and equal between seasons | | None | None | 5 | 1293.78 | 1303.78 | | Rejected |

[a] np: number of identifiable parameters; Dev: relative deviance; AIC: Akaikes' Information Criterion.

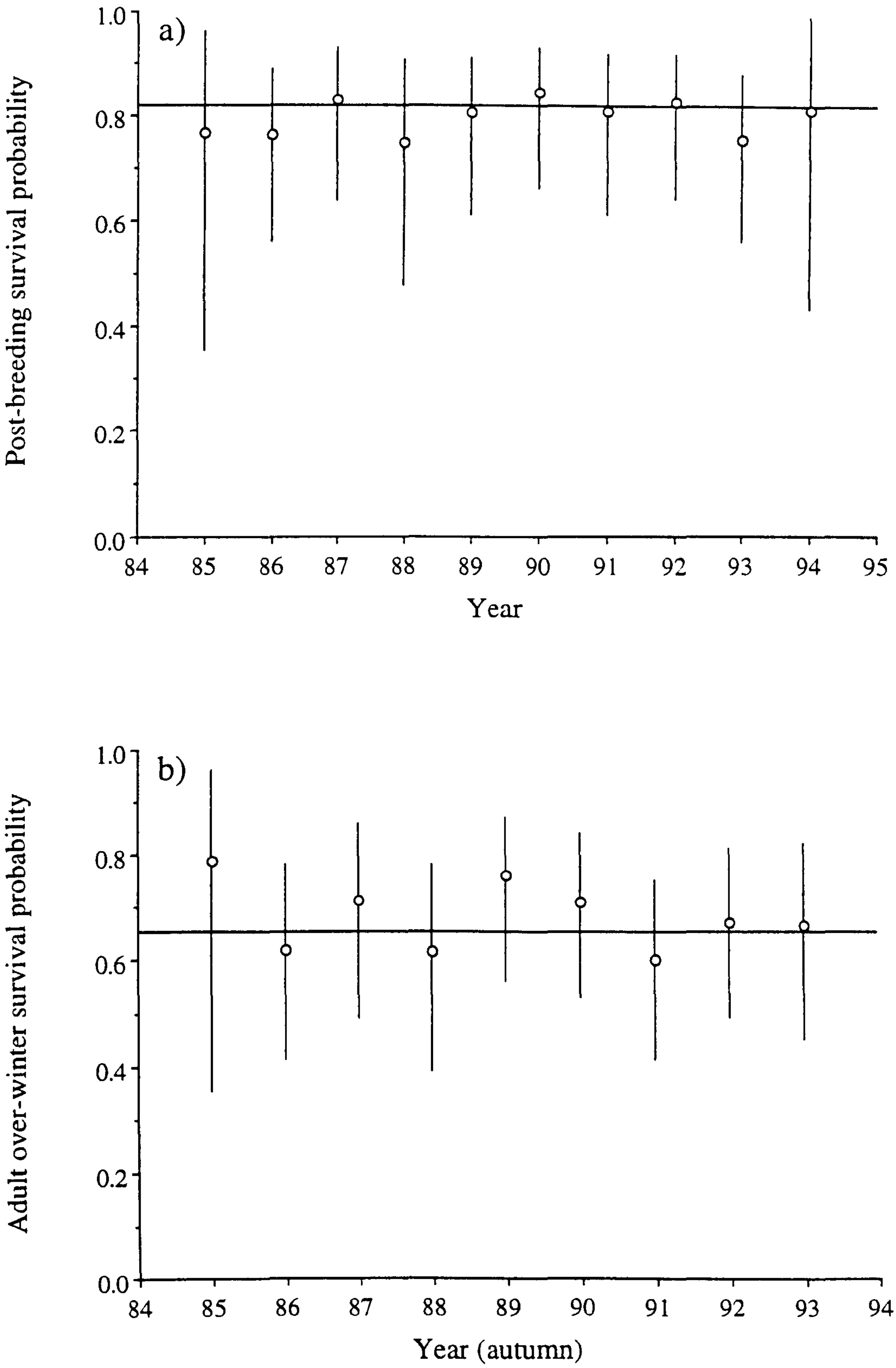


**Figure 4.1.** Estimates of post-breeding (a) and over-winter (b) survival for adult dippers within the Devon catchment between 1985-1994. Data points represent survival probabilities (±95% asymmetric confidence intervals) calculated with survival time dependent and recapture dependent on census effort only (Model 3, Table 4.3). The fitted lines represent survival probabilities derived from the final model (Model 5, Table 4.6).

This was considered an appropriate starting point for examining age specific breeding probabilities for dippers and passerines in general (Clobert *et al.* 1990).

### 4.3.4.1. Modelling recapture rates for immature birds (group 1)

Likelihood ratio testing revealed no evidence of sex differences in the autumn recapture probabilities of juveniles (Model 1 *vs* 2, Table 4.4, $\chi^2_8$=2.57, p=0.958) or effects between age classes (Model 2 *vs* 3, Table 4.4, $\chi^2_9$=12.29, p=0.197). Outwith breeding, all individuals appeared equally likely to be captured, irrespective of age and sex. Further testing indicated similar spring recapture rates, and hence breeding probabilities, for each sex in group 1 (Model 3 *vs* 4, Table 4.4, $\chi^2_9$=4.16, p=0.900). No attempt was made to examine group effects at this time, to allow age specific breeding probabilities to be addressed later in a more parsimonious way.

### 4.3.4.2. Modelling survival rates for immature birds (group 1)

Although not significant at $p \leq 0.05$, likelihood ratio testing suggested possible sex differences in the survival rates of group 1 birds (Model 4 *vs* 5 and 6, Table 4.5, $p \leq 0.105$) and sex effects were retained initially within the analysis. Whilst there was no evidence of between year differences in the local post-fledgling rate (Model 4 *vs* 7, Table 4.5, $\chi^2_{18}$=21.66, p=0.247), variation in over-winter survival appeared important. With *a priori* information on the probable importance of density-dependent processes in determining the population size at breeding (Newton 1989a), between year differences in juvenile over-winter survival appeared to be adequately explained by constraining survival to the lowland autumn population density with logistic regression equations fitted independently to each sex (Figure 4.2). In this model (Model 8, Table 4.5), survival probabilities for 1988 are estimated separately since, with only a partial census conducted at this time, population density could not be assessed in a comparable way to other years. No sex differences in juvenile over-winter survival were apparent, with a further model fitting this same density constraint to both sexes combined being selected (Model 8 *vs* 11, Table 4.5, $\chi^2_3$=2.50, p=0.475). Under the assumption of equal sex ratios at fledgling (see Chapter 7), sex differences in post-fledgling survival appeared significant, however, with a model retaining sex effects on post-fledging survival providing a significantly better fit to the data than one with equal rates for both males and females. The local post-fledging survival rate of males appeared significantly greater than for females (Model 11 *vs* 12, Table 4.5, $\chi^2_1$=9.77, p=0.0018).

### 4.3.4.3. Modelling age specific breeding probabilities

Initial likelihood ratio testing revealed significant variation between years in the recapture probabilities of first year birds. A model with a constant rate for juveniles (Model 2, Table 4.6) failed to describe the data as well as a fully time-dependent alternative (Model 1, Table 4.6). As expected given this result, a model representing full breeding at age 1, where all individuals shared the (constant) recapture rate of known breeders, was firmly rejected (Model 1 *vs* Model 3, $\chi^2_{11}$=24.17, p<0.0001 Table 4.6). A further model with age and time dependence on spring recapture until age 3 (Model 4, Table 4.6) also failed to describe the data significantly better than the initial model. It appeared that the spring recapture rates of first year dippers was significantly lower than for known breeders, although all birds shared similar recapture probabilities by their second year. Full breeding appeared to be achieved at age 2 for both sexes, with no sex differences in the breeding probabilities of first year birds.

### 4.3.4.4. Annual variation in first-year breeding probabilities

With previous studies highlighting the importance of river flows in determining both breeding success (Newton 1989a; Price and Bock 1983) and breeding probabilities (Clobert *et al.* 1990; Marzolin in prep.), a final model, selected with the lowest AIC of all those models fitted, constrained the spring recapture rates of juveniles to a logistic regression on peak river flow in March (Model 5, Table 4.6). The proportion of first year birds *recorded* making a breeding attempt appeared to be determined by the river flow conditions during the initiation of breeding (nest-building/laying), with fewer juveniles breeding in years with spring floods (Figure 4.4). A model with the spring recapture rate of known breeders constrained to a similar March flow effects within SURGE (see Figure 4.3) failed to describe the data better than the constant rate selected previously (Model 2, Table 4.2) suggesting that this flow effect was acting primarily on first year birds.

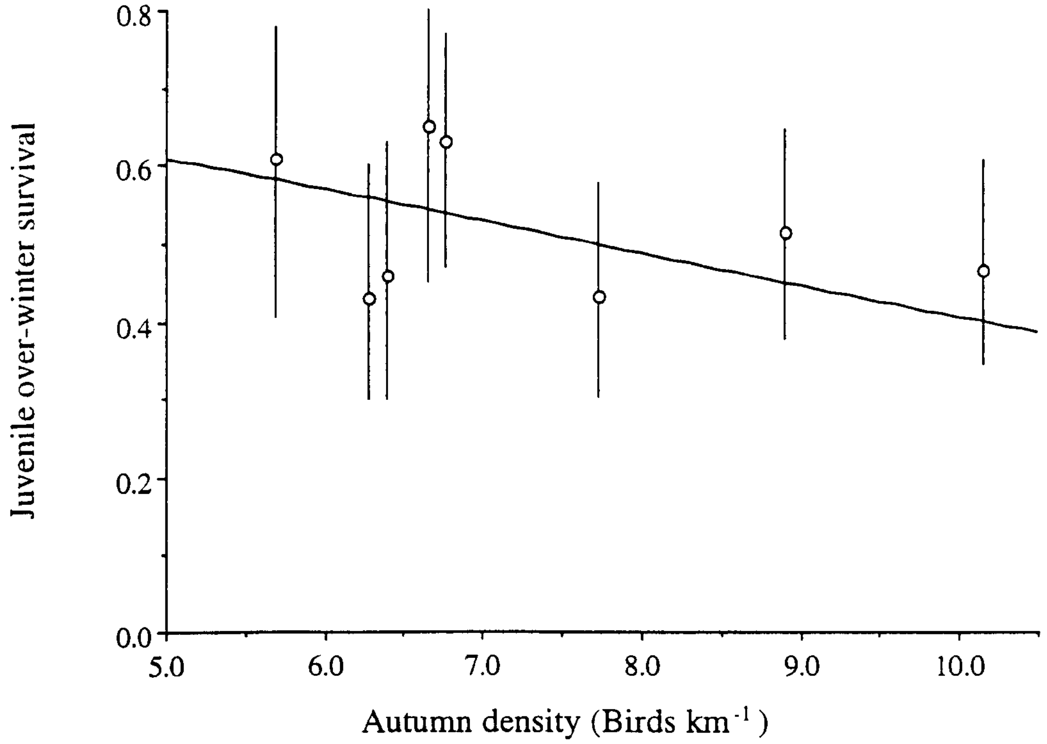


**Figure 4.2.** Estimates of local juvenile over-winter survival for dippers within the Devon catchment between 1985-1994. Data points represent survival probabilities (±95% asymmetric confidence intervals) estimated as in the final model (Model 5, Table 4.6) but with fully time dependent juvenile over-winter survival, estimated without density constraints. The fitted line represent survival probabilities derived from the final model (Model 5, Table 4.6) with juvenile survival dependent on Lowland autumn population density (birds 10km$^{-1}$), (logit (Φ)= 1.2561 - 0.1635*Lowland autumn population density*).

**Table 4.4.** Modelling recapture rates for group 1 (marked before maturity, until first recapture as breeder). All models are fitted assuming adult survival constant within seasons (no sex or group effects) and recapture rates dependent on season and census effort only (Model 4, Table 4.3). Initial models for group 1 assume age effects within 4 survival classes: post-fledging; juvenile over-winter; adult post-breeding; adult over-winter. Survival of adults within group 1 is assumed equal to known breeders (see methods). Initial models for recapture assume age, sex and time effects for first year birds, with individuals sharing similar rates to known breeders thereafter (full breeding at age=2).

| Model | Autumn | Spring | Sex Effects | np[a] | Dev[a] | AIC[a] | Test between models | |
|---|---|---|---|---|---|---|---|---|
| (1) | Variable | Variable | Both seasons | 79 | 2849.04 | 3007.04 | | Accepted |
| | | | | | | | (1)vs(2) $\chi^2_8=2.57$, p=0.958 | |
| (2) | Variable | Variable | Spring only | 71 | 2851.61 | 2993.61 | | Accepted |
| | | | | | | | (3)vs(2) $\chi^2_9=12.29$, p=0.197 | |
| (3) | Effort (as breeders) | Variable | Spring only | 62 | 2863.90 | 2987.90 | | Accepted |
| | | | | | | | (4)vs(3) $\chi^2_9= 4.16$, p=0.900 | |
| (4) | Effort (as breeders) | Variable | None | 53 | 2868.06 | 2974.06 | | |

[a] np: number of identifiable parameters; Dev: relative deviance; AIC: Akaikes' Information Criterion.

**Table 4.5.** Modelling survival for group 1 (marked prior to maturity, until first recapture as breeder). All models are fitted assuming constant post-breeding and over-winter adult survival (no sex or group effects) and recapture rates dependent on season and census effort. Autumn recapture rates are independent of age and sex (Model 4, Table 4.4). All models retain time and age effects on spring recapture for first year birds with individuals sharing similar rates to known breeders thereafter (full breeding at age=2).

| Model | Post-fledging | Juvenile over-winter | Sex Effects | np[a] | Dev[a] | AIC[a] | Test between models | |
|---|---|---|---|---|---|---|---|---|
| (4) | Variable | Variable | Both seasons | 53 | 2868.06 | 2974.06 | <br>(4)vs(5) $\chi^2_{18}$=25.76, p=0.105 | Accepted |
| (5) | Variable | Variable | Both seasons with parallelism between sexes | 35 | 2893.82 | 2963.82 | (5)vs(6) $\chi^2_{1}$= 2.05, p=0.152 | Rejected (initially) |
| (6) | Variable | Variable | None | 34 | 2895.87 | 2963.87 | (4)vs(6) $\chi^2_{19}$=27.81, p=0.087 | Rejected (initially) |
| (7) | Constant | Variable | Both seasons | 35 | 2889.72 | 2959.72 | (4)vs(7) $\chi^2_{18}$=21.66, p=0.247 | Accepted |
| (8) | Constant | Population density on each sex independently | Both seasons | 23 | 2900.54 | 2946.54 | (7)vs(8) $\chi^2_{12}$=10.82, p=0.544 | Accepted |
| (9) | Constant | Population density of same sex | Both seasons | 23 | 2899.41 | 2945.41 | (7)vs(9) $\chi^2_{12}$=9.69, p=0.6431 | Accepted |
| (10) | Constant | Constant | Both seasons | 19 | 2911.49 | 2949.49 | (8)vs(10) $\chi^2_{4}$=10.95, p=0.027 | Rejected |
| (11) | Constant | Population density | Spring only | 20 | 2903.04 | 2943.04 | (8)vs(11) $\chi^2_{3}$= 2.50, p=0.475 | Accepted |
| (12) | Constant | Population density | None | 19 | 2912.81 | 2950.81 | (11)vs(12) $\chi^2_{1}$=9.77, p=0.0018 | Rejected |

[a] np: number of identifiable parameters; Dev: relative deviance; AIC: Akaikes' Information Criterion.

**Table 4.6.** Modelling first year recapture probabilities and age specific proportions of breeders. All models fitted assuming constant post-fledging survival rates within each sex, with juvenile over-winter survival dependent on lowland autumn population density and constant post-breeding and over-winter adult survival. Autumn recapture rates for all individuals, and spring recapture rates of known breeders (groups 2 and 3) are dependent on census effort only (Model 11, Table 4.5).

| Model | Age of Full breeding | Spring recapture rates | np[a] | Dev[a] | AIC[a] | Test between models | |
|---|---|---|---|---|---|---|---|
| (1) | 2 | Variable | 20 | 2903.04 | 2943.04 | | Accepted |
| (2) | 2 | Constant | 12 | 2927.21 | 2951.21 | (1)vs(2) $\chi^2_8=24.17$, $p<0.0001$ | Rejected |
| (3) | 1 | As breeders (constant) | 9 | 2971.92 | 2989.92 | (1)vs(3) $\chi^2_{11}=68.88$, $p<0.0001$ | Rejected |
| (4) | 3 | Variable | 28 | 2896.11 | 2952.11 | (1)vs(4) $\chi^2_8=6.93$, $p=0.2721$[b] | Rejected |
| (5) | 2 | Peak spring flow | 14 | 2910.69 | 2938.69 | (1)vs(5) $\chi^2_6=7.65$, $p=0.2647$ | **Final Model** |

[a] np: number of identifiable parameters; Dev: relative deviance; AIC: Akaikes' Information Criterion.

[b] One-tailed test.

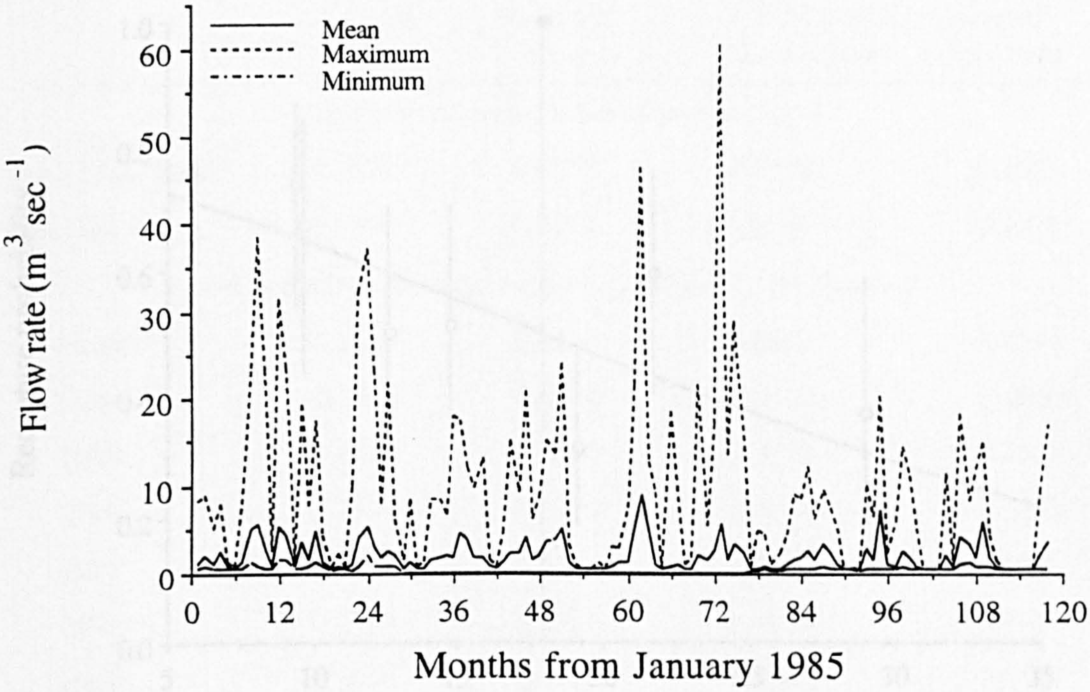


**Figure 4.3.** Patterns of river discharge on the River Devon (metered at Castlehill reservoir) between 1985 and 1994.

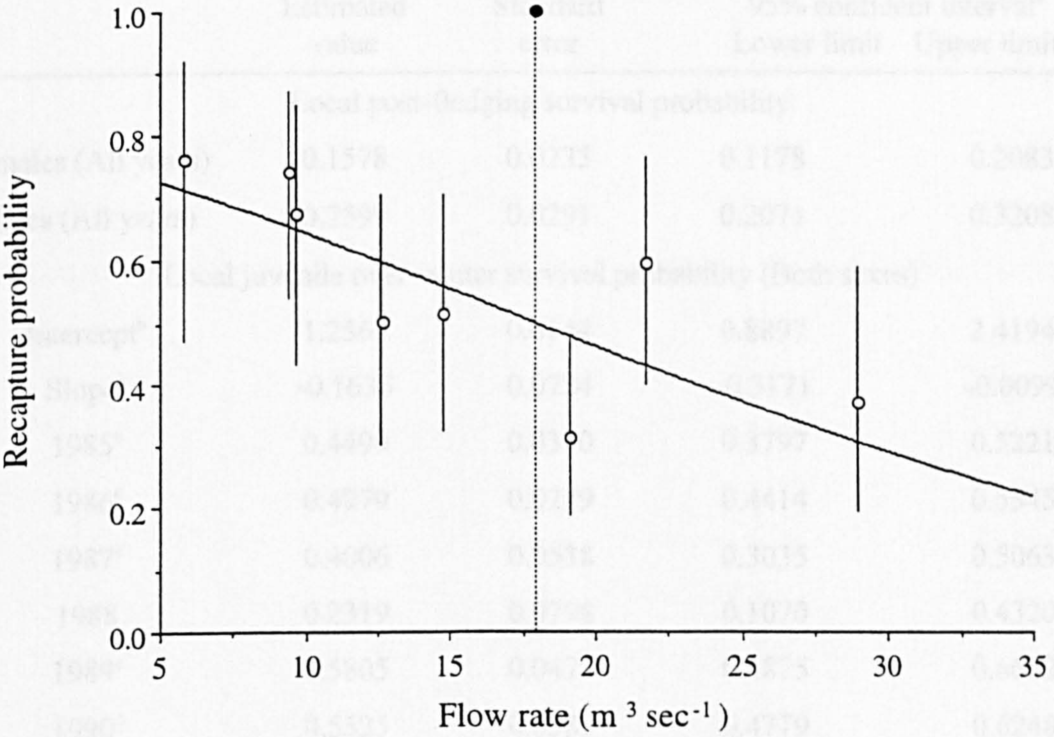


**Figure 4.4.** Estimates of juvenile recapture probabilities for dippers within the Devon catchment between 1985-1994. Data points represent recapture probabilities (±95% asymmetric confidence intervals) fitted as in the final model (Model 5, Table 4.6) but with fully time dependent juvenile recapture rates, estimated without flow constraints. The fitted line represent recapture probabilities derived from the final model (Model 5, Table 4.6) with juvenile spring recapture rates dependent on peak river flow in March ($m^3sec^{-1}$), (logit (p)= 1.3328 - 0.0744*Peak river flow*). The shaded point (1989) is not included within the calculation of the fitted line because too few juveniles were marked in 1988 and later recaptured to allow first-year breeding probabilities to be estimated for this cohort (see text).

**Table 4.7.** Survival probabilities from the final model (Model 5, Table 4.6). The model is fitted with constant post-fledging survival rates within each sex, juvenile over-winter survival dependent on lowland autumn population density and constant post-breeding and over-winter adult survival. Autumn recapture rates for all individuals, and spring recapture rates of known breeders (groups 2 and 3) are dependent on census effort only. The spring recapture rates of first year birds are dependent on the peak river flow ($m^3sec^{-1}$) during March (Table 4.6).

| | Estimated value | Standard error | 95% confident interval[a] Lower limit | Upper limit |
|---|---|---|---|---|
| | Local post-fledging survival probability | | | |
| Females (All years) | 0.1578 | 0.0235 | 0.1178 | 0.2083 |
| Males (All years) | 0.2599 | 0.0291 | 0.2071 | 0.3208 |
| | Local juvenile over-winter survival probability (Both sexes) | | | |
| Intercept[b] | 1.2561 | 0.6144 | 0.8897 | 2.4194 |
| Slope[b] | -0.1635 | 0.0784 | -0.3171 | -0.0099 |
| 1985[c] | 0.4499 | 0.0370 | 0.3797 | 0.5221 |
| 1986[c] | 0.4979 | 0.0289 | 0.4414 | 0.5545 |
| 1987[c] | 0.4006 | 0.0538 | 0.3035 | 0.5063 |
| 1988 | 0.2319 | 0.0798 | 0.1070 | 0.4320 |
| 1989[c] | 0.5805 | 0.0475 | 0.4875 | 0.6682 |
| 1990[c] | 0.5525 | 0.0382 | 0.4779 | 0.6248 |
| 1991[c] | 0.5373 | 0.0339 | 0.4709 | 0.6025 |
| 1992[c] | 0.5569 | 0.0395 | 0.4797 | 0.6314 |
| 1993[c] | 0.5417 | 0.0351 | 0.4731 | 0.6087 |
| | Post-breeding survival probability of breeders (Both sexes) | | | |
| All years | 0.8157 | 0.0296 | 0.7488 | 0.8679 |
| | Over-winter survival probability of breeders (Both sexes) | | | |
| All years | 0.6522 | 0.0296 | 0.5905 | 0.7091 |

[a] Asymmetric confidence intervals, back transformed from a logit scale

[b] Derived from logistic linear regression on autumn lowland population density (fitted within SURGE 4.2)

[c] Derived from logit ($\Phi$)= 1.2561 - 0.1635*Lowland autumn population density.*

**Table 4.8.** Recapture probabilities from the final model (Model 5, Table 4.6). The model is fitted with constant post-fledging survival rates within each sex, juvenile over-winter survival dependent on lowland autumn population density and constant post-breeding and over-winter adult survival. Autumn recapture rates for all individuals, and spring recapture rates of known breeders (groups 2 and 3) are dependent on census effort only. The spring recapture rates of first year birds are dependent on the peak river flow ($m^3sec^{-1}$) during March (Table 4.6).

| | Estimated value | Standard error | 95% confident interval[a] Lower limit | Upper limit |
|---|---|---|---|---|
| Autumn capture probabilities (All birds) | | | | |
| "High" effort years[b] | 0.7306 | 0.0262 | 0.6766 | 0.7785 |
| "Low" effort years[b] | 0.4246 | 0.0711 | 0.2955 | 0.5649 |
| Spring recapture probabilities of individuals not yet observed as breeders (Both sexes) | | | | |
| Intercept[c] | 1.3328 | 0.3939 | 0.5288 | 2.1368 |
| Slope[c] | -0.0744 | 0.2269 | -0.1204 | -0.2847 |
| 1986[d] | 0.4772 | 0.0436 | 0.3932 | 0.5625 |
| 1987[d] | 0.4286 | 0.0508 | 0.3330 | 0.5299 |
| 1988[d] | 0.6486 | 0.0484 | 0.5454 | 0.7396 |
| 1989 | 1.0000 | 0.0000 | 0.0000 | 1.0000 |
| 1990[d] | 0.5963 | 0.0421 | 0.5097 | 0.6772 |
| 1991[d] | 0.3043 | 0.0714 | 0.1827 | 0.4611 |
| 1992[d] | 0.6529 | 0.0490 | 0.5481 | 0.7448 |
| 1993[d] | 0.7104 | 0.0571 | 0.5820 | 0.8121 |
| 1994[d] | 0.5581 | 0.03962 | 0.4785 | 0.6347 |
| Spring recapture probabilities of known breeders (Both sexes) | | | | |
| "High" effort years[b] | 0.8005 | 0.0319 | 0.7324 | 0.8548 |
| "Low" effort years[b] | 0.8030 | 0.0711 | 0.5998 | 0.9173 |

[a] Asymmetric confidence intervals, back transformed from a logit scale

[b] High effort includes all years except 1988, low effort indicates 1988

[c] Derived from logistic linear regression on autumn population size (fitted within SURGE 4.2)

[d] Derived from logit (p)= 1.3328 - 0.0744*Peak river flow* (*$m^3sec^{-1}$*) *during March.*

## 4.4. Discussion

### 4.4.1. Assessing survival for dippers

The linear nature of the stream habitat and restricted territory requirements of dippers allow populations to be readily and reliably censused through much of the year (Bryant and Newton 1996; Logie *et al.* 1996; Newton 1989a; Ormerod *et al.* 1985, 1988). Dippers are generally sedentary, conspicuous in their habits and show strong fidelity to both nest and roost sites (Hewson 1967; Galbraith and Tyler 1982; Ormerod and Tyler 1990a). The mean distance moved between breeding years within the Devon catchment, for example, was 281±404m (maximum 4760m) and 306±675m (maximum 8260m) for males and females respectively, whilst Tyler *et al.* (1990) found that less than 3.6% of dippers moved more than 2500m between breeding attempts in upland Wales. Although mortality and permanent emigration can rarely be separated, it seems that losses from the adult population are likely to represent true mortality rather than movements outwith the core census area, and, at least for adults, local and true survival rates should be matched closely (see Chapter 1).

A number of autumn-captured birds were known to undertake altitudinal movements to breed in upland sites. However, testing within RELEASE (Burnham *et al.* 1987) gave no indication of heterogeneity within the data sets (Table 4.1), and it appears unlikely that such seasonal movements had an important influence on parameter estimates. True dispersal will be of greater importance for first-year birds, however, possibly carrying some individuals outwith the study area. Indeed, the influx of unringed juveniles into the summer populations suggests that cross-watershed movements during post-natal dispersal may not be infrequent. As such, post-fledging and juvenile over-winter survival estimates should be considered to represent local, and hence minimum, probabilities in all years.

#### 4.4.1.1. Annual adult survival

Approximately 81% of all adult birds survived from spring to the following autumn, with 65% of the autumn population then surviving over-winter (Table 4.7). These figures lead to annual adult survival probabilities of 53.2%, consistent with estimates for dippers in Britain and elsewhere (Clobert *et al.* 1990; Hewson 1969; Galbraith and Tyler 1982; Price and Bock 1983 for *Cinclus mexicanus*). Hewson (1969) estimated mean minimum ages for roosting dippers in Banffshire of 32.1 and 35.1 months for a sample of 12 males and 10 females respectively, equivalent to annual survival rates of 55% and 59%. Galbraith and Tyler (1982) calculated average adult survival at 54%, based on BTO records of ringing recoveries and controls.

Although it is possible that subtle differences remain undetected within these analyses, likelihood ratio testing provided no evidence of variation in adult survival between years (Model 3 *vs* 4, Table 4.3, $\chi^2_{17}$=7.56, p=0.975; Figure 4.1). Rather, the analysis suggests a strong consistency, reflecting the findings of national UK population monitoring programmes (Dobinson and Richards 1964; Marchant *et al.* 1990).

#### 4.4.1.2. Flow influences on adult survival

The importance of river flow in determining the survival of both adult and juvenile dippers has been highlighted in a number of previous studies (Clobert *et al.* 1990; Marzolin in prep.; Price and Bock 1983; Wilson 1996). Clobert *et al.* (1990) and Marzolin (in prep.) have shown consistent rates in 'normal' years for a population in north-eastern France, but with survival and breeding probabilities depressed under unusually high or low flows. A similar reduction in both adult and juvenile post-fledging survival during extreme flows have also been suggested for dippers in upland Wales (George 1993; Tyler and Ormerod 1994) and Scotland (Wilson 1996). However, direct comparisons between independent studies remain difficult, particularly because factors known to influence dipper populations, such as topography and water quality, may vary even between adjacent catchments (Logie *et al.* 1996; Ormerod *et al.* 1985; Vickery 1991). The flow regimes influencing mortality for dippers thus remain difficult to quantify; a problem often compounded by subjective flow classifications such as 'flood' and 'drought' made relative only to the local hydrological conditions. Indeed, some studied populations are clearly more likely than those in the UK to experience particular environmental extremes, such as floods, droughts or the freezing of river habitats (cf. Anderson and Wester 1972; Price and Bock 1983; Sarà *et al.* 1994).

If, as seems to be the case, river flow is the principal influence on adult mortality rates (Clobert *et al.* 1990; George 1993; Marzolin in prep.; Price and Bock 1983; Tyler and Ormerod 1994; Wilson 1996), the absence of annual variations in survival may reflect stable or benign conditions, either generally within the catchment or simply during the course of this study. Without reference to climatic variation, the artificial regulation of flow on the River Devon would be an obvious source of consistency. The upper and mid Devon holds five major reservoirs, three on the main river and two on principal tributary streams (Figure 2.1.b), where the retention of water during floods and compensatory discharges in summer dampen natural flow fluctuations (SEPA unpubl.). Although no significant flow effects were demonstrated in this analysis, the importance of occasional extreme events cannot be discounted, either under natural conditions within the Devon catchment or locally on other unregulated rivers.

### 4.4.1.3 Environmental influences on adult survival

No attempt has been made to relate adult survival to external or climatic variables other than river flow, since likelihood ratio testing gave no indication of differences in mortality between years (Model 3 *vs* 4, Table 4.3, $\chi^2_{17}$=7.56, p=0.975), and formal analyses would not then have been of value. The importance of environmental influences on survival other than river discharge, however, remain to be confirmed. Low temperatures and severe winter weather are known to cause increased mortality in many other passerine species (Arcese and Smith 1991; Ekman 1984; Nilsson 1987; Perrins 1966; Tinbergen *et al.* 1985), although similar effects have not been shown for dippers (Dobinson and Richards 1964; Marchant *et al.* 1990).

Dippers are tolerant of a wide range of ambient temperatures (Murrish 1970), with their dense plumage helping to insulate them in winter streams and at high altitudes, although the increased number of birds seeking the thermal advantages of 'prime' roosts on the coldest nights illustrates the importance of temperature in the maintenance of a positive energy balance (Ormerod and Tyler 1990; Shaw 1979). Dementiev and Gladkov (1954, cited in Tyler and Ormerod 1994) found dippers over-wintering at -40°C, for example, where ice free waters remained, and Marzolin (in prep.) has even suggested enhanced survival for some birds in 'cold' years. Possibly, periods of frost are associated with low rainfall and reduced river discharges maintaining, or even enhancing, access to riffle sites.

In many species, environmentally determined variations in food availability and accessibility may also be important components influencing over-winter survival (e.g. Arcese *et al.* 1991; Ekman 1984; Haftorn 1992; Nilsson 1987; Tinbergen *et al.* 1985). In many small raptors for example, marked declines in numbers associated with heavy mortality occur in years of prolonged snow cover when rodents remain hidden for long period (Newton 1991; Village 1990). Many estuarine species may suffer high mortality in severe winters related to low prey availability when mudflats freeze (e.g. Dobinson and Richards 1964; Evans and Pienkowski 1982), and most probably, dippers suffer from reduced access to foraging sites or reductions in foraging efficiency where streams freeze, rather than from temperature stresses alone (c.f. Da Prato 1981). Generally, the fast flowing riffles within the Devon catchment do not freeze, although dippers breeding on hill burns often move towards the main river prior to the worst of the winter weather (Bryant *et al.*, unpubl.; Newton 1989a). Since late autumn is known to be a period of escalating territoriality of the lowland river, it seems likely that this reflects a deterioration in local conditions on upland streams, possibly in terms of changing temperature or flow regimes (Bryant and Tatner 1988).

### 4.4.2. Seasonal differences in adult survival

Lack (1966) suggested that over-winter mortality primarily determined population size in passerines, and it is widely reported that mortality over this period accounts for the greatest numbers of adult losses in many species (e.g. Dhondt *et al.* 1990; Krebs 1970; Lack 1966; Tinbergen *et al.* 1985). Yet, previous field studies of European dippers (and many other passerines), have considered only annual censuses and have been unable to partition mortality between seasons (Dobson 1987; Galbraith and Tyler 1981). While Price and Bock (1983) suggested that the majority of losses from their population of *Cinclus mexicanus* occurred during winter, only one previous British study has attempted to describe mortality patterns throughout the year. Galbraith and Tyler (1982), in an analysis of BTO ringing recoveries suggested that early and mid summer losses accounted for the greatest mortality of both adults and recently fledged young.

Undoubtedly, body condition and an individual's ability to cope with energetic stresses, as well as the energetic demands placed on a bird, and the availability of prey, will vary throughout the annual cycle (Bryant and Tatner 1988, Galbraith and Broadly 1980; O'Halloran *et al.* 1993; Ormerod *et al.* 1986b). Indeed, there is considerable empirical evidence that most songbirds adopt 'winter fattening' strategies, and that, within this, variance in food availability is critical (Haftorn 1989; Gosler 1996; Gosler *et al.* 1995; Lehikoinen 1986, 1987; Rogers 1987; Rogers and Smith 1993). In support of the level of high post-breeding losses in their study, Galbraith and Tyler (1982), suggested that dippers may be susceptible to flow extremes during the post-breeding stage when body masses are at a minimum. Equally, throughout breeding, territory maintenance may leave breeders unable to seek foraging refuges outwith the territory boundaries due to strict territory defence by neighbours, and for many passerines, female mortality is greatest during egg-laying and incubation through increased physiological stress and susceptibility to predation (Dobson 1987). Territory acquisition and defence may place considerable demands on breeding males (e.g. McCleery *et al.* 1996). Yet, while it seems certain that these reproductive investments are energetically costly for breeders, in contrast to Galbraith and Tyler's (1982) findings, the results of this study suggest that a greater number of adults, as well as a greater proportion of the adult population, died over-winter than during early and mid summer.

Breeding is known to pose the greatest energetic demands of the annual cycle (Bryant and Tatner 1988), but increasing day-lengths and low summer discharges generally provide extended access to foraging sites to satisfy daily energy demands. In contrast, the rate of gain required to achieve energy balance is at a maximum during the winter months, at almost twice the peak level during breeding (Bryant and Tatner 1988). This reflects a combination of increased thermoregulatory and foraging costs and the short active-days. Winter daily energy expenditure is generally governed by the nature and duration of energy-costly activities (Bryant *et al.* 1985) with these patterns determined by the prevailing river flows (Tyler and Ormerod 1994). Spates with high turbulence, turbidity or reduced access to river sites will all act to reduce food availability and increase foraging costs, pushing birds closer to energetic imbalance.

Whether or not winter losses also include a proportion of birds suffering from a persistent reduction in 'condition' resulting from previous breeding stresses remains unknown. Dobson (1989) has shown an increase in female, although not male mortality in autumn for a number of passerine species, suggesting that breeding stresses may not become apparent until conditions deteriorate later in the year. Indeed, evidence linking reproductive effort to senescence and reduced future survival demonstrates that breeding costs can affect survival, either later in life (Bryant 1991; McCleery *et al.* 1996; Nilsson 1994) or under unfavourable conditions (Dhondt *et al.* 1990; Tinbergen *et al.* 1985). For males, over-winter losses may also reflect territorial investments made prior to the breeding season (e.g. McCleery *et al.* 1996).

The patterns of mortality identified appear at odds with those suggested from ringing recoveries (Galbraith and Tyler 1982). However, of more than 10000 dippers ringed by 1974 only 1.4% had been recovered (Galbraith and Tyler 1982). Given the nature of habitat occupied by dippers, it seems probable that recoveries are most likely at or near the nest, aided by the increased recreational use of riparian sites during the summer months. Possibly, 'census effort' and the chances of losses being reported are biased towards this time.

### 4.4.3. First year survival

#### 4.4.3.1. Juvenile over-winter survival

Entry to autumn populations is known to be a competitive process in many species, with the proportion of juvenile recruiting being shown to depend on the number of young fledged or the number of potential spaces created through adult mortality (Dhondt 1979; Ekman 1984; Kluyver 1971; Nilsson 1987; Southern 1970; Tinbergen *et al.* 1985; Van Balen 1980) Tinbergen *et al.* (1985) have shown that in an island population of great tits (where movements to and from the population were negligible) entry to the autumn population was dependent on the numbers of young fledged, whilst Ekman (1984) found the survival of juvenile willow tits *Parus montanus* to be negatively related to density. Drent (1984), for example, showed that when territorial great tits were removed in autumn and winter, previously subordinate juveniles rapidly established territories in the same area.

Investigating the recruitment dynamics of dippers on the River Devon, Newton (1989a) suggested that autumn juvenile losses probably involved density dependent processes, with dominance-related territorial intolerance leading to the exclusion of subordinates to fringe sites. With this *a priori* information, a logistic relationship with juvenile survival dependent on autumn population density (birds 10km$^{-1}$) appeared to explain the variation in juvenile over-winter survival (Model 11, Table 4.5). The survival of juveniles, although not adults, was negatively related to population density across all years. Murdoch (1970) suggests that experimental manipulations of population size can provide a test of density dependence, with regulatory processes being implicated if populations return to the pre-experimental levels. Newton's (1989a) introductions of juveniles into the autumn populations in 1985, 1986 and 1987 to examine the importance of the timing of arrival on recruitment, provide further incidental support for density-dependence in over-winter survival.

No sex differences in juvenile over-winter survival were apparent, in spite of young females being generally subordinate to all other age/sex classes (Bryant and Newton 1994, 1996). Competition for winter resources such as roost or foraging sites is known to occur between all members of the population rather than within age or sex classes alone (Cramp 1988; Bryant and Newton 1996; Shaw 1979). Yet, intra-sexual conflict may ultimately determine which individuals survive to gain breeding territories through a combination of dominance, social interactions and body condition (Bryant and Newton 1996; Newton 1989a, 1993). Smith (1994), for example, has shown the winter survival of black-capped chickadees *Parus atricapillus* to be independent of sex but strongly affected by within-sex rank and it seem likely that similar mechanisms operate within dipper populations (Bryant and Newton 1996). In line with this, SURGE models with juvenile survival dependent on the density of the same sex only, (Model 8, Table 4.5) appeared to describe the data better than models fitting total density (all birds) independently to each sex (Model 9, Table 4.5, with lower AIC). Although survival rates were shown not to differ between the sexes

(Table 4.5), it remains impossible to determine if this simply reflects near-equal sex ratios in all autumn populations, or if independent density constraints based only on the abundance of the same sex might be more appropriate if autumn sex ratios differed.

The inclusion of flow effects in the logistic regression failed to describe juvenile survival rates better than a model based on population density alone. Territorial activity increases noticeably in the October and November, following the completion of moult and the resurgence of song (Bryant and Tatner 1988), with this period in late autumn appearing to account for the majority of over-winter losses of first year birds (Newton 1989a). Environmental influences on juvenile over-winter survival have been shown to be a major causes of pre-breeding mortality in some passerine species (Arcese *et al.* 1992; McCallum 1990; Nilsson 1987; Tinbergen *et al.* 1985), and although such effects could be obscured by density dependent processes in this study, at least for first year birds, peak over-winter mortality did not appear to coincide with the worst of the winter weather (Newton 1989a).

#### 4.4.3.2. Age effects on over-winter survival

Many studies have highlighted the importance of dominance and competition on dispersal and juvenile over-winter survival (Davies and Houston 1981; De Laet 1985; Dhondt 1979; Ekman 1984; Newton 1989a), and, across all years, the over-winter local survival probabilities of first year dippers, were consistently lower than for adults (Table 4.8). Juvenile dippers are known to be subordinate to adult birds (Bryant and Newton 1994, 1996; Newton 1989a), and juvenile survival often depends on the creation of 'gaps' through the mortality of dominant territorial adults (e.g. Nilsson 1987; Southern 1970; Van Balen 1980), and/or dominance related access for food and other resources (Ekman 1984; Ficken *et al.* 1990; Hake 1996). However, it also seems likely that inefficient foraging, and an incomplete knowledge of the distribution of prey species may limit the ability of juvenile birds to detect or gather prey to meet daily energetic demands, even in the absence of competitive effects, and particularly under unfavourable conditions (Greig-Smith 1985; Sullivan 1989; Yoerg 1994). Recently fledged dippers are known to take more time to handle food items and to be more likely to drop prey before handling is complete (Yoerg 1994). Whether or not this inexperience persists until winter in unknown, although Desrochers (1992) has suggested that, even a year after fledging, a poorer foraging efficiency may account for the lower reproductive success of juveniles in blackbirds, and possibly other passerine species. Wilson (1996) noted that a disproportionate number of first-year dippers were lost during severe winter floods.

#### 4.4.3.3. Post-fledging survival

Post-fledging survival probabilities (see Chapter 2) were significantly lower in all years amongst females (15.8%) compared to males (26.0%) under the assumption of equal sex ratios at fledging (see Chapter 7). Yet, with no sex differences in adult survival rates, a consistent sex difference in juvenile survival would ultimately lead to an excess of males in the adult population. Although in all years, females accounted for the majority of immigrant juveniles, comprising an mean of 58% of all the unringed juveniles captured between 1985 and 1997, it appears unlikely that adjacent catchments would be consistently producing surplus females to compensate for the excess males suggested here. More likely, while local post-fledging survival rates may differ between the sexes, true survival rates may not.

For practical reasons, it remains impossible to partition losses between true mortality and permanent emigration. This problem is likely to be most important post-independence, when juveniles undertake dispersal movements (Newton 1989a; Tyler *et al.* 1990). Females are known to have longer dispersal distances within the Devon catchment (Newton 1989a) and to be more likely to cross watersheds than males (Tyler *et al.* 1990). Indeed, juvenile males rarely move more than 10km from their natal site with the majority (over 70%) remaining within 6km of the nest (Newton 1989a, Tyler *et al.* 1990). Survival differences may reflect greater female mortality or, more probably, a greater tendency for females to move outwith the study area.

#### 4.4.3.4. Annual variation in post-fledging survival

No significant differences were identified between years in the survival probabilities of juvenile dippers from fledging to their first autumn (Table 4.5). In part, this may reflect the low return rates within this period, and with relatively few fledglings resighted, it remains difficult to identify subtle differences between years. However, territorial activities are known to start in late summer (Bryant and Tatner 1988), and is seems likely that, to some extent, dipper numbers are matched to resources even before the late autumn census (Logie 1995, Logie *et al.* 1996; Ormerod *et al.* 1988). Ormerod and Tyler (1994), for example, have also shown that, on average, juvenile males dispersed 30% further in years of high population density. Differences between years in survival in the weeks immediately post-fledging may be subsumed by competitive effects in the following months. Indeed, the limited variation in autumn numbers within the Devon catchment is consistent with some density/resource dependence on establishing a place in the autumn population. The importance of individual variation in body-size and/or condition and the timing of fledging as determinants of post-fledging survival are considered in Chapter 7.

### 4.4.4. Age specific proportions of breeders.

In most studies, age specific breeding probabilities describe the proportion of individuals with the opportunity to breed, assuming that all individuals given this opportunity will subsequently take it. However, if breeding is confirmed only once a required stage in the breeding cycle is reached, birds attempting to breed but failing early may remain unrecorded. Where conditions at the initiation of breeding have an important influence on the subsequent success of any attempt, separating the proportion of individuals excluded from breeding, from those breeding but failing early may be impossible, particularly if age-classes are affected differentially. In spite of these problems, comparisons of recapture probabilities may still provide valuable information on population processes if *a priori* information is available concerning probable influences on early breeding success (e.g. McCleery *et al.* 1996).

#### 4.4.4.1. Breeding records and breeding attempts

Over all years, the recapture probabilities of first year birds were significantly lower than for known breeders, indicating that with recapture dependent on clutch initiation, either more first year birds failed during the initial stages of nesting of full breeding was not achieved at age one (Table 4.6, see methods). All adults had similar recapture rates, however, suggesting full breeding by the age of two.

Assuming, as appears to be the case, that the number of breeding territories did not differ greatly over time, breeding opportunities should be similar in each year with approximately constant numbers of potential first time breeders (from juvenile recruitment) available to fill a constant number of 'gaps' from adult mortality. This is the expected outcome if juvenile survival is matched to available breeding resources as suggested by Newton (1989a) and the survival estimates from SURGE. However, modelling in SURGE suggested significant differences between years in first-year breeding rates with a logistic regression based on river flow conditions at the initiation of breeding best describing this variation. The final model (Model 5, Table 4.6) predicted that all adults, and in favourable (i.e. low flow) years up to 89% of juveniles (96% of all birds), initiated breeding (Figure 4.4). Thus, the indications were that in some years, and possibly most others, only a small proportion of the population was actively excluded from making a breeding attempt.

With significant density-dependent juvenile over-winter mortality, it appears unlikely that regulatory processes would not have acted most strongly before spring. Importantly, flow effects on survival would be expected to reduce the non-breeding surplus, either by removing non-breeding birds or by creating 'gaps' through the loss of territory holders (see Clobert *et al.* 1990 for example). Further, there was no evidence that the lower recapture rates of first year birds represented breeding attempts in fringe upland territories followed by movements to 'prime' main river sites in later years. Only 13 individuals changed breeding sites between the uplands and lowlands during the course of this study. Of these, 10 birds simply moved between adjacent territories on the upland/lowland boundary, although three females did make longer movements between breeding attempts, failing to return to upland sites after over-wintering on the main river. The relative scarcity of such records, coupled with the absence of unringed birds entering the populations during breeding, suggests that substantial movements of this kind occur only infrequently. Hence, birds failing before laying, and not subsequently recorded near their original site, truly appear to be foregoing breeding for the season. While emigration from the study area to renest cannot be ruled out, again, such permanent movements would be reflected in survival rather than recapture rates.

#### 4.4.4.2. Flow influences on breeding 'probabilities'

In some situations, nest failures induced by environmental extremes many comprise a significant proportion of all nest losses. These may be directly attributable to nest destruction (e.g. Arcese *et al.* 1992; Storey *et al.* 1988) or result from increased energetic stress on breeders where food availability is depressed and/or foraging or thermoregulatory demands increase during unfavourable weather conditions (e.g. Clamens and Isenmann 1989; Coulter and Bryan 1995; Nilsson 1994; Siikamaki 1996; Wiktander *et al.* 1994). Although energetic stresses are generally reported in the later stages of the breed cycle when the broods demands are highest (e.g. Clamens and Isenmann 1989; Nilsson 1994; Siikamaki 1996; Wiktander *et al.* 1994), the strong relationships between food availability, weather conditions and laying dates in many species (see Martin 1987 for review) also imply important energetic constraints during the initial stages of breeding (Nilsson 1994; Perrins 1970). Dippers of both sexes increase body mass in early spring (Bryant and Tatner 1988; Galbraith and Broadly 1980; Ormerod *et al.* 1986b), and severe weather at, or immediately prior to, this time is known to extend the period required to reach breeding condition (Efteland 1975; Ormerod and Tyler 1985; Price and Bock 1983; Sackl and Dick 1988).

If the foraging commitments required to meet the daily energetic demands cannot be satisfied at any stage during breeding this will ultimately result in an energetic imbalance and a reliance on stored reserves. Decreases in reserves at an early stage in the breeding cycle must then be met either by decreased investment in offspring, in terms of number or 'quality', or increased dependence on exogenous resources with a further diversion of time and energy away from the nest and young (Martin 1987). This, in turn, has possible implications for nest predation, hatching date, hatching success, nestling development and/or future survival of both adults and young (Bakacincka *et al.* 1996; Drent 1975; Lijjeld and Slagsvold 1986; Zicus *et al.* 1995). The extent to which a bird will be prepared to incur any cost will then depend on the trade-offs between current and future reproduction and adult and chick survival (Michod 1979; Pianka and Parker 1975; Ricklefs 1977; see Chapter 7).

### 4.4.4.3. Age effects and nest failure

Price and Bock (1983) found mean precipitation during the nestling period and the total age of both parents to be the most important predictors of seasonal production for their population of American dippers. These effects were attributed to reduced foraging efficiencies for provisioning parents under high river flows, the flooding (and loss) of some nests and age differences in the quality of territory held. Older birds tended to hold territories with nest-sites less susceptible to flooding (Price and Bock 1983). Moller (1991) showed that in blackbirds *Turdus medula*, yellowhammers *Emberiza citrinella*, chaffinches *Fringilla coelebs* and black-billed magpies *Pica pica*, nest predation rates decreased with increasing patch size while the proportion of juvenile breeders decreased, suggesting that inexperienced or subordinate birds may be likely to use poorer nest sites. This pattern seems common in territorial species (e.g. Alatalo *et al.* 1985; Dias *et al.* 1992; Hatchwell *et al.* 1996; Holmes *et al.* 1996; Monkkonen 1990; Newton 1991; Verhulst *et al.* 1997), and if exclusions to poor sites is coupled with some elements of inexperience then it may go some way to explaining why juveniles appear to be most severely affected by spring floods.

Desrochers (1992) suggested that the later breeding of juvenile blackbirds was related to their lower foraging abilities, and with the provision of supplementary food, laying by juveniles although not older breeders was advanced relative to controls. Similar results have been seen in great tits (Kallander 1974), although no age differences in response were evident for dunnocks *Prunella modularis* (Davies and Lundberg 1985). Desrochers suggested that these differences were attributable to the complexity of the foraging methods employed by each species, with great tits and blackbirds using 'difficult' methods. Clearly, the foraging techniques of dippers are demanding, particularly under adverse flow condition, and any foraging inefficiencies are likely to be particularly important in species, like dippers, that employ energy-costly foraging habits (Bryant 1991). It also seems possible that juveniles could be under greater energetic stresses throughout breeding, and previous work within this population has shown that older females are able to adopt more efficient incubation regimes (Bryan 1996; Ward 1992) and maintain lower levels of energy expenditure during brood-provisioning than younger birds (Bryant and Tatner 1988).

#### 4.4.4.4. Habitat quality and breeding probabilities

Because breeding activities depend on an adequate (and continuous) supply of food, inexperienced or low quality birds may only be able to breed under favourable conditions. Such conditions may occur at good sites in all years, although perhaps only infrequency in marginal habitats. The occasional use of some fringe sites, both within the uplands and lowlands (Figures 8.2, 8.3), did not appear to result from annual differences in recruitment because there appeared to be at least some non-breeders in all years. Rather, the relationship between first year breeding probabilities and river flow conditions suggested that the suitability of some marginal sites differed between years depending on the prevailing flow conditions.

It seems likely that both nest destruction and flow-dependent effects on body condition will be of greatest importance for first year birds and provide mechanisms to account for at least a part of the low juvenile success in 'flood' years. The relative importance of these factors remains unclear, although the processes need not be mutually exclusive. Flooding will restrict access to food, possibly coupling nest destruction with increased energetic stresses. Although there would appear to be sufficient time for birds failing early to lay replacement clutches, and some workers (e.g. Schmid 1985) have reported nest-building being completed in as little as 5 days where a nest is lost (although by birds of unspecified age), birds may be unwilling to resume a breeding attempt which has little chance of success. Where the decision to breed is only marginal, any interruption may be sufficient to lead to the complete abandonment of breeding for that season. Moreover, if poor individuals are excluded to fringe sites (Newton 1989a) some interaction is likely between individual and habitat quality, further restricting the ability of juveniles to prepare for the rigours of breeding.

Lack (1966) has suggested that birds should only delay breeding for a season if they have a reasonably high probability of surviving to breed in the future, and Drent and Daan (1980) suggest that there is little evidence that when feeding conditions are extremely poor birds will not breed at all. Subsequent studies of a number of short lived species have shown, however, that in any year, a significant proportion of first-year young may not make a breeding attempt (Clobert *et al.* 1990, 1993; Dhondt 1989; Marzolin in prep.; Sternberg 1989; Thompson 1992). Although within this population, dippers did not appear to be able to compensate for the 'lost' first-year production (see Chapter 6), evidence from other species that breeding attempts at poor sites may not only have low probabilities of success but may also reduce the subsequent survival chances of adults (Bryant 1991; Daan *et al.* 1996; Nilsson 1994) suggest that for lifetime success, the 'gains' from breeding at fringe sites may only be apparent in years of high habitat suitability.

# Chapter 5

# Breeding biology of dippers in the River Devon catchment

## 5.1. Introduction

Dippers have been ringed within the Devon catchment since the mid-seventies, and the breeding population has been continuously monitored since 1980 (Bryant *et al.* unpubl.; Shaw 1978). Initially, the breeding surveys considered only the section of the river between Glendevon reservoir and Crook O'Devon (Figure 2.1b), and in 1985 the study was extended to consider all suitable habitat within the catchment (Newton 1989a). At this time, some sites within the adjacent Teith and Allan catchments, assumed to be the most likely rivers for the exchange of dispersing juveniles, were also added to the study area.

Dippers are widespread within the Devon catchment throughout the year, (Newton 1989a), breeding on all major tributary streams and along the length of the main river where fast flowing, shallow waters provide the riffle areas favoured for foraging. Although many upland sites are abandoned outwith breeding, the circum-neutral waters of the catchment (mean pH 7.07, SEPA *unpubl.*) appear to provide ideal conditions for dippers, and studies of both breeding and non-breeding populations show densities on the main river to be among the highest recorded for any rivers in the British Isles (Logie 1995; Logie *et al.* 1996; Ormerod *et al.* 1985, 1986a, 1988; Newton, 1989; Vickery, 1991; Wilson 1996).

A brief account of the breeding biology of the population has been given elsewhere (Newton 1989a), although the extended data-sets now available allow a more complete description of breeding parameters. The analyses here are concerned principally with seasonal measures of breeding productivity. Demography, distribution, age-structure and individual variation in lifetime reproductive success are considered elsewhere (Newton 1989a; Chapters 3, 5, 6 and 7). Ormerod and Tyler (1985), Shaw (1978), Smiddy *et al.* (1995) and Wilson (1996) provide details of the breeding biology of some other dipper populations in Britain and Ireland (see Ormerod and Tyler 1985, Tyler and Ormerod 1994, and Wilson 1996 for general reviews).

## 5.2. Methods

### 5.2.1. Field methods

Nests were located as early as possible during the breeding season, either by searching traditional and potentially suitable sites, or by following adults carrying nesting material. After locating a nest, visits were made to record clutch size, brood size and the number of fledglings raised. Laying dates were recorded directly, or calculated from hatching dates or nestling biometrics after Shaw (1978). All nests were revisited to confirm successful fledging and, in the following weeks, territories were checked to record second or replacement breeding attempts. More complete descriptions of the field methods are given in Chapter 2.

### 5.2.2. Habitat variables

For each breeding territory, altitude, gradient and river width were recorded. Altitude referred to the site of the nest itself, whilst the mean river gradient was calculated for a 1000m river section extending 500m each side of the nest. Measures for both altitude and gradient were obtained directly from 1:25000 Ordnance Survey maps. Although the 1000m sections used in assessments of river gradient did not necessarily match the breeding territories directly, and complete descriptions of territory boundaries were not available in all years, it seems likely that they adequately represented the local river topography and the foraging sites available.

River width (the width of flowing water) was measured in 1995 only, to the nearest 0.5m at five 100m intervals each side of the nest. All distances between sampling were 'paced-out' to provide easily repeated sample intervals and to avoid subjectivity in the selection of sites points for habitat assessments (see also Chapter 3).

### 5.2.3. Data presentation

Since only a subset of the population of the River Devon was followed prior to 1985 (and a subset of the Allan Water and River Teith in all years), generally, analyses were restricted to data collected from the Devon catchment after this time. However, some analyses were undertaken pooling the data from all catchments or over all years to increase sample sizes. Analyses using pooled data were restricted to comparisons including either second and replacement breeding attempts, or individual breeding performance with age. Although these additional data were biased towards lowland sites, repeat breeding attempts were restricted to these lowland territories and thus, only records for equivalent river sites were pooled. Further, no inter-catchment differences were identified for any measure in any analysis, although in some cases, limited sample sizes prohibited rigorous testing.

To avoid pseudoreplication (Hulbert 1984), mean values were used in all analyses where repeated measures were available within the data-sets. For example, analyses examining the relationships between habitat variables and the time of laying were based only on the mean dates over all years within a single territory. Similarly, where an individual (or pair) bred in more than one season, only the mean value (e.g. laying date, clutch size) over all recorded attempts within an age-class were included.

### 5.2.4. Statistical analyses

Analyses of clutch size, brood size, and the number of fledglings raised were undertaken using Mann-Whitney and Kruskal-Wallis tests where appropriate since the non-normal variation in these breeding measures prohibited the use of parametric statistics (see below). Where paired comparisons were made, Wilcoxon matched-pairs tests have been applied. All age-class analyses compared first year birds with second year breeders and older. Parametric statistics were considered appropriate only where both measures lay on a continuous scale (i.e laying dates and habitat variables). Spearman's rank coefficients were used, therefore, in all correlational analyses examining clutch size, brood size or the number of fledglings raised.

## 5.3. Results

A total of 449 breeding attempts was recorded within the Devon catchment between 1985 and 1995, either with complete or partial data (Table 5.1). Breeding was confirmed from 10 to 425 metres above sea level, with 74% of the territories used (in at least one year) occurring below 250m a.s.l. and 87% below 350m (Figure 5.1).

### 5.3.1. Laying and hatching dates

Typically, laying started during the second half of March (Figures 5.2, 5.3), with the earliest clutches hatching during the first, or more usually the second week in April. Over all years, the earliest recorded date of clutch initiation was 6 March (1989), with the latest first eggs laid on 23 May (1986) and 1st June (1986) for first and second clutches respectively. Between 1985 and 1995, the median date of clutch initiation for first breeding attempts within the Devon catchment was 11 April.

Less than 20% of all clutches were started during March, and the frequency of laying increased sharply during the first and second weeks of April (Figure 5.2). By this time, approximately two-thirds of all lowland attempts (Figure 5.3a) and a quarter of upland clutches were initiated (Figure 5.3b). This was equivalent to more than 55% of all breeding attempts within the catchment each season (Figure 5.2), and generally, more than 35% of clutches were laid during this peak two week period. The frequency of nesting attempts declined sharply thereafter, interrupted only by a slight increase during the first two weeks in May. This coincided with the laying of second and replacement broods at a number of lowland sites, together with continued laying in the uplands (Figure 5.3). In many cases, pairs breeding at main river sites and laying a second clutch, did so even before the initiation of first attempts in the highest upland territories.

For birds making second and replacement breeding attempts, median laying dates were 17 May and 11 May respectively (all data combined). True second clutches were laid significantly later than replacements (ANOVA $F_{1,63}=20.8$, $p<0.001$), reflecting the additional time required to raise the first brood before initiating the second attempt. Birds laying early also appeared significantly more likely to attempt a second brood than those breeding later in the season (Analysis of co-variance, $F_{1,210}$=47.7, p<0.001, year entered as covariate (see below)), and over all years, no birds initiating a first clutch after the 9th of April and successfully fledging at least one chick, were recorded as attempting a second brood within the same year.

### 5.3.1.1. Annual variation in laying dates

The median date of clutch initiation for first broods ranged between 2 April (1990) and 20 April (1986). Differences in laying dates were significant between years (Kruskal-Wallis H=36.0, n=378, $p \leq 0.001$), with breeding delayed in 1986, following a period of severe weather (Newton 1989a). A similar delay in laying was also noted in the same year on the River Esk, Midlothian (Wilson 1996).

Although nationally, a trend towards increasingly early laying has been suggested for many birds, including dippers (Crick *et al.* 1995), no evidence of this was found within any of the catchments studied (Pearson's correlation coefficients <-0.420, p>0.10 in all cases). Relationships remained non-significant when restricting the analysis to the Glendevon-Crook O'Devon river section, for which the longest continuous records were available (1980-1996).

### 5.3.1.2. Habitat influences on the laying date

Considering only first clutches, laying dates were strongly related to river width, altitude and gradient (Table 5.5). These three measures of habitat structure were all strongly correlated, with rivers becoming increasingly steep and narrow at higher altitudes (Table 5.2). A multiple regression analysis of laying date against these three habitat variables included river width as the principal factor, explaining 48.3% of the variance, with altitude and gradient (both after $\log_{10}$ transformation) together explaining a further 4.3% (Table 5.3).

### 5.3.1.3. Age effects on laying dates

For females, there was no significant difference in the mean laying dates between age classes (Mann-Whitney, U=11069.5, n=307, p=0.366). In part, this result may reflect the high variation

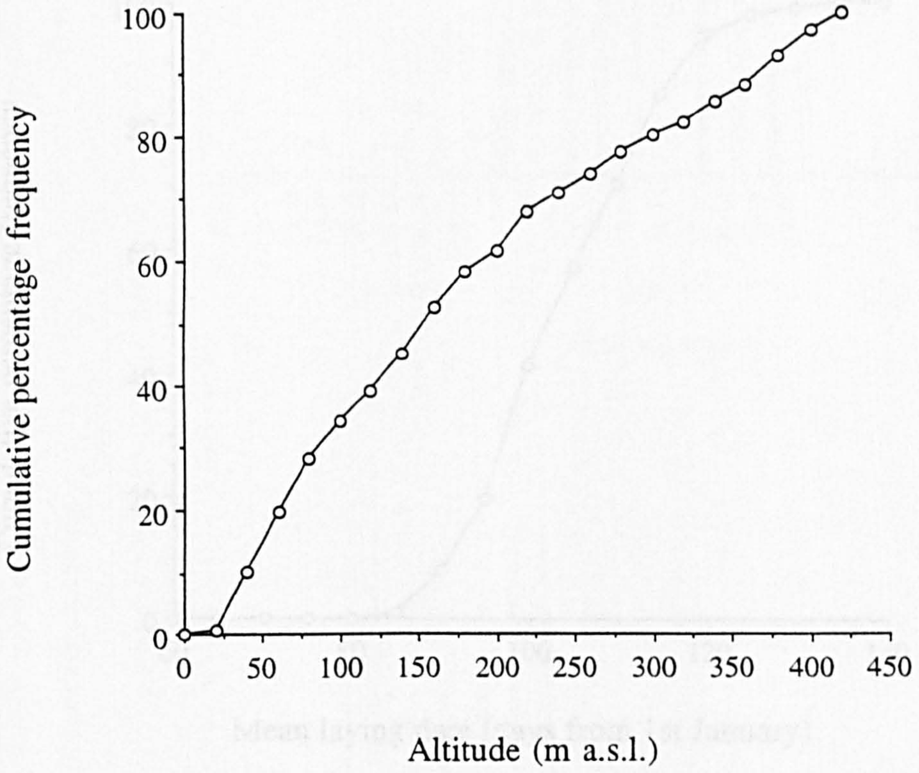


**Figure 5.1.** Cumulative percentage frequency distribution of nests (sites used in at least one year between 1985 and 1995) with altitude (m a.s.l.) within the River Devon catchment.

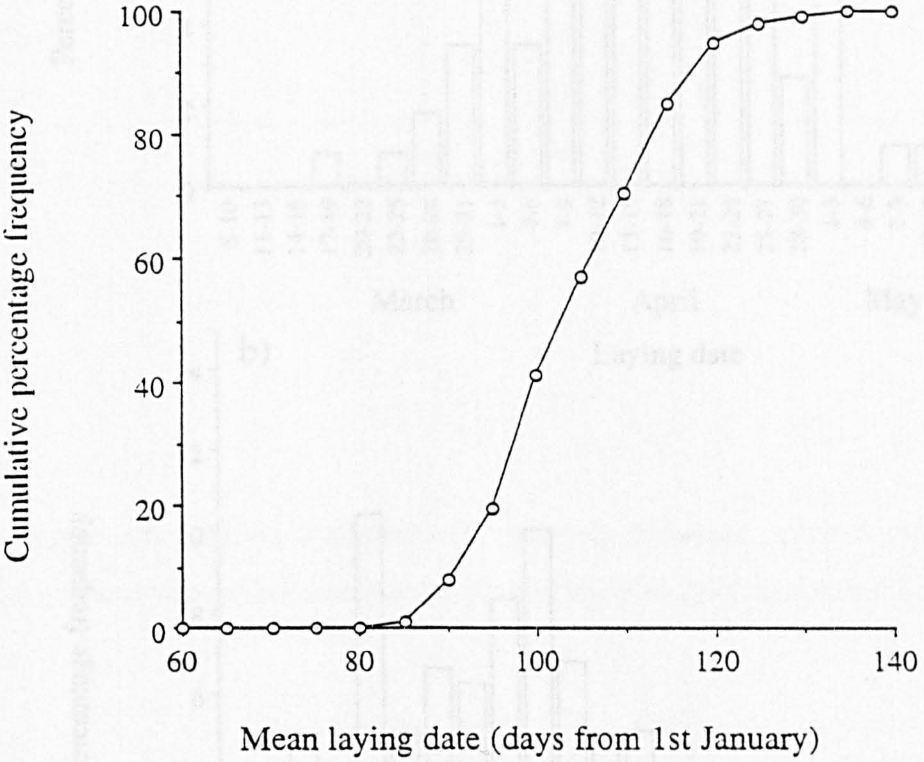


**Figure 5.2.** Cumulative percentage frequency of laying dates (mean date for sites used in at least one year between 1985 and 1995) within the River Devon catchment.

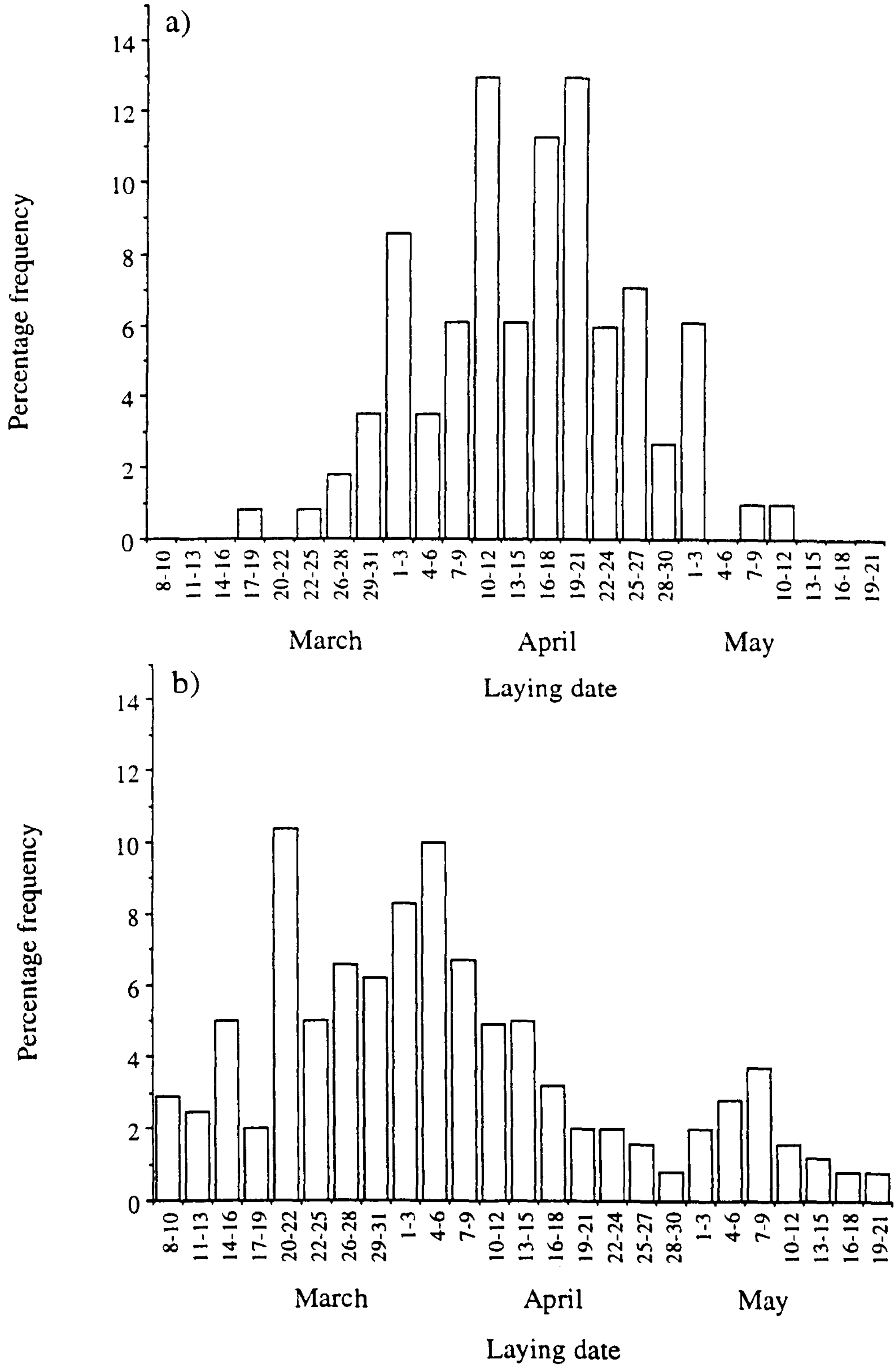


**Figure 5.3.** Dates of clutch initiation for dippers at upland (a) and lowland (b) site within the River Devon catchment between 1985 and 1995 (all attempts).

**Table 5.1.** Numbers of breeding attempts recorded in the Devon, Allan and Teith catchments from 1985-1995 (inclusive).

| | Lowland Attempts | | | Upland Attempts | | | All |
|---|---|---|---|---|---|---|---|
| | First | Second | Repl't | First | Second | Repl't | |
| River Devon | 250 | 33 | 13 | 149 | 3 | 1 | 449 |
| Allan Water | 63 | 12 | 2 | 14 | 0 | 0 | 91 |
| River Teith | 33 | 2 | 1 | 0 | 0 | 0 | 36 |
| All Rivers | 346 | 47 | 16 | 163 | 3 | 1 | 576 |

**Table 5.2.** Pearsons correlation coefficients for measures of habitat structure and laying date. Altitude and gradient were transformed ($\log_{10}$) prior to analysis. All correlations were significant at $p<0.001$.

| | Mean laying date | Altitude (m.a.s.l.) | Gradient (m $km^{-1}$) | Width (m) |
|---|---|---|---|---|
| Mean laying date | 1.000 | | | |
| Altitude | 0.574 | 1.000 | | |
| Gradient | 0.603 | 0.518 | 1.000 | |
| Width | -0.699 | -0.699 | 0.603 | 1.000 |

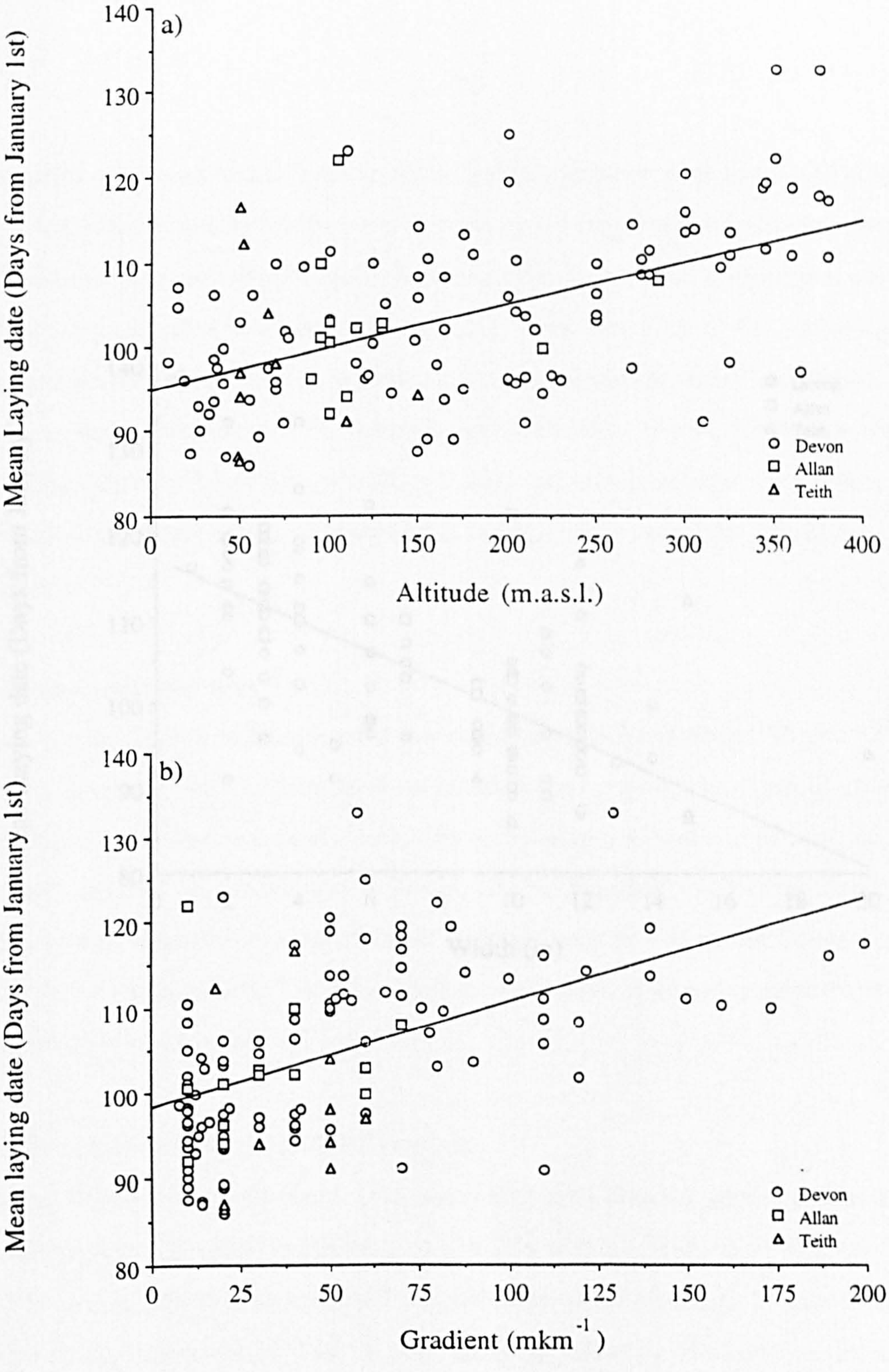


**Figure 5.4.** Mean laying dates (first egg) for first breeding attempts in catchments in central Scotland between 1985 and 1995, in relation to a) altitude (m.a.s.l.), b) gradient (m km$^{-1}$) and c) river width (m). For sites within the River Devon catchment (n=105), Laying date=94.757+0.0051*Altitude* ($r^2$=0.374), Laying date=98.108+0.124*Gradient* ($r^2$=0.313), Laying date=116.98-1.819*Width* ($r^2$=0.448). Including all catchments (n=128), Laying date=95.162+0.0049*Altitude* ($r^2$=0.339), Laying date=97.797+0.124*Gradient* ($r^2$=0.279), Laying date=115.46-1.565*Width* ($r^2$=0.381). The fitted lined are for the Devon catchment only.

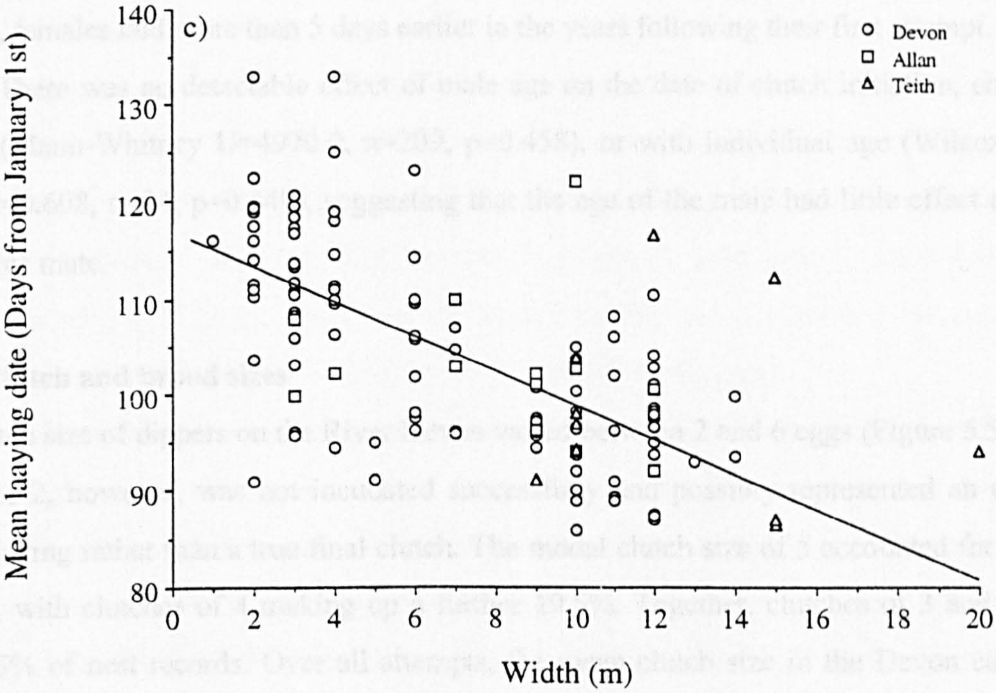


**Figure 5.4.** (continued)

between territories (see above), or between birds within a territory, relative to individual differences with age. Accordingly, paired comparisons between the laying dates of individual females in their first year and the mean date of subsequent breeding attempts revealed a significant advancement of laying following their first year (Wilcoxon matched pairs, Z= -2.13, n=48, 2-tailed p=0.034). On average, females laid more than 5 days earlier in the years following their first attempt.

There was no detectable effect of male age on the date of clutch initiation, either between classes (Mann-Whitney U=4970.0, n=209, p=0.458), or with individual age (Wilcoxon Matched pairs Z=-0.608, n=24, p=0.449), suggesting that the age of the male had little effect on the laying date of his mate.

### 5.3.2. Clutch and brood sizes

The clutch size of dippers on the River Devon varied between 2 and 6 eggs (Figure 5.5). The single clutch of 2, however, was not incubated successfully and possibly represented an abandonment during laying rather than a true final clutch. The modal clutch size of 5 accounted for 73.0% of all records, with clutches of 4 making up a further 19.5%. Together, clutches of 3 and 6 comprised only 7.5% of nest records. Over all attempts, the mean clutch size in the Devon catchment was 4.68±0.62 (mean±S.D., n=345, Table 5.4) with no significant differences between years (Kruskal-Wallis H=14.19, n=345, p=0.164; Figure 5.6.).

#### 5.3.2.1. Seasonal trends in clutch and brood size

Considering all attempts in all years, first and replacement clutches appeared significantly larger than second clutches (Kruskal-Wallis H=33.41, n=298, p<0.001, Table 5.5). Mean clutch size also appeared to change significantly through the breeding season (Figure 5.6, Kruskal-Wallis H=16.20, n=298, p=0.003), with clutches laid in May being significantly smaller than those initiated in March and April, at the peak of laying (Table 5.7). This effect persisted when restricting the analysis to first attempts (Kruskal-Wallis H=8.45, n=260, p=0.015), suggesting that the reduction in mean clutch size was not due solely to the inclusion of smaller second clutches laid late in the season. Seasonal trends in both brood size and the numbers of chicks fledged paralleled those for clutch size with late broods holding significantly less chicks at hatching (Kruskal-Wallis H=10.672, n=285, p=0.005) and fledging significantly fewer young (Kruskal-Wallis H=6.069, n=270, p=0.048). Brood size and the numbers of fledglings were also significantly reduced in second relative to first attempts (Kruskal-Wallis H=11.241, n=265, p=0.004 for brood size; H=7.640, n=262, p=0.022 for fledglings).

Although, upland breeders laid significantly later than birds on the main river (Table 5.2, Figure 5.3), the smaller late clutches did not appear to be due to a differences in territory structure (clutch size, brood size and number of fledglings with altitude, gradient or river width; Spearman's correlation coefficient <0.047, p>0.207, n=140 in all cases). Additionally, there was no evidence that the numbers of eggs, chicks or fledglings within broods differed between the broad upland/lowland classes (Mann-Whitney, p>0.467, n=140 in all cases).

Although all measures of brood size at fledgling were based on the number of chicks at the time of ringing, and did not account for losses between ringing and fledgling (Mayfield 1961, 1975), no significant differences in the numbers of fledglings per nest were apparent between years (Kruskal-Wallis p>0.2625, n>339), or between the periods 1985-1992 and 1993-1995 (Mann-Whitney p>0.1121, n=339) when all nests were visited when the chicks were 18 days old, immediately prior to fledgling. It seems likely, therefore, that if nesting success has been over-estimated in the early years of this study, any differences in mean brood size are likely to be small.

### 5.3.2.2. Age effects on clutch and brood sizes

The mean clutch size laid by first year females was slightly smaller than for older breeders (4.59±0.76 compared to 4.65±0.67), although no significant differences were detected between age classes (Mann-Whitney U=9698.5, n=287, p=0.3582). There was no evidence that territory quality masked true age effects (Wilcoxon matched pairs, first year birds vs older breeders in the same territory, Z=-1.0418, n=56, p=0.2975) or that the clutch size of an individual female changed following her first year (Wilcoxon matched pairs Z=-0.5247, n=40, p=0.5998). Again, male age did not appear to affect the clutch size of his mate (Mann-Whitney U=4164.5, n=188, p=0.7091 comparison between age classes; Wilcoxon matched pairs Z=-0.6083, n=28, p=0.5430 clutch size

**Table 5.3.** Stepwise multiple regression analysis for laying date (mean for each territory over all years) in relation to selected habitat variables ($y=a+bx_1+bx_n$). Gradient (m $10km^{-1}$) and altitude (m a.s.l) were transformed ($\log_{10}$) prior to analysis.

| Variables in Equation | b±s.e. | Beta±s.e. | Cum $r^2$ | F (Eqn) | p |
|---|---|---|---|---|---|
| 1. Width | -0.913±0.317 | -0.330±0.115 | 0.4831 | 127.15 | 0.0001 |
| 2. Gradient | 9.11±2.786 | 0.315±0.096 | 0.5125 | 71.967 | 0.0001 |
| 3. Altitude | 0.419±0.192 | 0.177±0.081 | 0.5260 | 50.934 | 0.0001 |
| Constant | 18.856±7.257 | | | | |

**Table 5.4.** Mean clutch sizes, brood sizes and numbers of fledglings raised (±S.D.) on the River Devon, Allan Water and River Teith between 1985-95 inclusive.

| First Attempts | Clutch | Brood | Fledglings |
|---|---|---|---|
| River Devon | 4.68±0.62, n=345 | 3.63±1.64, n=388 | 3.21±1.84, n=386 |
| Allan Water | 4.67±0.77, n=70 | 3.95±1.48, n=78 | 3.46±1.75, n=72 |
| River Teith | 4.60±0.86, n=42 | 3.59±1.68, n=39 | 3.25±1.90, n=36 |
| Second[1] | 4.13±0.70, n=38 | 3.23±1.46, n=47 | 2.76±1.65, n=45 |
| Replacement[1] | 4.38±1.30, n=8 | 3.80±1.62, n=10 | 2.60±2.17, n=10 |

[1] All nests, including those from Allan water and River Teith.

**Table 5.5.** Mean clutch size, brood size and number of fledglings raised (±S.D.) on the river Devon 1985-95, relative to time of laying.

| | March | April | May |
|---|---|---|---|
| Clutch size | 4.57±0.66, n=54 | 4.75±0.56, n=191 | 4.67±0.61, n=30 |
| Brood Size | 3.49±1.59, n=67 | 3.82±1.48, n=232 | 3.53±1.71, n=34 |
| Fledglings | 3.13±1.76, n=69 | 3.19±1.84, n=228 | 3.18±1.66, n=34 |

**Table 5.6.** Clutch sizes, brood sizes and numbers of fledglings raised for four pair-age combinations on the River Devon, 1985-95 inclusive (FY, first year; AD, adult; m, male; f, female).

| Pair Combination | Mean Clutch±SD | Brood size±SD | Fledglings±SD |
|---|---|---|---|
| FYf/FYm | 4.58±0.79, n=38 | 4.09±1.36, n=43 | 3.27±1.99, n=44 |
| FYf/ADm | 4.70±0.72, n=27 | 3.56±1.87, n=32 | 2.88±2.06, n=33 |
| ADf/FYm | 4.63±0.59, n=38 | 3.61±1.53, n=46 | 3.26±1.69, n=50 |
| ADf/ADm | 4.61±0.81, n=96 | 3.86±1.52, n=104 | 3.51±1.75, n=106 |

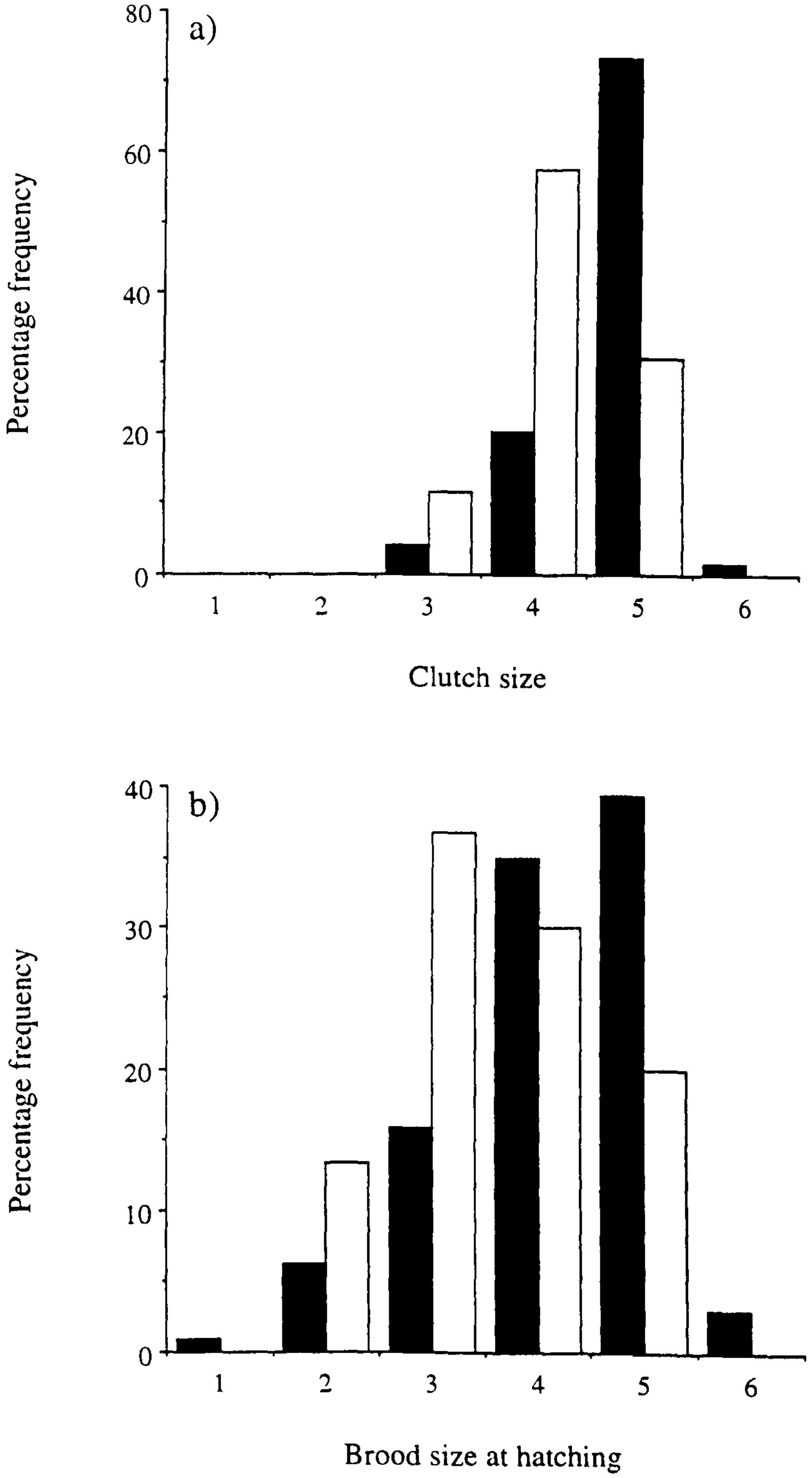


**Figure 5.5.** Percentage frequency distributions of a) clutch size, b) brood size and c) numbers of fledglings raised for first (shaded bars) and second (open bars) breeding attempts within the River Devon catchment between 1985 and 1995 (n=345 first attempts, 33 second attempts).

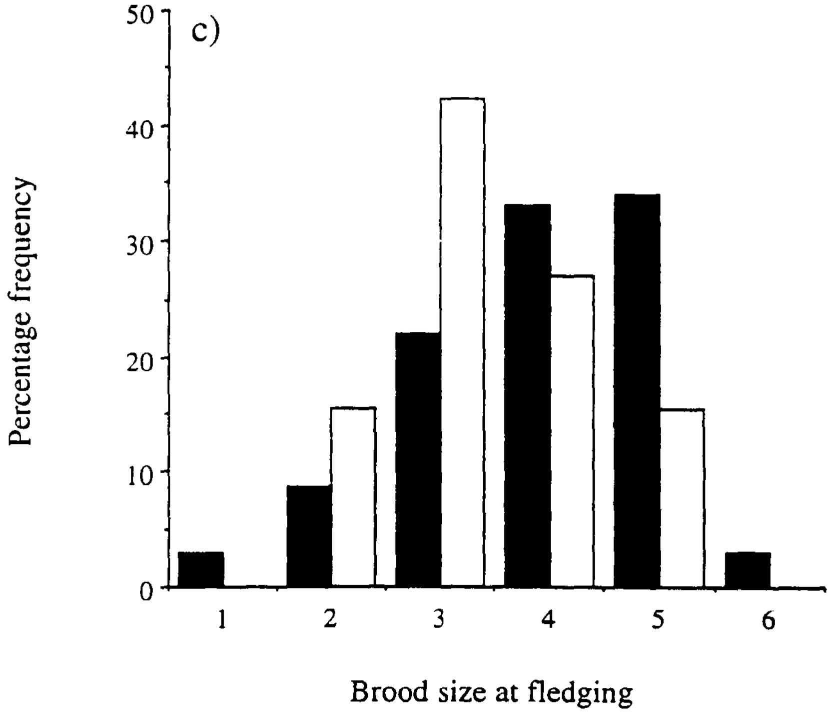


**Figure 5.5.** (continued)

with individual age), or any other measure of breeding productivity until fledging (Mann Whitney $U<4979.5$, $n>204$, $p>0.6632$; Wilcoxon matched pairs $Z>-0.3620$, $n>21$, $p>0.6155$, comparisons of first year and mean adult measures between age classes and for individual breeders respectively as juveniles/adults respectively). The exclusion of complete breeding losses, failed to affect the statistical significance of any of these analyses.

In contrast to findings on the River Esk (Wilson 1996), the age composition of a pair did not appear to affect any measure of breeding production until fledging (Table 5.6, Kruskal-Wallis, $H<2629.0$, $p>0.353$, $n=199$ in all cases).

### 5.3.3. Nest success

Over all years, 90% of nests which were followed from the initiation of laying, successfully hatched at least one chick, with 92% of these surviving nests (81% of total) then producing at least one fledging. Overall, 79% of eggs produced chicks and 78% of all chicks (62% of all eggs) survived until fledging. Of unsuccessful nests, the precise cause of the nest failure was not known in most cases. Flooding and the loss of poorly anchored nests was important in many cases, although predation by rats, corvids and mustelids was also recorded. At a few man-made sites, nest destruction or egg collection by humans may also have accounted for some nest failures, although the relative importance of each of these factors remains unclear.

### 5.3.4. Total Seasonal productivity

Lowland birds were significantly more likely than upland pairs to be double-brooded within a season (Wilcoxon $Z=-2.80$, $p=0.005$), and including second clutches at some sites, lowland breeders laid significantly more eggs (Mann-Whitney $U=12656.0$, $p=0.001$, $n=204$; Figure 5.8) and hatched more chicks each year than upland pairs (Mann-Whitney $U=13649.5$, $p=0.040$, $n=210$). Although, on average, lowland birds raised more fledglings within a season, and during the course of this study only lowland birds successfully fledged young from second broods, differences in total fledgling production between habitats classes were not significant (Mann-Whitney $U=14540.5$, $p=0.250$, $n=210$, Table 5.7; Figure 5.7).

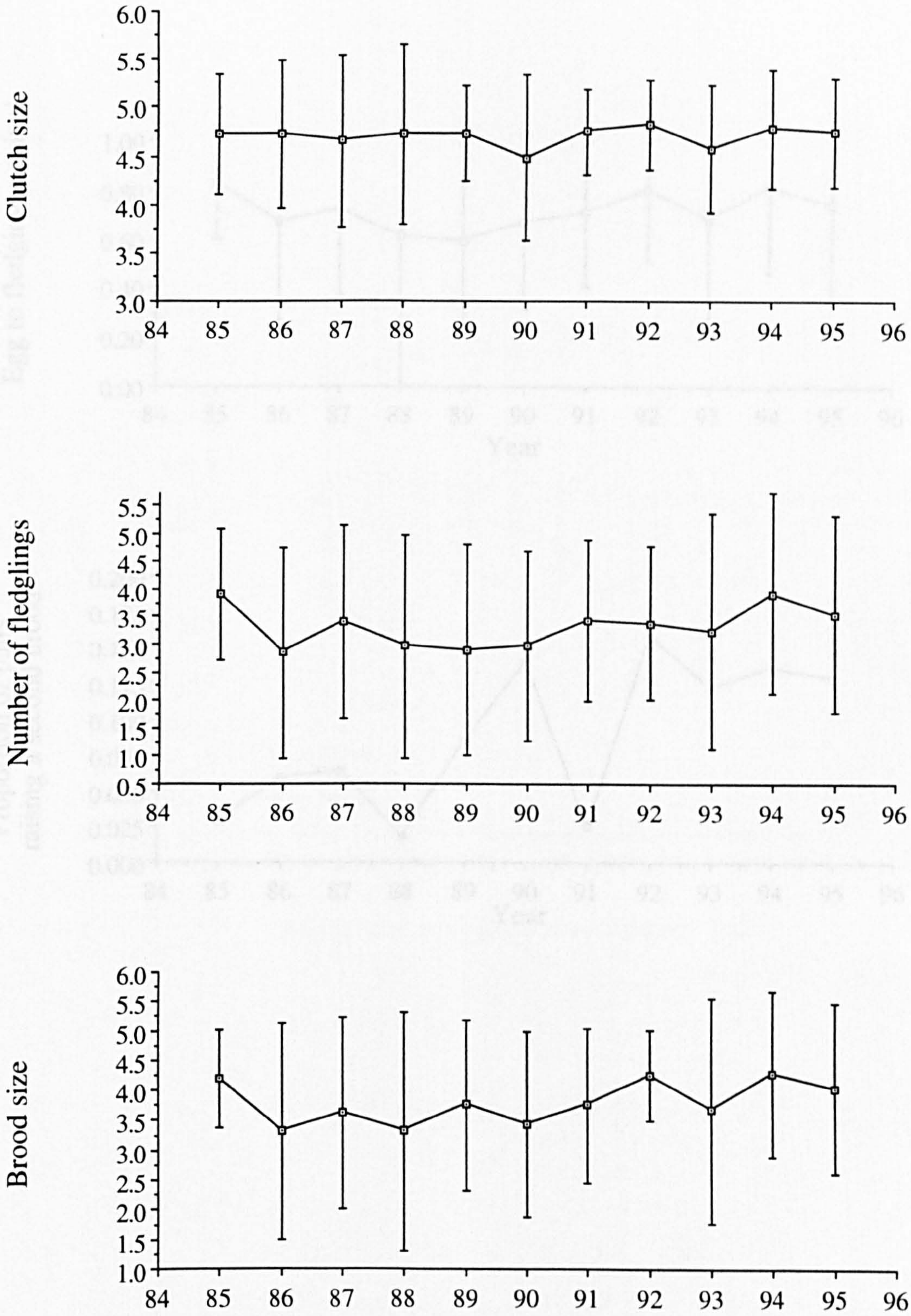


**Figure 5.6.** Annual variation in clutch size, brood size, numbers of fledglings raised and egg to fledging survival from first attempts only (±S.D.), and the proportion pairs attempting 'true' second broods within the River Devon catchment between 1985 and 1995 (n≥333 in all cases).

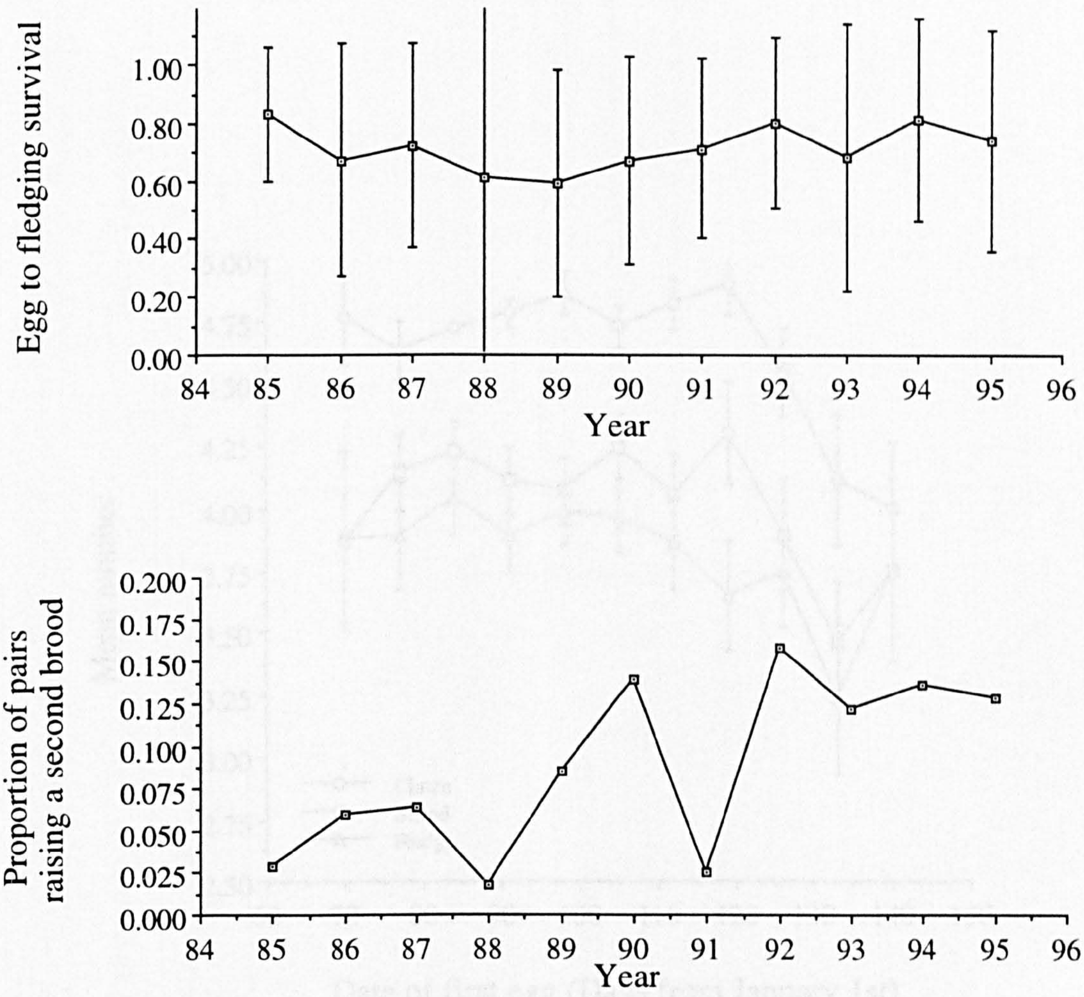


**Figure 5.6** (continued).

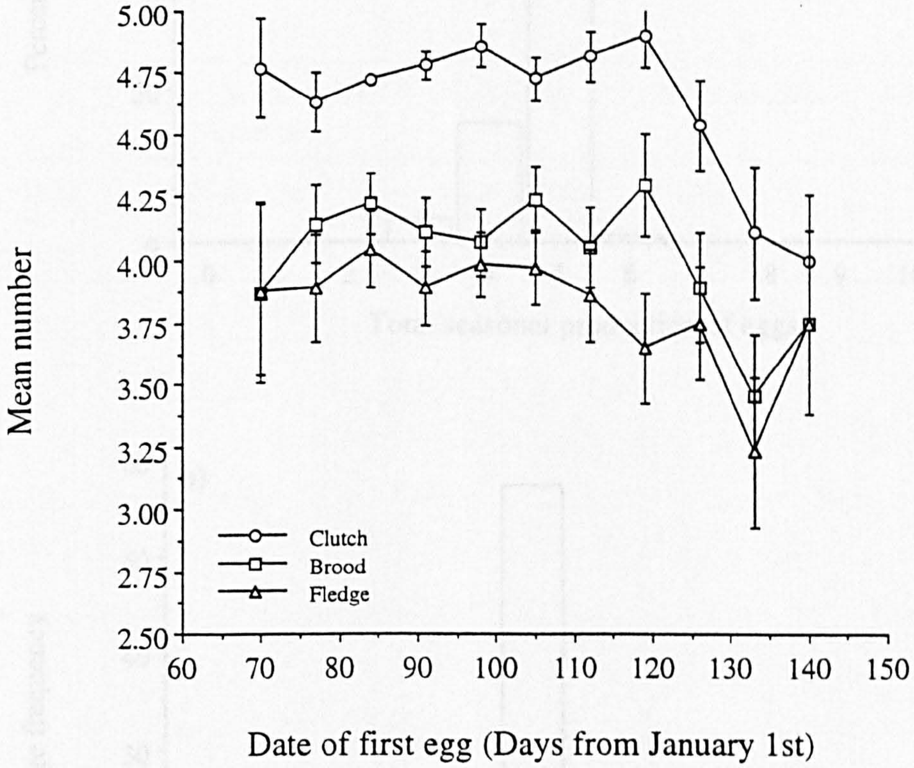


**Figure 5.7.** Seasonal trends in clutch size, brood size and the numbers of fledglings raised within the River Devon catchment between 1985 and 1995 ($n \geq 333$).

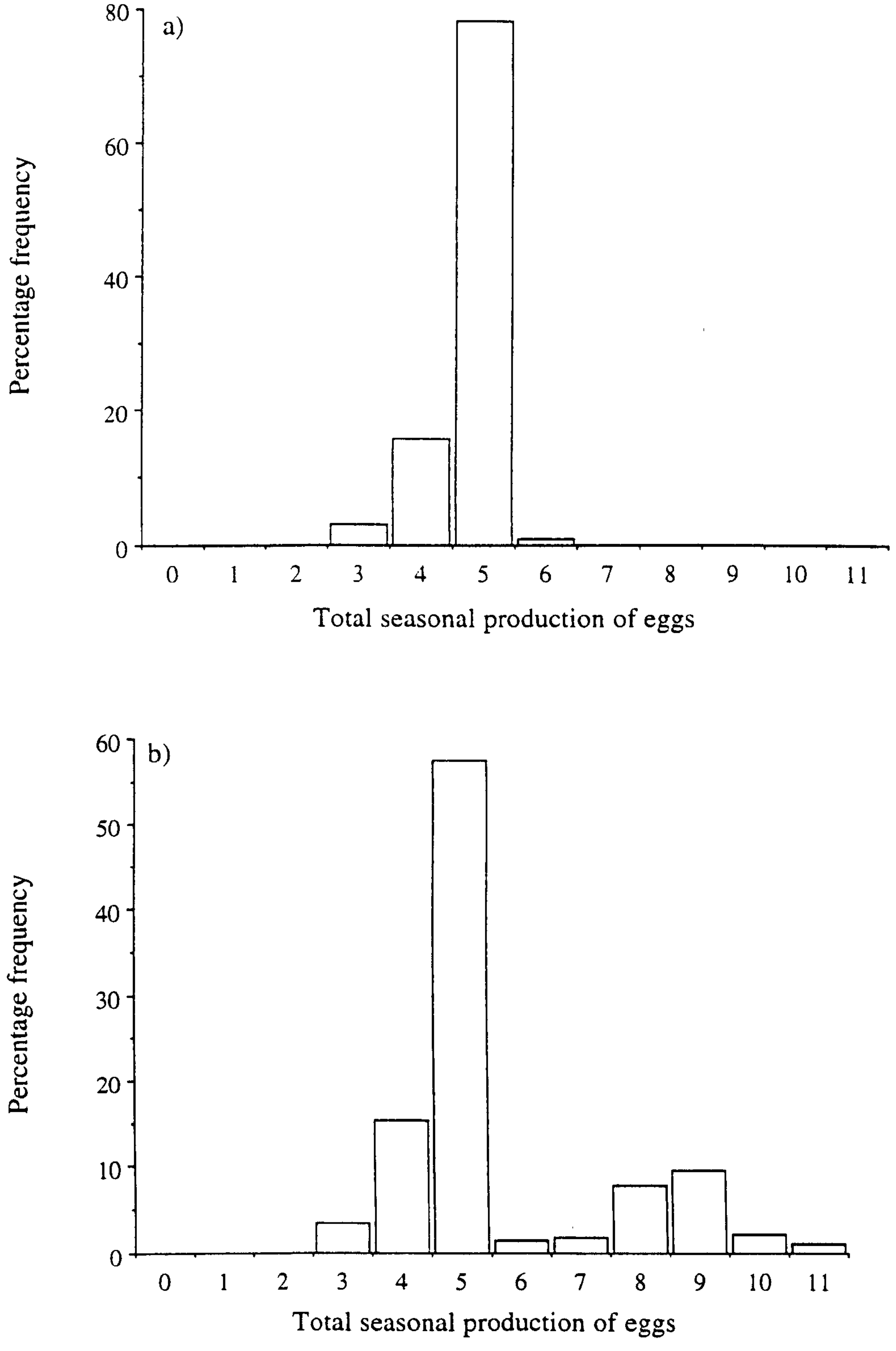


**Figure 5.8.** Percentage frequency distribution of the total seasonal production of eggs for a) upland and b) lowland sites within the Devon catchment between 1985 and 1995 (n=149 upland pairs, n=250 lowland pairs).

**Table 5.7.** Comparison of total seasonal reproductive success (Mean±S.D.) for upland and lowland breeders. Second attempts refer to the proportion of breeders initiating true second attempts. 'Difference' refers to the statistical significance of tests between habitat means (Wilcoxon matched paired test by year for Second attempts, Mann-Whitney for all measures of breeding productivity).

| | Second attempts | Eggs laid | Chicks hatched | Chicks fledged |
|---|---|---|---|---|
| Uplands (n=103) | 0.01±0.01 | 4.75±0.59 | 3.83±1.72 | 3.46±1.85 |
| Lowlands (n=305) | 0.12±0.08 | 5.57±1.74 | 4.51±2.06 | 3.88±2.44 |
| Difference | p=0.0050 | p=0.0007 | p=0.0396 | p=0.2505 |

## 5.4. Discussion

### 5.4.1. Regional variation in laying dates

Laying dates on the River Devon, and in the adjacent Teith and Allan catchments, were approximately two weeks later than those reported for similar studies in Wales and Southern Ireland (Smiddy *et al.* 1995; Tyler and Ormerod 1985). This delay did not appear to reflect differences in habitat quality or site topography. Water quality is known to be a principal determinant of laying dates, and population densities, clutch size and breeding success were consistent with those for dippers on high quality, circum-neutral rivers elsewhere (Ormerod *et al.* 1985, 1986, 1988; Vickery 1991, 1992). The altitudinal distribution of nests in the Devon catchment closely matched that described in Wales by Tyler and Ormerod (1985). Shaw (1978) failed to detect any regional differences in laying dates within Britain, although subsequent studies have suggested that southern populations in both Britain and Ireland may breed significantly earlier than those further north (Smiddy *et al.* 1995; Tyler and Ormerod 1985; Wilson 1996). Recent analyses of BTO nest record cards have confirmed this as a general pattern across species, and dippers in Scotland appear to lay, on average, 4-5 days later than those in England (Crick *et al.* 1995).

The remarkable similarities in the long-term median laying dates of the two studies in central Scotland (and the three catchments within this study), together with their consistent differences from more remote populations, support the existence of important regional effects (this study; Smiddy *et al.* 1995; Tyler and Ormerod 1985; Wilson 1996). It seems likely that these general differences reflect the milder weather conditions early in the year at southern and western sites and the ability of breeders to prepare for the onset of breeding. Within populations, for example, annual variations in the severity of the weather at, or prior to, the breeding season are known to influence the timing of clutch initiation (Efteland 1975; Ormerod and Tyler 1985; Price and Bock 1983; Sackl and Dick 1988; Schmid 1985), and studies in Wales (Tyler and Ormerod 1985) and mainland Europe (Efteland 1975; Sackl and Dick 1988; Schmid 1985) have shown advanced laying following mild winters, with breeding delayed after severe weather or high water levels. In 1986, laying dates on both the River Devon and Esk were approximately two weeks later than for 'normal' years following a period of exceptionally cold and wet weather (Newton 1989a; Wilson 1996). Early laying on the Esk in 1991 (the only other year highlighted by Wilson (1996)) was also recorded within the Devon, Allan and Teith catchments, although in this year the effect was less pronounced.

### 5.4.2. Habitat influences on the timing of breeding

The breeding season in birds is generally assumed to match the optimal conditions for raising young (Lack 1947, 1954). Yet, although the timing is determined to a great extent by the seasonality of resources (Bryant 1975; Perrins 1965, 1970), differences in laying date between individuals may reflect variation in food availability on a local scale and the ability of parents to form and incubate eggs or adequately provision nestlings (Boutin 1990; Daan *et al.* 1990; Drent and Daan 1980; Kluyver 1951; Lack 1966; Nilsson 1994; Perrins 1965, 1970). Indications that in many species birds would breed earlier if more food was available comes from experimental studies showing that with supplementary feeding females often advance laying and in some cases increase clutch sizes relative to control nests (see Daan *et al.* 1988; Boutin 1990 and Martin 1987 for reviews). Mean laying dates are often advanced in years of high food availability and within populations birds breeding in habitats with greater food abundance generally breed earlier than those elsewhere (see Martin 1987 for review; Ormerod *et al.* 1985a, 1986b, 1986; Vickery 1991, 1992). River width, gradient and altitude were all strongly inter-correlated and negatively related to laying dates (Table 5.2). Yet, for habitat differences in food availability to explain the patterns of laying within the Devon catchment it is necessary to show that these trends, related to habitat structure, were consistent with variation in resource abundance.

Estimates of prey abundance were not available for upland sites within the Devon catchment, although generally, both invertebrate numbers and biomass are known to be highest within riffles, and intermediate gradients and wide rivers are known to provide these shallow, fast-flowing river sections favoured by foraging dippers (Marchant and Hyde 1980; Ormerod *et al.* 1985; Price and Bock 1983; Round and Moss 1984; Shooter 1970). It seems likely that the extent of these foraging sites may be generally reduced on upland streams due to the narrow, steep nature of the stream channels (Logie and Bryant 1994; Chapter 1), because at increasing gradients, rivers channels tend to change from riffles to rapids; faster, more turbulent waters, less suitable for both invertebrates and foraging dippers (Price and Bock 1983).

Lennon (1988) calculated territory areas of between c.1700m$^2$ and c.2500m$^2$ for all birds breeding on the River Devon between Glendevon Reservoir and Vicar's Bridge (Figure 2.1b). A mean territory area of 3670m$^2$ was calculated for breeders on the Burn of Sorrow, the only upland burn considered. The indications were that the reduction in river width was insufficient to account for differences in territory size and that birds on upland streams occupied larger, and not just longer, territories. Territory size is often inversely related to resource abundance (Enoksson and Nilsson 1983; Gill and Wolf 1975; Ormerod *et al.* 1985; Vickery 1991), and in this respect, these findings parallel conditions on acid streams, where the lower prey availability means that birds persist only by utilising more dispersed resources and by covering greater distances to find sufficient food for breeding activities (O'Halloran *et al.* 1990). Birds on acid rivers also lay consistently later than those on circum-neutral streams (Ormerod *et al.* 1985, 1986; Vickery 1991).

Habitat trends in resource abundance may be strengthened further by differences in prey availability associated with riparian vegetation. The lowland river invariably held some deciduous fringe, whilst upland streams invariably flowed across open moorland, and a number of studies have shown elevated dipper densities on deciduously lined streams, independently of other habitat features (Logie *et al.* 1996; Ormerod *et al.* 1986, Buckton and Ormerod 1997). The input of deciduous litter as a source of food and shelter is known to be important for many stream insects and tree roost may also help to trap and retain detritus within the stream system (Dobson and Hildrew 1992; Richardson 1991). In some cases, the direct supply of terrestrial prey may also be significant (Mason and MacDonald 1982).

O'Halloran *et al.* (1990) showed that although daily energy expenditure did not differ between habitats, birds on acid streams were forced to devote a greater proportion of the active day to foraging than those on circum-neutral streams. Thus, energetic constraints need not be represented solely in food abundance, and for birds occupying territories including few riffles, maximum prey capture rates may be important, particularly if the time devoted to foraging conflicts with that required for breeding activities. In dippers, for example, the energetic demands of incubation are not significantly lower than at other times of the year (Bryant and Tatner 1988), although Bryan (1996) has shown that with the time required on the nest, incubating females have only 19% of the foraging time available to males (or non-breeders). Such constraints may be particularly important for early breeders like dippers, since the active day is still short at the start of breeding.

The significant advancement in laying date between the first and subsequent years suggests that, at least for females, individual differences in 'quality' in terms of breeding (or other) experience or the ability to exploit resources may also be important components determining the timing of breeding (see Curio 1983, Desrochers 1992 and Saether 1990 for reviews). There is also evidence that in many species young or subordinate birds may be forced to occupy the poorest breeding territories (e.g. Holmes *et al.* 1996; Moller 1991; Newton 1991; Price and Bock 1983), and if, as suggested by Newton (1989a), upland birds were forced to these sites due to their competitive inferiority as juveniles, the roles of individual and territory quality may be non-independent and additive in the delayed laying of birds at many upland nests.

### 5.4.3. Clutch and brood sizes

Studies within Britain and Ireland have recorded mean clutch sizes ranging between 4.78±0.61 (Mean±S.D.) in Wales and 3.40 (S.D. not reported) in Northern Scotland (Hewson 1967; Tyler and Ormerod 1985; see Wilson 1996 for complete listings of mean clutch and brood sizes for European studies). The mean size of first clutches within the Devon, Allan and Teith catchments (Table 5.4), were all amongst the highest recorded within the British Isles, and approximately equal to the mean of 4.63±0.66 recorded on the River Esk (Wilson 1996).

Clutch size has been shown to be positively related to food availability in many species (Hogstedt 1980, 1981; Perrins and Birkhead 1983; see Davies and Lundberg 1985 and Martin 1987 for reviews), although evidence from experimental manipulations of food availability have been equivocal (see Boutin 1990 and Martin 1987 for reviews). Boutin (1990), for example, found an increase in clutch size following the provision of additional food in only 4 of 13 avian studies with laying date. However, at least in part, this may reflect the timing, duration and quality of food supplementation. Evidence for increased production is more convincing comparing the performance of individuals in relation to variation in natural food availability, either between years or habitats (see Martin 1987 for review).

Extensive studies within the UK have shown considerable local variation in the breeding production of dippers, related to water quality and its influence on prey availability. Generally, these effects have reflected stream acidity (Ormerod and Tyler 1987; Vickery 1991, 1992), although additional influences such as organic pollution, organochlorines or mercury may also be important in some instances (Smiddy *et al.* 1995). The large mean clutches reported in this study and from independent and remote studies undertaken in (assumed) high quality circum-neutral habitats throughout the UK suggest that local food availability (or its correlates) provides the most appropriate predictor of clutch size and breeding success (Ormerod and Tyler 1987; Tyler and Ormerod 1985; Vickery 1991, 1992; Wilson 1996; this study). However, some measures of habitat structure may also be important (Ormerod and Tyler 1985; Shaw 1978).

Shaw (1978) suggested that, on average, nests built below 100m tended to contain slightly more eggs than nests at higher altitudes, and brood size tended to increase to a maximum at nests built between 300 and 400m. However, as in this study, Smiddy *et al.* (1995) and Tyler and Ormerod (1985) failed to identify any trends in clutch or brood size in relation to physical habitat structure. Similarly, Tyler and Ormerod (1991) found no evidence of altitudinal effects on the clutch size of grey wagtails nesting along streams in Wales, although laying dates were significantly later at upland sites. Recently, Fargallo and Johnson (1997) and Sanz (1997) have shown similar altitudinal effects on laying dates, although with no effects on clutches size, for pied flycatchers *Ficedula hypoleuca* and blue tits *Parus caeruleus*.

Zang (1981) reported that clutch size in dippers nesting in the Harz mountains of Germany decreased by c.0.2 eggs for every 100m increase in altitude. This finding may be confounded by the effects of laying date, however, and the effect of territory structure on production seems most likely to be apparent through its influence on the timing of breeding and the probability of birds initiating a second clutch. Studies in this, and a number of other species, have shown that the latest breeders are unlikely to attempt repeat breeding within a season (Desrochers 1992; Harvey *et al.* 1985; Kluyver *et al.* 1977; Ormerod and Tyler 1985; Smiddy *et al.* 1995; Smith *et al.* 1988; Thompson 1992; Vickery 1991; Wilson 1996). Desrochers (1992) for example, suggested that juvenile blackbirds fledged fewer young than adults solely because they started breeding, on average, two weeks later, resulting in them raising fewer broods each year.

Each season, lowland birds bred significantly earlier, laid significantly more eggs and hatched more young than upland birds. Similar trends were evident in the numbers of chicks fledged, although these differences were not statistically significant. Nevertheless, the known habitat differences in the frequency of second clutches within this population, suggests that some lowland breeders contributed disproportionately to the total annual fecundity (Figures 5.7 and 5.8) due primarily to their ability to initiate laying early in the season.

### 5.4.4. Age effects on production

Many studies of birds have suggested increased reproductive success with age (see Curio 1983, Saether 1990 for reviews). In passerines, these effects are generally most pronounced between the first and subsequent breeding seasons with adults breeding earlier, laying larger clutches, fledging more young and, in some cases, making a greater number of breeding attempts each season than juveniles (e.g. Bryant 1979, 1989; Dhondt 1987; Desrochers 1992; Nol and Smith 1987; Perrins and McCleery 1985, 1989; Thompson 1992). There is also increasing evidence of senescence tied to age and/or past reproductive effort (see Newton 1995 for review), even within relatively short-lived species, although as yet has only been convincingly demonstrated for a small number of passerine species (great tits, Perrins and Moss 1975; Dhondt 1985, 1987, 1989; blue tits, Dhondt 1987, 1989; collared flycatchers *Ficedula albicollis*, Gustafsson and Part 1990, Part *et al.* 1992; black-capped chickadee, Loery *et al.* 1987).

Evidence of enhanced reproductive success with age (at least between juvenile and adult breeders, Saether 1990), appears to be widespread for passerines, yet within this study, age had no detectable influence on any measure of breeding productivity until fledging. Efteland and Kyllingstad (1984) found that dipper pairs including at least one first year bird laid slightly smaller clutches than those where both were adults, although this difference was not significant. Wilson (1996) found no age effects on clutch size for dippers in Midlothian, although adult breeders tended to fledge more offspring than pairs including at least one first year bird. He attributed this to a greater parental ability of adult birds in raising young. However, similar patterns were not evident within this study, and Ward (1992), for example, found significant correlations between both the clutch size and egg volume (a measure often correlated with hatching success, nestling growth rates and offspring survival probabilities (e.g. Bryant 1978; Lundberg and Vaisanen 1979; Magrath 1992; Martin 1987)) of individual females between years, but no age-effects in either measure. It seems likely, however, that while no significant differences in breeding productivity were apparent for confirmed breeders, including first-year non-breeders (or those failing prior to clutch initiation), important differences in mean reproductive output are still likely to exist between age-classes as a whole (see Chapter 4).

Individual females did initiate laying significantly earlier in the years following their first breeding attempt. The timing of breeding is often an important component of breeding success and individual fitness (Clutton-Brock 1988; Daan *et al.* 1990; Perrins and Birkhead 1983). Its significance within this population is considered in chapter 7.

### 5.4.5. Seasonal patterns in production

As in previous studies of dippers (Shaw 1978; Smiddy *et al.* 1995; Tyler and Ormerod 1985) and many other passerine species (see Crick *et al.* 1993 for review), a seasonal decline in clutch size was evident within the Devon catchment. Clutches laid in May contained fewer eggs, and hatched and fledged fewer chicks than those in March and April. Although both second and replacement clutches were significantly smaller than first clutches, the seasonal trend persisted when restricting the analysis to first attempts, suggesting that the reduction was not due solely to the inclusion of small repeat clutches or second attempts.

Laying dates were significantly related to habitat structure (see above) and it has been suggested that the birds occupying the poorest territories have been competitively excluded to these sites (Newton 1989a). Thus, variation in clutch size could reflect differences in female or territory quality, with low quality individuals or those in poor habitats laying later and producing smaller clutches than those elsewhere (Smith 1993). Recent experimental manipulations of laying date, however, have suggested that differences in individual quality may be insufficient to fully explain variation in clutch size in great tits (Verhulst and Tinbergen 1991) and fledging success in coots *Fulica atra* (Brinkhof *et al.* 1993). Moreover, there were no significant differences in fecundity with age, and thus no indications that differences in laying date between age-classes affected this result. Similar seasonal trends have been shown to remain even after accounting for age in marsh tits *Parus palustris* (Smith 1993) and tree swallows *Tachycineta bicolor* (Stutchbury and Robertson 1988). These findings suggest that the season progression itself may be important (Brinkhof *et al.* 1993; Norris 1993; Verhulst and Tinbergen 1991).

Trends in clutch size may reflect a decline in food availability within a season (Perrins 1965). For tits, this has been suggested in relation to the decline in the availability of caterpillars (Smith 1993; Van Balen 1973), and in dippers this could be tied to the emergence of many aquatic insects (Shaw 1978). Yet, in most passerines variation in female body mass during laying is small relative to the mass of the clutch (Perrins 1970), and Ward (1992) suggested that eggs were formed principally from the food consumed each day in a study of dippers and swallows *Hirundo rustica.* Thus, a seasonal decline in clutch size is unlikely to reflect a scarcity of food at the time of egg formation, since often late breeders are laying at the time when earlier birds are raising chicks, near the presumed peak of food abundance (Perrins 1970; Ormerod *et al.* 1993). Rather, this appears to be tied to the ability of parents to adequately provision nestlings, and be adaptive, since small late clutches produce more surviving offspring than large ones (Perrins 1970). Many species are known to show a seasonal decline in chicks survival (e.g. Kestrel *Falco tinnunculus*, Cave 1968; goldeneye *Bucephala clangula*, Dow and Fredga 1984; song sparrows Hotchachka 1990; great tits, McCleery and Perrins 1989, Verhulst and Tinbergen 1991; sparrowhawks, Newton and Marquis 1984; marsh tits, Smith 1993), and since birds breeding later in the season have less chance of raising young, they start with fewer eggs and each offspring receives proportionately more parental care (e.g. Daan *et al.* 1988).

From studies in upland Wales, Ormerod and Tyler (1991) have suggested that the growth rate of chicks may decline as the season progresses. The low subsequent survival probabilities of these young (Ormerod and Tyler, 1993; Chapter 7) also implies a lower 'value' of young from late broods, particularly if the additional effort involved in raising young late in the season, or under poor conditions, results in some costs to parents, such as delayed moult, poor autumn body condition or reduced survival or future fecundity (Askenmo 1979; Bryant 1991; Daan *et al.* 1996; Ekman 1984; McCleery *et al.* 1996; Tinbergen *et al.* 1985). The importance of chick growth and the timing of fledgling as measures of offspring ‘quality’ within this population form the basis of Chapter 7.

# Chapter 6

# Lifetime reproductive success of dippers

## 6.1. Introduction

Previous chapters have considered mean survival rates, breeding probabilities and seasonal reproductive success (Chapter 4 and 5), the components that combine to determine an individuals breeding lifespan and seasonal fecundity, the two elements of individual lifetime reproductive success. Yet, although of undoubted importance for an understanding of population dynamics, mean rates fail to consider the relative 'fitness' of individuals or the effects of phenotype on breeding success. Within populations, for example, the numbers and 'quality' of offspring raised, both within a season, and across a lifespan, generally varies considerable between breeders, and it has been commonly reported that in many species, a minority of the population raise the majority of the next generation (Clutton-Brock 1988 and Newton 1989b, 1995 for reviews).

Breeding success may be strongly related to both extrinsic and intrinsic factors such as habitat quality (Hogstedt 1981), food availability (Bryant 1975; Korpimaki 1990 a,b; Martin 1989 for review; Ormerod and Tyler 1985; Vickery 1991), age, experience, body size, dominance status and body condition (e.g. Clutton-Brock 1988, Houston and McNamara 1996 and Newton 1989b for reviews). In many species, even from the earliest stages of development, individual traits play an important role in the probability of survival or entry to the breeding population (e.g. Daan *et al.* 1988; Hochachka and Smith 1991; Smith *et al.* 1989; Magrath 1991 for review). And, if breeding status is itself dependent on phenotype, then the breeders may not even be representative of all survivors (Grafen 1988). To attempt to determine and explain differences in the reproductive performance of animals within populations, it is important to assess the factors, conditions and phenotypic traits that influence individual success.

Variation in individual success is unlikely to be adequately described in seasonal studies since they consider only a portion of a breeding lifespan, and often individuals of differing ages.

Whilst comparisons between age-classes may be sufficient to highlight some differences with age (e.g. Dhondt 1989b), if the birds surviving to old age are qualitatively different from others within each cohort, these effects may not be adequately assessed in cross-sectional studies (Newton 1989b; Perrins and McCleery 1985). By placing less emphasis on single breeding attempts, which themselves may simply reflect chance events or current environmental conditions, LRS allows the importance of individual attributes to be assessed more easily (Newton 1989b). Moreover, many recent studies have highlighted the importance of current reproductive effort in determining future fecundity and survival (Gustafsson and Sutherland 1988; McCleery *et al.* 1996; Nur 1984; Reid 1987; Williams 1966). Where reproduction entails some costs, natural selection should favour reductions in current reproductive effort if this increases lifetime success, and increased effort as future breeding opportunities decline (Charnov and Krebs 1974; Pianka and Parker 1975; Williams 1966). In birds, this may be reflected in differences in clutch size or the number of breeding attempts made each year. The compound effect of small seasonal differences in breeding production, may be significant over a lifetime (Newton 1989b), and the full extent of reproductive costs for life-histories, and the components and causes of variance in individual success, can only be assessed by following known birds throughout their lifetimes and comparing the reproductive performance in one season with subsequent success and/or survival (Clutton-Brock 1988; Newton 1989b; Stearns 1976). Lifetime reproductive success (LRS) allows the most complete assessment of individual variation in reproductive performance (Clutton-Brock 1988; Newton 1989b), and provides the best approximation of individual 'fitness' (Kemp 1984).

Although to date, published work on dippers has mainly focused on the average seasonal success within populations (Shaw 1978; Smiddy *et al.* 1995; Tyler and Ormerod 1985; Wilson 1996), the sedentary and conspicuous habits of dippers allow lifetime reproductive success (LRS) be to measured reliably (Chapter 1). Bryant and Newton (1994, 1996) and Newton (1989, 1993) have considered individual survival, recruitment and dominance in relation to age, sex, phenotype and physiology within this population, although a complete synthesis of LRS has yet to be undertaken. Within this chapter, the extent and determinants of variation in reproductive success are examined between individual dippers of each sex. Estimates were made of the proportions of birds failing to reproduce, before considering variation in success between breeders. The importance of some phenotypical and ecological factors are considered as influences on individual LRS.

## 6.2. Methods

### 6.2.1. Individuals included within the analyses

Analyses of lifetime reproductive success are based on dippers of known age fledging between 1979 and 1991 and breeding between 1980 and 1996. Five of these birds (2 males, 3 females) were known to have been alive in the autumn of 1996 and may have had their LRS underestimated. However, accounting for likely over-winter losses, it seems that at least some of these birds will have died before the next breeding season and that their LRS will, therefore, be equal to their production to date. Moreover, although these individuals represent less that 2% all birds included for both sexes, they already represent the upper extremes of LRS and their exclusion would be likely to have a greater influence on the validity of results presented.

### 6.2.2. Components of lifetime reproductive success

Since juvenile dippers (particularly females) are known to move between catchments during post-natal dispersal (Newton 1989a; Tyler *et al.* 1990), it was not possible to assess offspring survival (and hence breeding success) based on local information on recruitment alone. Indeed, the local pre-breeding survival rates estimated for the Devon catchment (Chapter 4) were insufficient to match adult losses (see Chapter 8). Because of this, LRS was initially measured only in terms of success until fledging since few birds ever raised offspring that successfully recruited to the breeding population of the Devon catchment. However, for both sexes, individual lifetime fledgling production was strongly correlated with the lifetime number of young surviving to autumn (Spearman's correlation coefficients $\geq 0.426$, including all breeders; correlation coefficient $\geq 0.378$ including only birds raising at least one fledgling; $p \leq 0.001$ in all cases; Figure 6.1), and Newton (1989a) has suggested that all autumn birds have apparently equal probabilities of surviving to breed. Thus, it seems likely that total fledgling production provided an adequate measure of individual success. The components of success are considered to be lifespan, age at first breeding

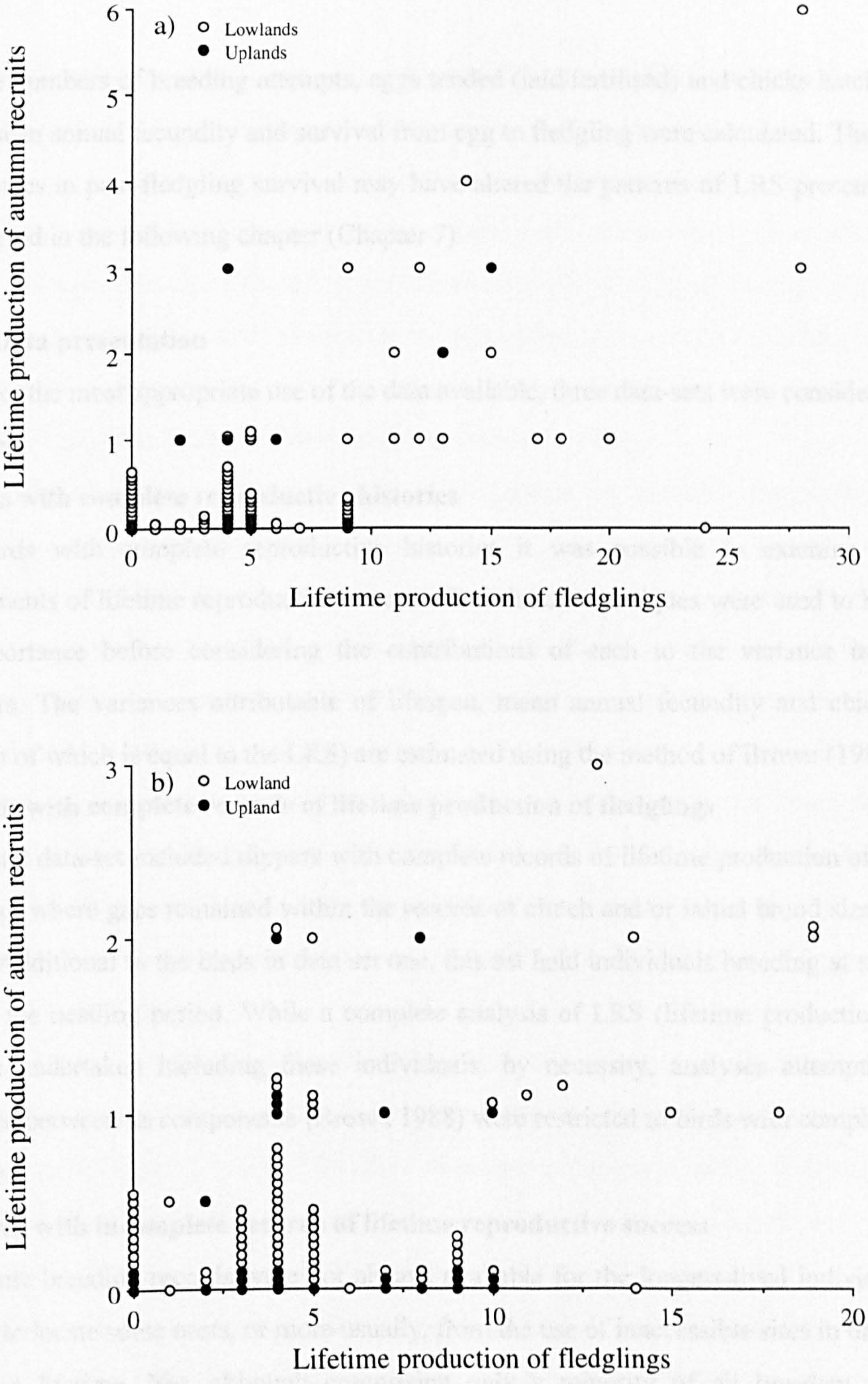


**Figure 6.1.** The relationship between lifetime production of fledglings and lifetime total of autumn recruits for a) male and b) dippers (upland and lowland birds combined). Spearman correlation coefficients ≥0.426, including all breeders; correlation coefficient ≥0.378 including only birds raising at least one fledgling; p≤0.001 in all cases). All analyses exclude birds from the Allan and Teith catchments where juvenile survival could not be adequately assessed.

and the numbers of breeding attempts, eggs tended (laid/fertilised) and chicks hatched. From these data, mean annual fecundity and survival from egg to fledgling were calculated. The possibility that differences in post-fledgling survival may have altered the patterns of LRS presented here will be considered in the following chapter (Chapter 7).

### 6.2.3. Data presentation

To make the most appropriate use of the data available, three data-sets were considered within these analyses;

**i) Birds with complete reproductive histories**

For birds with complete reproductive histories it was possible to examine all (measured) components of lifetime reproductive success. Correlation techniques were used to highlight factors of importance before considering the contributions of each to the variance in LRS between breeders. The variances attributable of lifespan, mean annual fecundity and chick survival (the product of which is equal to the LRS) are estimated using the method of Brown (1988).

**ii) Birds with complete records of lifetime production of fledglings**

A second data-set included dippers with complete records of lifetime production of fledged young, although where gaps remained within the records of clutch and/or initial brood size in one or more years. Additional to the birds in data set one, this set held individuals breeding at sites first located during the nestling period. While a complete analysis of LRS (lifetime production of fledglings) can be undertaken including these individuals, by necessity, analyses attempting to partition variance between its components (Brown 1988) were restricted to birds with complete reproductive histories.

**iii) Birds with incomplete records of lifetime reproductive success**

Complete breeding records were not always available for the longest-lived individuals due to the failure to locate some nests, or more usually, from the use of inaccessible sites in one or more years within a lifetime. Yet, although comprising only a minority of all breeders, these birds are particularly important since, in many cases, they represented the extremes in LRS and could, therefore, help to identify attributes of the most successful individuals. Thus, a final data-set was considered, including some birds with only partial data on LRS. Here, gaps in breeding records were 'filled' for individuals followed for several seasons but with missing data in one or more years. The following additional categories of birds were included within this third data-set;

i) Individuals occasionally breeding at inaccessible nest sites where clutch and brood sizes could not be assessed directly, although observations of birds feeding chicks throughout the nestling period, or parents with recently fledged juveniles, confirmed successful breeding.

ii) Individuals from nests that could not be located, although where parents were later seen on the river with dependent fledglings, confirming successful breeding.

ii) Individuals breeding at inaccessible sites were the nest was known to have fallen, failed or been predated, confirming nesting failure.

iv) Exceptionally, birds known to have bred repeatedly at the same site were allocated to a nest, if the breeder of this sex remained unidentified, and this usual occupant was not recorded breeding elsewhere within that season, but subsequently resighted and, therefore, known to have been alive.

In most cases, birds with gaps in their breeding records were allocated the median annual clutch size, brood size and numbers of fledglings from the population as a whole, although if a pair bred successfully in three or more years median values for that pair were included in the LRS records (see Ward 1992). Birds not recorded breeding in a year, and where all breeders in surrounding territories were identified, were considered to have forgone breeding and raised no young within that season.

It appears unlikely that the use of 'constructed' data led to significant differences between the true and assumed LRS for any individual. Generally, constructed records were only included for birds where the breeding outcome (in terms of success or failure in raising fledglings) was recorded with certainty, and where the majority of lifetime reproductive history was already known. Moreover, the limited variation in brood size at fledging within this population suggests that, for most birds, mean population production and individual success should be closely matched. However, because it remains possible that small differences in seasonal production may accumulate over a lifetime, no attempt was made to reconstruct more than one third of the breeding record of any bird. Accordingly, no individual had the success of more than two attempts estimated over its lifetime.

Analyses including birds with reconstructed histories (data-set iii, and in come cases, ii) are intended only to supplement the results from more complete data-sets and, hence no results will be presented based of these birds alone. All results were thus based on birds with complete records unless this is stated to be otherwise.

### 6.2.4. Body measures

Comparisons of body measures for individuals captured as both juveniles and adults suggested that body mass, wing, keel, tarsus and head&bill lengths and the area of the chestnut breast plumage increased between the first and subsequent years (Paired t-tests, $p \leq 0.084$ in all cases split by sex; $p \leq 0.06$ combining all birds for body size measures; Wilcoxon matched pairs $Z \leq -3.634$, $p \leq 0.003$, $n \geq 85$ for each sex for plumage measures). There was also some indication that the richness of the colour increased for females (Wilcoxon matched pairs $Z=-1.9534$, $p=0.0508$, $n=93$), although not for males (Wilcoxon $Z=-1.1728$, $p=0.2409$, all test results 2-tailed). Consequently, analyses including body measures were repeated including three means for each of these measures; the mean for each bird as a juvenile, the mean as an adult and the mean over an individual's lifetime. As expected, all mean measures were strongly correlated (Pearson's correlation for body size, Spearman's correlation for plumage measures, $p<0.001$ in all cases).

Mean body mass was usually based on autumn measurements since to avoid disturbance, few individuals were captured during spring. In all years, however, a number of previously unringed birds were handled for the first time during breeding. Although body masses are more variable at this time than in autumn, particularly for females (Newton 1989a), no significant differences in mean mass were identified for individuals captured in both seasons (Paired t-test, $p \geq 0.426$, $n \geq 25$ for each sex (analyses restricted to adults to avoid age effects)) and again, spring and autumn masses were strongly correlated (Pearson's correlation coefficient=0.6311, $p<0.001$, $n \geq 25$ adults for each sex).

### 6.2.5. Ecological influences on LRS

Having entered the adult population, ecological and site specific factors seem important in determining some elements of seasonal, and possibly lifetime, reproductive performance (Chapter 5). Lifetime success was therefore examined in relation to habitat type before considering the importance of first year breeding status and site fidelity.

## 6.3. Results

In total, complete reproductive histories (data-set i) were available for 241 birds (116 males and 156 females) with complete records of lifetime production of fledglings (data-set ii) available for a further 13 males and 18 females.

### 6.3.1. Individuals failing to breed

#### i) Birds dying before reaching maturity

Of all chicks fledged between 1985 and 1993, only 10.4-14.5% of males and 6.3-9.2% of females survived locally to breeding age (Chapter 4). Therefore, approximately 85-90% of males and 91-94% of females which were raised within the Devon catchment reared no young on this river through their failure to reach maturity. Including losses prior to fledgling, only c.6.5% of all eggs subsequently lead to breeding adults. In all cases, these figures represent local and hence minimum survival estimates.

#### ii) 'Non-breeders' of reproductive age

With 53% adult survival between 1985 and 1995 and a mean first year breeding probability of c.0.69 within the Devon catchment over this period (Chapter 4), on average, for every 100 birds recorded each spring there were 62.1 breeding adults and 37.9 breeding juveniles, but with a further 26.1 non-breeding first year birds apparently remaining unrecorded. With 53% adult survival (and full breeding at age two) potentially 13.8 of these non-breeders then survived to be recorded breeding in their second year, leaving 12.3 birds to die before the next breeding season. Thus, on average, for every breeder recorded with a lifespan of one year, an estimated 0.41 birds survived to reproductive age but died having made no breeding attempt or an attempt that failed prior to hatching (see Chapter 4). Overall, this was equivalent to 15.6% of all birds reaching maturity. Including birds failing to survive to breeding age, on average only 8.7-12.1% of male and 5.3-7.3% of female fledglings raised locally ever initiated breeding within the Devon catchment.

### 6.3.2. Variation in the lifetime reproductive success of breeders

The percentage frequency of lifetime production of fledglings for male and female dippers surviving to breeding age is displayed on Figure 6.2 (from data-set ii). The most prominent peaks represent lifetime production of zero, with 22.3% of males and 22.1% of females raising no young (11.5 and 10.8% of male and female breeders respectively). Further peaks of 4 and 5, then 8 and 10, represent birds successfully rearing one and two broods respectively. Less than 23% of breeding males and 22% of breeding females fledged more than 10 chicks within their lifetimes.

Breeding dippers fledged between 0-10 young each year with, on average, each pair raising 3.37 young from 1.08 annual breeding attempts. Over a lifetime, male and female breeders raised an average of c.6.8 and 6.1 fledglings from c.2.1 and 2.0 breeding attempts respectively (Tables 6.5 and 6.6), although most birds only ever initiated a single breeding attempt (Table 6.1 and 6.2). There was no evidence that lifespan, seasonal production or LRS differed between the sexes (Mann-Whitney $p \geq 0.333$ in all cases)

The two most successful males with complete reproductive histories each raised 28 fledglings, from 7 and 8 attempts over 5 and 7 years respectively (Table 6.1, Figure 6.2). The most successful female raised 28 fledglings from 7 breeding attempts over 5 years (Table 6.2, Figure 6.2). This bird was known to be alive in the autumn of 1996. For each sex, however, birds with incomplete records were believed to have fledged more chicks over their lifetime. One male fledged an estimated 31 chicks from 9 attempts over 6 years (Table 6.1), whilst a female fledged 32 chicks from 7 attempts over 6 years (Table 6.2). In each case, the number of chicks fledged was only estimated for a single breeding attempt during the lifetime of the bird, and these figures seem likely to represent faithfully the maximum lifetime production over the period of study.

### 6.3.3. Components of LRS for breeders

The correlation matrices for five components of lifetime reproductive success are displayed in Tables 6.3 and 6.4. As expected, for both males and females, the birds fledgling the most young were those tending the greatest number of eggs and hatching the most chicks. This higher production, however, resulted from an increased number of reproductive attempts, either within a season or more usually throughout a lifetime (Figure 6.3), rather than from variation clutch or brood sizes between individuals (Chapter 5).

### 6.3.4. Means and variance of the components of LRS

The mean and variance for three components of LRS (lifespan, mean annual fecundity and egg to fledgling survival) and their two- and three-way products are given in Tables 6.5. and 6.6. For both males and females, the majority of variance in lifetime reproductive success was attributable to differences in total lifespan and offspring survival from egg to fledgling (Tables 6.5b and 6.6b). Lifespan appeared of greatest importance, explaining c.33% and 44% of the overall variance for males and females respectively, with offspring survival accounting for a further 29 and 31%. In agreement with the low variation in clutch size within the population (Chapter 5), differences in fecundity (numbers of eggs laid/fertilised per season) appeared rather less important, accounting for only 19% and 14% of the overall variation for males and females breeders. As expected within a generally monogamous population, the number of eggs tended within a season was approximately equal for each sex, although both mean fecundity and its variance were slightly higher for males, possibly reflecting the greater annual production of a few polygynous birds (Tables 6.5a and 6.6a). For both sexes, the two- and three-way interaction terms accounted for comparatively little of the total variance (Tables 6.5b and 6.6b).

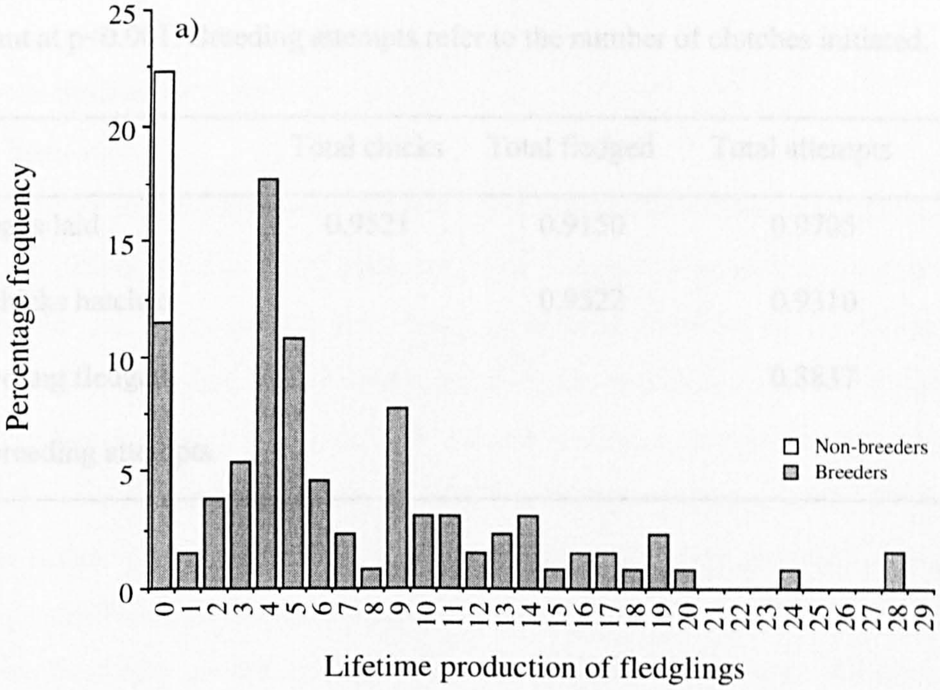
Slightly less than 85% of the overall variance in LRS was attributable to breeders for both sexes (Tables 6.5c and 6.6c), although as discussed later, this proportion is likely to vary between cohorts.

**Table 6.1.** Lifetime reproductive success of breeding male dippers. All figures were calculated for birds with complete reproductive histories, except 'corrected' maxima which were calculated including some birds with constructed data in one or more years (see section 5.2.3).

| | Min | Mode | Max | Corrected max | Mean±S.D. |
|---|---|---|---|---|---|
| Total eggs fertilised | 3 | 5 | 36 | 43 | 8.81±6.28 |
| Total chicks hatched | 0 | 4 | 30 | 35 | 7.25±5.75 |
| Total young fledged | 0 | 4 | 28 | 31 | 6.29±5.76 |
| Total breeding attempts | 1 | 1 | 8 | 9 | 1.97±1.23 |
| Lifespan (years) | 1 | 1 | 7 | 7 | 2.25±1.23 |
| Variance in fledgling success | 0.839 | | | | |

**Table 6.2.** Lifetime reproductive success of breeding female dippers. All figures were calculated for birds with complete reproductive histories, except 'corrected' maxima which were calculated including some birds with constructed data in one or more years (see section 5.2.3.).

| | Min | Mode | Max | Corrected max | Mean±S.D. |
|---|---|---|---|---|---|
| Total eggs laid | 3 | 5 | 31 | 36 | 8.67±5.92 |
| Total chicks hatched | 0 | 4 | 28 | 32 | 6.90±5.92 |
| Total young fledged | 0 | 4 | 28 | 32 | 5.96±5.35 |
| Total breeding attempts | 1 | 1 | 8 | 8 | 2.15±1.19 |
| Lifespan (years) | 1 | 1 | 6 | 7 | 1.90±1.31 |
| Variance in fledgling success | 0.806 | | | | |



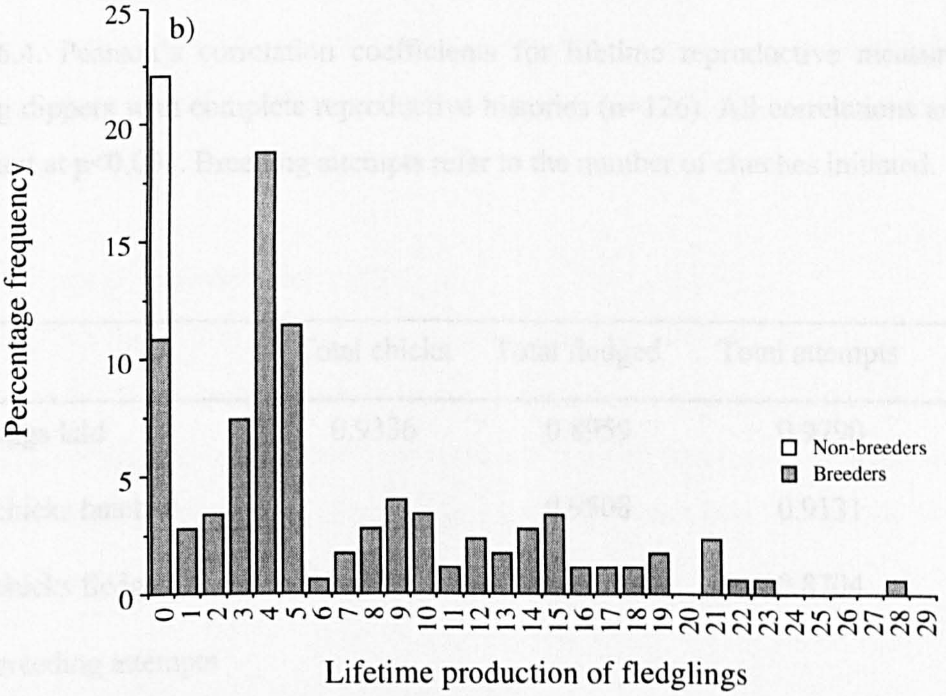


**Figure 6.2.** The percentage frequency of lifetime production of fledglings for a) male and b) female dippers surviving to maturity.

**Table 6.3.** Pearson's correlation coefficients for lifetime reproductive measures in male breeding dippers with complete reproductive histories (n=84). All correlations are statistically significant at p<0.001. Breeding attempts refer to the number of clutches initiated.

| | Total chicks | Total fledged | Total attempts | Lifespan |
|---|---|---|---|---|
| Total eggs laid | 0.9521 | 0.9150 | 0.9705 | 0.7500 |
| Total chicks hatched | | 0.9522 | 0.9310 | 0.7182 |
| Total young fledged | | | 0.8837 | 0.6592 |
| Total breeding attempts | | | | 0.7435 |

**Table 6.4.** Pearson's correlation coefficients for lifetime reproductive measures in female breeding dippers with complete reproductive histories (n=126). All correlations are statistically significant at p<0.001. Breeding attempts refer to the number of clutches initiated.

| | Total chicks | Total fledged | Total attempts | Lifespan |
|---|---|---|---|---|
| Total eggs laid | 0.9336 | 0.8959 | 0.9790 | 0.7375 |
| Total chicks hatched | | 0.9508 | 0.9131 | 0.7106 |
| Total chicks fledged | | | 0.8704 | 0.6690 |
| Total breeding attempts | | | | 0.7512 |

### 6.3.5. Determinants of LRS

#### 6.3.5.1. Body size

Few significant relationships were evident using either simple and quadratic regression, between lifespan or lifetime production of eggs, chicks or fledged young and any measure of body size. In all cases, the use of mean first year, adult or lifetime measures or the inclusion of birds with reconstructed data in some years had little effect on the statistical significance of these results.

For females, there was an indication that a quadratic function fitted to adult mass explained some of the variation in the numbers of breeding attempts and eggs laid ($r^2 \leq 0.08$, $p \leq 0.045$; Figure 6.4). For males, a quadratic function on mean first year mass provided a significant fit to the lifetime production of fledglings ($r^2 = 0.08$, $p = 0.040$; Figure 6.5). In all cases, the body size measures accounted for little of the overall variation between individuals, however, and Bonferroni adjustment of critical probabilities suggested that no measure of body size significantly predicted any component of LRS for either sex.

For birds surviving into their second year (i.e. those known to have been alive during the breeding season), there were no consistent differences in any body measure relative to first year breeding status (t-test for differences in body size between first-year breeders and non-breeders, $p \geq 0.114$, $n \geq 56$ in all cases for each sexes).

#### 6.3.5.2. Plumage variation and LRS

There were no significant relationships between plumage area or intensity and LRS, or any of its components for either male or female breeders (Spearman's correlation $p \geq 0.165$, $n \geq 63$ for females; $p \geq 0.423$, $n \geq 61$ for males). Similarly, for birds surviving to two years, no differences were apparent in either plumage measure relative to first year breeding status (Mann-Whitney $U \leq 332.0$, $p \geq 0.3114$, $n \geq 58$ for females; $U \leq 403$, $p \geq 0.3018$, $n \geq 63$ for males).

#### 6.3.5.3. Cohort effects and age of first breeding

Analyses entering LRS (after $\log_{10}$ transformation), total lifespan, cohort and age of first breeding into a General Linear Model confirmed the importance of breeding lifespan on LRS, including total

**Table 6.5.** Mean and variance of the components of lifetime reproductive success in male dippers.

a) Mean and variance of lifespan (L), Fecundity (eggs fertilised per year, F) and egg survival to fledging (S) and their products for male dippers

| | Original | | |
|---|---|---|---|
| | Mean | Variance | Standardised variance |
| L | 2.1064 | 1.4780 | 0.3331 |
| F | 4.6757 | 3.0371 | 0.1586 |
| S | 0.6943 | 0.1178 | 0.2445 |
| LF | 8.8507 | 41.5339 | 0.4889 |
| LS | 1.5236 | 1.3387 | 0.6260 |
| FS | 3.0183 | 3.5286 | 0.3823 |
| LFS | 6.8576 | 34.0876 | 0.8325 |

b) Percentage contributions to variation in lifetime reproductive success ($V(LFS)/(LFS)^2$) among female breeding dippers.

| | L | F | S |
|---|---|---|---|
| L | 40.02 | | |
| F | -0.34 | 19.05 | |
| S | 5.81 | -2.49 | 29.37 |
| LFS | 8.59 | | |

c) Inclusion of non-breeders

| | |
|---|---|
| Proportion of breeders | 0.855 |
| Overall variance | 34.31 |
| Percentage of variance due to non-breeders | 15.24 |
| Percentage of variance due to breeders | 84.76 |

**Table 6.6.** Mean and variance of the components of lifetime reproductive success in female dippers.

a) Mean and variance of lifespan (L), Fecundity (eggs laid per year, F) and egg survival to fledging (S) and their product for female dippers.

| | Original | | |
|---|---|---|---|
| | Mean | Variance | Standardised variance |
| L | 1.9915 | 1.3473 | 0.3397 |
| F | 4.4557 | 2.3225 | 0.1071 |
| S | 0.6576 | 0.1099 | 0.2408 |
| LF | 9.0165 | 37.6225 | 0.4376 |
| LS | 1.4057 | 1.1922 | 0.6586 |
| FS | 3.1233 | 3.4966 | 0.3534 |
| LFS | 6.1479 | 30.2497 | 0.7709 |

b) Percentage contributions to variation in lifetime reproductive success ($V(LFS)/(LFS)^2$) among female breeding dippers.

| | L | F | S |
|---|---|---|---|
| L | 44.07 | | |
| F | -1.20 | 13.90 | |
| S | 10.11 | 0.70 | 31.24 |
| LFS | 1.17 | | |

c) Inclusion of non-breeders

| | |
|---|---|
| Proportion of breeders | 0.855 |
| Overall variance | 30.86 |
| Percentage of variance due to non-breeders | 16.30 |
| Percentage of variance due to breeders | 83.70 |

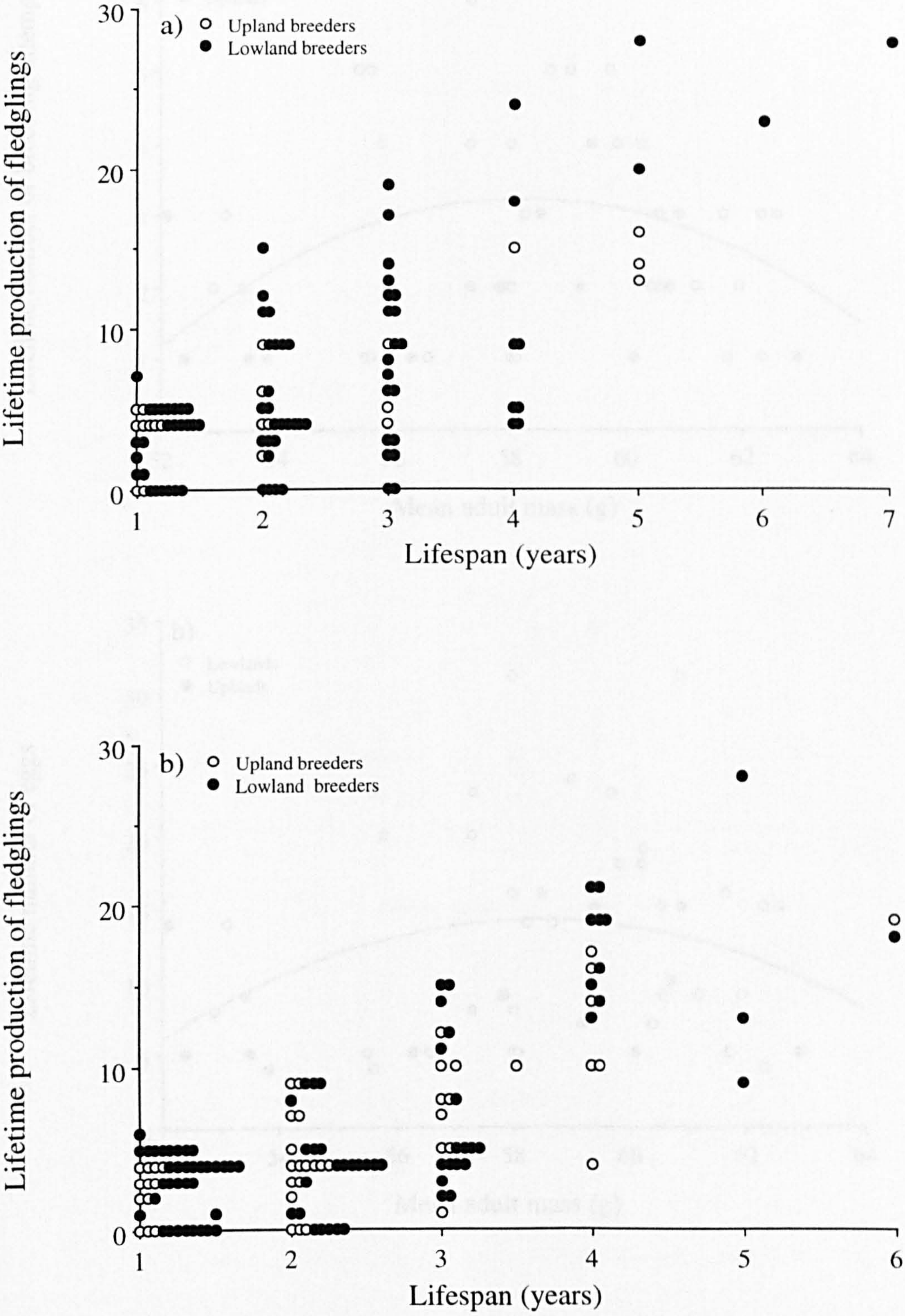


**Figure 6.3** The relationships between lifetime production of fledglings (LRS) and lifespan for a) male and b) female dippers. For males LRS=3.08**Lifespan*-0.605, n=107, p<0.001; for females LRS=2.95**Lifespan*-0.546, n=137, p<0.001 (upland and lowland birds combined in each case).

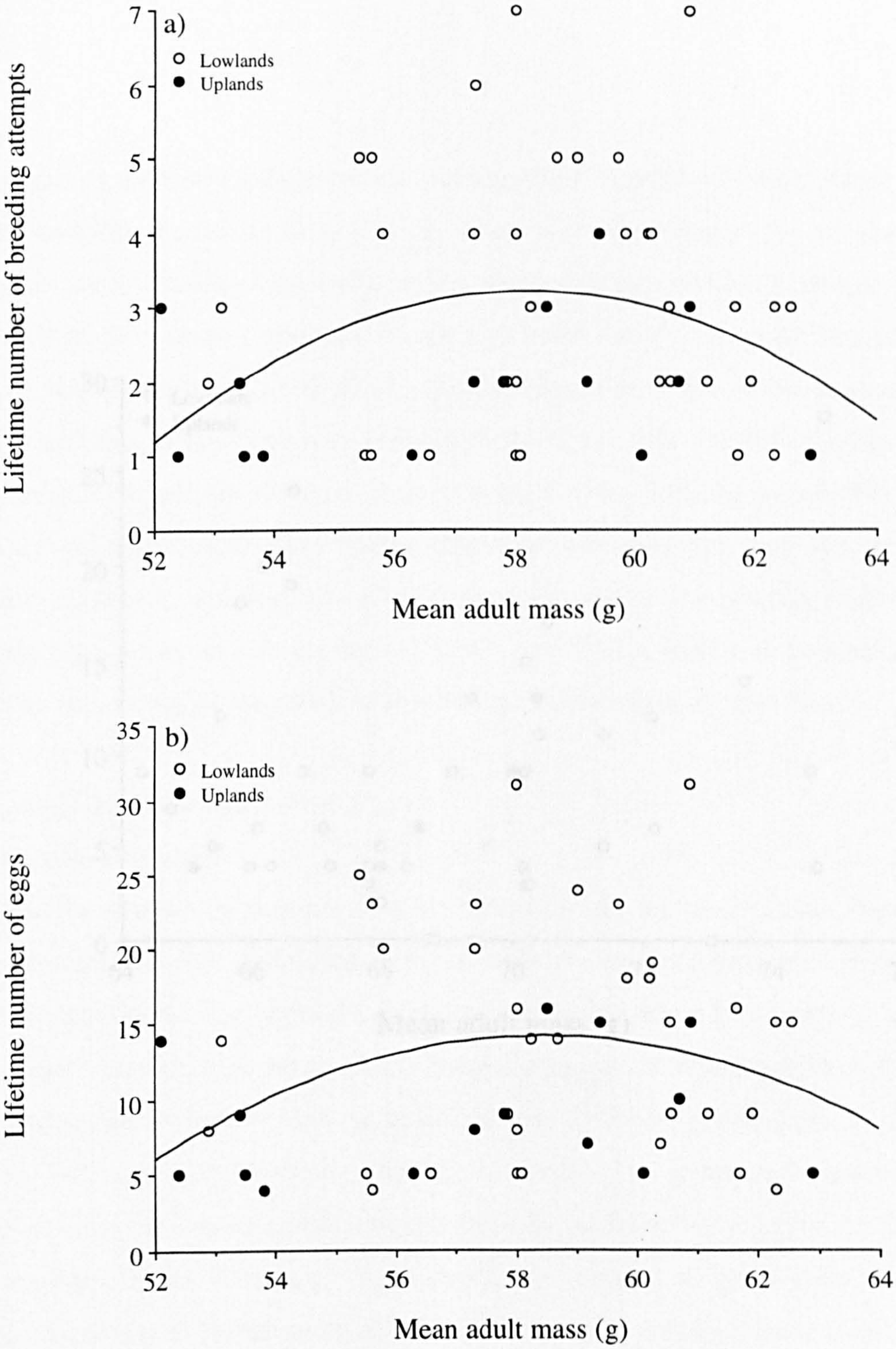


**Figure 6.4.** The relationship between mean adult mass (g) and a) lifetime number of breeding attempts and b) lifetime number of eggs laid, for female dippers (upland and lowland birds combined in each case). Lifetime attempts=-175.32+6.132*Mass*-0.0526*Mass*$^2$, $r^2$=0.085, p=0.042, n=54. Lifetime eggs= -655.43+22.917*Mass*-0.196*Mass*$^2$, $r^2$=0.075, p=0.045, n=54.

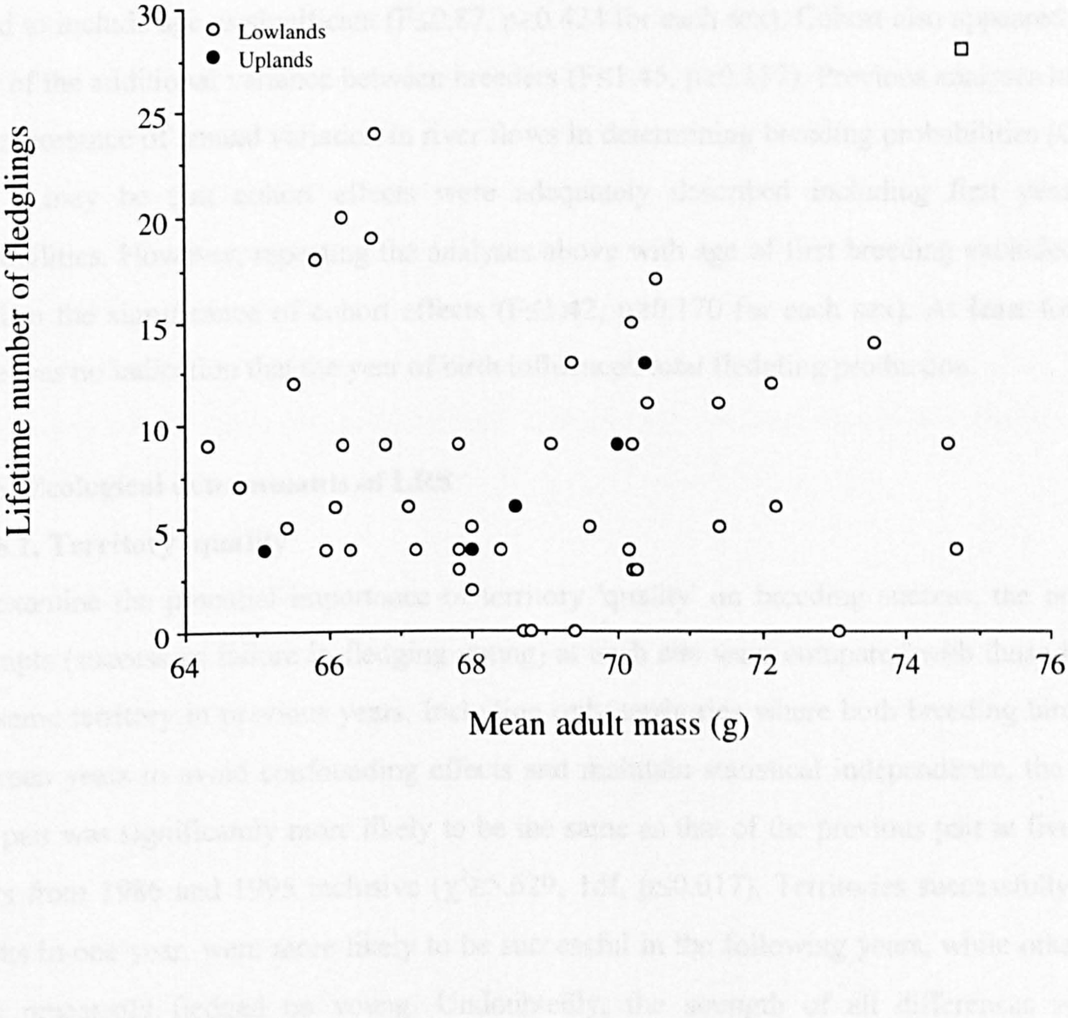


**Figure 6.5.** The relationship between mean adult mass (g) and lifetime number of fledglings for male dippers (upland and lowland birds combined). Lifetime fledglings=1157.0-33.132*Mass*+0.239*Mass*$^2$, $r^2$=0.085, p=0.042, n=48 including all birds;

Lifetime fledglings=3.88.07-10.822*Mass*+7.685*Mass*$^2$, $r^2$=0.018, p=0.198, n=47 excluding the single outlying lowland male (denoted by the open square).

lifespan ($F \geq 19.71$, $p<0.001$) and age of first breeding ($F \geq 2.75$, $p \leq 0.046$) as significant components of lifetime fledgling production for both sexes. There was no evidence, however, that age of first breeding had any influence of lifetime fledgling production that was not explained by breeding, rather than total, lifespan (see result above). General linear models with these two factors entered failed to include age as significant ($F \leq 0.87$, $p \geq 0.424$ for each sex). Cohort also appeared to explain little of the additional variance between breeders ($F \leq 1.45$, $p \geq 0.157$). Previous analyses have shown the importance of annual variation in river flows in determining breeding probabilities (Chapter 4), and it may be that cohort effects were adequately described including first year breeding probabilities. However, repeating the analyses above with age of first breeding excluded, failed to confirm the significance of cohort effects ($F \leq 1.42$, $p \geq 0.170$ for each sex). At least for breeders, there was no indication that the year of birth influenced total fledgling production.

### 6.3.6. Ecological determinants of LRS

#### 6.3.6.1. Territory 'quality'

To examine the potential importance of territory 'quality' on breeding success, the outcomes of attempts (success or failure in fledging young) at each site were compared with those for birds in the same territory in previous years. Including only territories where both breeding birds changed between years to avoid confounding effects and maintain statistical independence, the success of any pair was significantly more likely to be the same as that of the previous pair in five of the ten years from 1986 and 1995 inclusive ($\chi^2 \geq 5.629$, 1df, $p \leq 0.017$). Territories successfully 'fledgling' chicks in one year, were more likely to be successful in the following years, while other occupied sites repeatedly fledged no young. Undoubtedly, the strength of all differences would have increased markedly with the inclusion of 'territories' repeatedly left vacant and hence 'fledging' no chicks. In practice, the consistency of success is likely to be underestimated even for occupied sites, since if the same birds remained at the same site they were excluded to maintain independence. They too tended to have the same breeding outcome (success or failure) in one year as in the previous season ($\chi^2 \geq 14.94$, 1df, $n \geq 56$, $p \leq 0.002$ for each sex, based only on first two attempts of each bird to avoid pseudo-replication (Hulbert 1984)).

#### 6.3.6.2. Site fidelity

For birds breeding in the same territory in two consecutive years, there was no significant difference in the numbers of chicks fledged in the first and second years of site occupation (Wilcoxon matched pairs, $Z \geq -0.8769$, $p \geq 0.2016$, $n \geq 44$ for each sex). Breeders changing territories, however, were significantly more likely to be successful in the year following the territory shift (Wilcoxon matched pairs $Z \leq -1.8681$, $p \leq 0.0617$, $n \geq 56$ for each sex). Yet, birds that remained within the same breeding territory throughout their lifetime, had significantly greater LRS than those making a comparable number of breeding attempts but moving between years (Mann-Whitney $p \leq 0.05$, $n \geq 43$, for birds breeding in two and three years). It seems likely that this result reflects a greater probability of unsuccessful breeding in the year before a territory shift. Only 10% of all birds that remained within the same territory failed to raise at least one chick in the previous year, compared to 24% of those birds making territory movements (Table 6.7).

#### 6.3.6.3. Upland and lowland breeders

For both sexes, lowland birds tended to make more breeding attempts, lay more eggs, hatch more chicks and fledge more young than those breeding at upland sites. In no case, however, were these differences statistically significant (Tables 6.9 and 6.10).

## 6.4. Discussion

### 6.4.1. Birds failing to enter the breeding population

From the population survival and breeding records (Chapters 4 and 5), it was clear that the vast majority of all fledglings raised in any single year produced no surviving offspring themselves. This resulted from exclusions from breeding (Chapter 4), possibly the inability of some birds to locate a mate (c.f. Arcese *et al.* 1992; Bulmer and Perrins 1973; Newton 1986), from unsuccessful breeding attempts or, most usually, from the failure of fledglings to survive to reproductive maturity. With offspring survival from egg to fledgling at c.65% (See Tables 6.5a and 6.6a and

**Table 6.7.** Percentage frequencies of chicks fledged in the first year for birds followed over two consecutive breeding seasons. 'Changed' refers to birds moving territories between years, 'remained' refers to birds breeding at the same site in both years (n=220, based on all birds followed in two consecutive years, not only those included within the LRS analyses).

| Chicks fledged | Remained | Changed |
|---|---|---|
| 0 | 10.0 | 24.6 |
| 1 | 3.2 | 0.0 |
| 2 | 5.9 | 4.9 |
| 3 | 16.4 | 22.1 |
| 4 | 30.0 | 23.8 |
| 5 | 30.0 | 23.8 |
| 6 | 4.5 | 0.8 |
| Total successful | 90.0 | 75.4 |

**Table 6.8.** Mean numbers of chicks fledged each year for birds followed over two consecutive breeding seasons. 'Changed' refers to birds moving territories between years, 'remained' refers to birds breeding at the same site in both years (n=220, based on all birds followed in two consecutive years, not only those included within the LRS analyses). Significance refers to the results of Kruskal-Wallis tests between groups.

| Chicks fledged | Changed | Remained |
|---|---|---|
| First year | 2.95±1.88 | 3.61±1.62 |
| Second year | 3.46±1.92 | 3.38±1.74 |
| Significance | p=0.029 | p=0.110 |

**Table 6.9.** Comparison of lifetime reproductive success and its components for upland and lowland breeding male dippers. Significance refers to result of Mann-Whitney U test between groups.

| | Uplands (n=28) | Lowlands (n=75) | Significance |
|---|---|---|---|
| Lifespan | 2.07±1.35 | 2.29±1.19 | p=0.091 |
| Attempts | 1.82±1.19 | 2.26±1.63 | p=0.171 |
| Eggs laid | 8.18±5.73 | 10.28±7.47 | p=0.092 |
| Chicks hatched | 7.00±5.84 | 8.54±6.73 | p=0.151 |
| Chicks fledged | 6.54±5.30 | 7.41±6.76 | p=0.531 |

**Table 6.10.** Comparison of lifetime reproductive success and its components for upland and lowland breeding female dippers. Significance refers to result of Mann-Whitney U test between groups.

| Females | Uplands (n=53) | Lowlands (n=85) | Significance |
|---|---|---|---|
| Lifespan | 2.23±1.12 | 2.11±1.22 | p=0.606 |
| Attempts | 1.70±0.99 | 2.33±1.74 | p=0.166 |
| Eggs laid | 7.98±4.68 | 10.62±7.80 | p=0.321 |
| Chicks hatched | 6.38±4.47 | 8.63±7.13 | p=0.515 |
| Chicks fledged | 5.55±4.23 | 7.60±7.09 | p=0.338 |

Chapter 5), less than 6.5% of all eggs laid locally ever produced breeding adults within the Devon catchment.

The pre-breeding survival rates of c.10-15% for male and c.6-9% for female fledglings were consistent with those reported for dipper populations elsewhere (Clobert *et al.* 1990; Hewson 1969; Galbraith and Tyler 1982; Moss 1975; Price and Bock 1983), although the figures only represent local survival estimates. Predictions for the Devon catchment suggest that for both sexes, c.25% first-year survival would maintain the population with current levels of production and adult mortality (Chapter 8). With 25% of fledglings reaching maturity and accounting for the probabilities of an individual breeding in its first year, and of this, or any subsequently attempt, being successful, an estimated 16% of fledglings would be expected to raise young within their lifetime, either in the Devon catchment or elsewhere. If immigration and emigration are matched and similar processes to those within the Devon catchment operated on adjacent rivers, slightly less than one out of every ten eggs or one of every six fledglings would lead to a successfully reproducing adult. These figures may be subject to some error since adjacent catchments elsewhere are known to show contrasting population patterns (Ormerod and Tyler 1994). Indeed, the River Devon appears to represent 'prime' habitat (Logie 1995; Logie *et al.* 1996), and may be more productive than some surrounding sites (see Battarbee 1992, 1993; Logie *et al.* 1996; Ormerod and Tyler 1993; Vickery 1991). Nevertheless, the indications were that, on average, only every second clutch produced a fledgling that eventually survived to breed itself. With most breeders only making a single attempt within their lifetime (Tables 6.1 and 6.2), at least half of all breeders seem to raise no offspring that survive to breed. The highly skewed lifetime production figures suggest that others are likely to contribute disproportionately to future generations (Figures 6.2 and 6.3).

### 6.4.2. Components of LRS for breeders

For breeding birds, lifespan has been identified as the principal component of LRS in all studies to date where lifetime production of fledglings has been taken as the measure of individual success (Clutton-Brock 1988; Newton 1989b). Its importance is obvious, since together with age specific breeding probabilities, it determines the number of breeding opportunities available to each individual. Less that 6% of all breeding attempts involved polygynous males, and less than 8% of all pairs attempted to raise a second brood year. Consequently, more than 87% of all breeding attempts involved monogamous, single brooded birds, and breeding lifespan largely determined the number of breeding attempts initiated. Similar patterns have been reported for a variety of species (Bryant 1989; Coulson and Thomas 1985; Hotker 1989; Newton 1985), although in contrast so some studies (e.g. Bryant 1979, 1989; Dhondt 1989; Holmes *et al.* 1996; Newton 1991; Saether 1990 for review; Thompson 1992) there was no indication that older individuals gained a disproportionate advantage through increased seasonal production with age (see section 6.3.5.3 and Chapter 5). Reflecting the limited variation in clutch and brood sizes within the population (Chapter 5), differences in individual fecundity accounted for little of the variation in the lifetime fledgling production (Tables 6.5b and 6.6b).

### 6.4.3. Sex Differences in LRS

The breeding population of the River Devon was predominantly monogamous and showed no sex differences in survival or breeding probabilities (Chapters 4 and 5). Consequently, LRS and its components were approximately equal for each sex. Mean lifespan, annual fecundity and chick survival all appeared higher for males than females, the combined effect being that male dippers, on average, raised c.0.71 more chicks during their lifetime than females (Tables 6.5a and 6.6a), although none of these differences was statistically significant. The fact that all differences pointed to males being slightly more successful may reflect, in part, the increased seasonal production of the small number of polygynous males, although more likely, it arises from the tendency for more males than females to remain undetected at nests failing early. If these birds were in their first year and died before the next breeding season, they would not enter the LRS calculations. Consequently, the proportion of males with short lifespans and zero LRS may be underestimated slightly.

### 6.4.4. Age of first breeding

Approximately 15% of the overall variance in LRS for both male and female dippers of reproductive age appeared to be attributable to the non-breeders. Of all birds surviving to maturity but raising no young, approximately half did so through their failure to breed in their first year and their subsequent death before the next breeding season. Although age-specific breeding probabilities still remain poorly studied in many species, the mean first-year breeding probability of 69% estimated in this study is consistent with that obtained for a dipper population in north-eastern France (Clobert *et al.* 1990) and with those obtained for some other passerines species. Clobert *et al.* (1990) estimated that c.40% of first-year dippers failed to breed in 'normal' years, although the non-breeding fraction was often smaller if severe winter floods created additional breeding opportunities through elevated adult mortality. Dhondt (1989) suggested that c.16-18% of blue tits failed to breed as juveniles, whilst Clobert *et al.* (1993) estimated that c.42% of great tits raised no young in their first year. Thompson (1992) suggested that approximately one third of swallows failed to breed as juveniles.

There was no evidence that juvenile non-breeders surviving into their second year and beyond, compensated for their 'lost' first year production by fledging more chicks than other breeders in the following years. No differences were detected in later years in mean clutch size, brood size or numbers of chicks fledged between birds of different first year breeding status (Mann Whitney $U \leq 977.0$, $p \geq 0.575$, $n \geq 79$ for each sex in second year; $U \leq 147.5$, $p \geq 0.2641$, $n \geq 38$ for third year birds). As noted above, age had no effect on LRS that was attributable in breeding lifespan. Thus, on average, individuals making the same numbers of breeding attempts raised the same numbers of chicks, independently of their age at first breeding. Consequently, failure to breed as a juvenile lead to a reduced lifetime production of fledglings relative to first-year breeders with similar lifespans.

If current reproductive effort was traded against future survival and hence first-year non-breeders had longer lifespans (Bryant 1979; Linden and Moller 1989; McCleery *et al.* 1996), birds failing to breed as juveniles may still have raised a comparable number of young to first-year breeders. However, likelihood ratio testing within SURGE indicated that having entered the breeding population, birds first breeding as juveniles did not have significantly different survival or recapture (breeding) probabilities from birds breeding for the first time as adults (Comparisons between Groups 2 and 3; Survival, $\chi^2_{19}=14.88$, $p=0.730$, Table 4.2; Recapture, $\chi^2_6=2.88$, $p=0.824$,

Table 4.3; Chapter 4). Indeed, results from dipper populations elsewhere have suggested that some non-breeding or unsuccessful juveniles may have significantly lower survival probabilities than breeders of an equivalent age (Marzolin in prep.). If non-breeders are qualitatively inferior to breeders and/or relegated to low quality territories, survival need not be correlated negatively with breeding success (Hogstedt 1980, 1981; Matthysen 1990; Newton 1989c; Partridge and Harvey 1985).

### 6.4.5. Cohort effects

Although the age of first breeding was an important component of LRS (Section 6.3.5.3) and first year breeding probabilities were known to differ significantly between years (Chapter 4), General Linear Modelling provided no evidence of significant inter-cohort variation in lifetime fledgling production (section 6.3.5.3). Such analyses may not address the full extend of cohort difference, however, since the very birds that were most strongly affected i.e. non-breeders, were not considered unless they survived to breed in later years (Grafen 1988). Clearly, breeders as a group have some opportunity to raise young whereas non-breeders, by definition, do not.

To illustrate the potential importance of cohort differences for 'average' individuals, the probability of any chick fledged raised between 1985 and 1993 surviving on breed successfully within the Devon catchment was estimated. This was calculated as the product of four components; the probabilities of surviving to maturity, of breeding as a juvenile, of any breeding attempt subsequently leading to fledged young and of then surviving to breed again (from Chapters 4 and 5). From these figures (Figure 6.6a), it is clear that the probability of any fledgling breeding successful in its first year differed markedly between cohorts (Chapter 4). The differences were due partly to annual variation in first-year survival, although the main contributing factor appeared to be the probability of birds making a (successful) breeding attempt as juveniles (Chapter 4). Indeed, in spite of losses between breeding seasons, with full breeding at age two, birds from some cohorts were more likely to raise young in their second year than they were as juveniles. This was particularly apparent for cohorts such as 1990, where birds survived relatively well in their first winter although first-year breeding probabilities were low. For all birds, however, the probability of

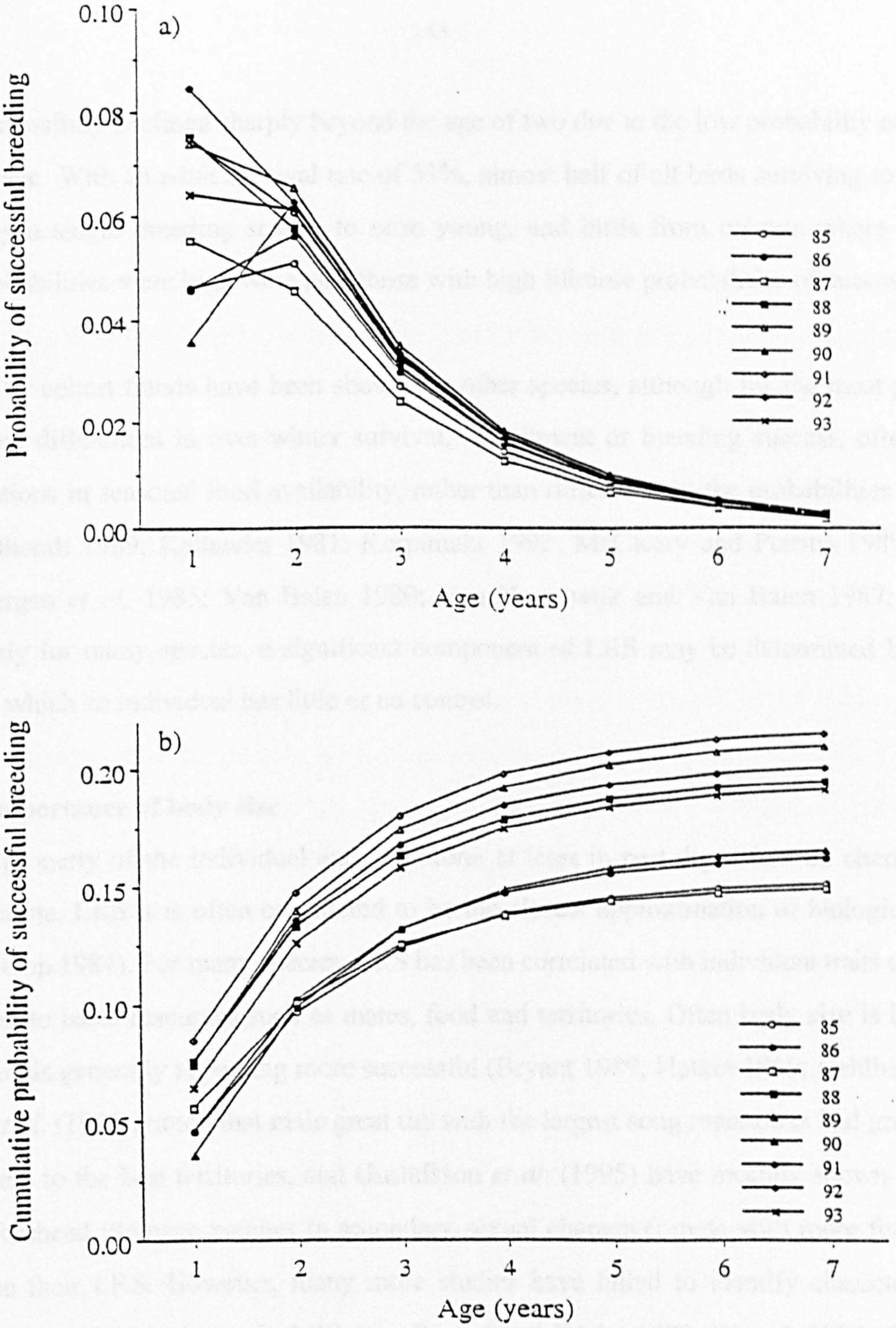


Figure 6.6 The seasonal (a) and cumulative probabilities (b) of male fledglings raised between 1985 and 1993 surviving to breed successfully within the Devon catchment. Figures are calculated from the final model of Chapter 4, assuming constant post-fledgling and adult survival. Juvenile over-winter survival is dependent on the lowland population density and first-year breeding probabilities are dependent on peak march river flows. Breeding success is considered constant at 81% (Chapter 5) to allow cohorts with incomplete data to be included (e.g. data were only available for three years of the potential lifespan of birds raised in 1993). Trends for females parallel those for males, although for all cohorts the probabilities of females surviving to breed successfully are significantly reduced due to their lower local post-fledgling survival.

breeding successfully declined sharply beyond the age of two due to the low probability of survival beyond this age. With an adult survival rate of 53%, almost half of all birds surviving to breeding age had only a single breeding season to raise young, and birds from cohorts where first-year breeding probabilities were high were also those with high lifetime probabilities of success (Figure 6.6.b).

Similar cohort trends have been shown for other species, although for the most part, they have reflected differences in over-winter survival, recruitment or breeding success, often tied to annual variations in seasonal food availability, rather than difference in the probabilities of clutch initiation (Dhondt 1989; Kallander 1981; Korpimaki 1992; McCleery and Perrins 1989; Perrins 1965; Tinbergen *et al.* 1985; Van Balen 1980; Van Noordwijk and Van Balen 1987; Verhulst 1992). Clearly for many species, a significant component of LRS may be determined by chance events, over which an individual has little or no control.

### 6.4.6. The importance of body size

Although a property of the individual and, therefore, at least in part dependent on chance events within a lifetime, LRS it is often considered to be the closest approximation of biological fitness available (Kemp 1984). For many species, LRS has been correlated with individual traits that play a role in access to basic resources such as mates, food and territories. Often body size is important, with larger birds generally appearing more successful (Bryant 1989; Hotker 1989; Gehlbach 1989). McGregor *et al.* (1981), noted that male great tits with the largest song repertoires had greater LRS through access to the best territories, and Gustafsson *et al.* (1995) have recently shown the males with large forehead plumage patches (a secondary sexual character) mate with more females and thus increase their LRS. However, many more studies have failed to identify characteristics of individuals that explain variation in LRS (e.g. Bunzel and Druke 1989; Dhondt 1989; Gustafsson 1989; McCleery and Perrins 1989), and even where important individual traits have been identified, often their advantage has been weak or inconsistent (Bryant 1989; Hotker 1989).

This study failed to identify any traits that appeared to confer 'fitness' or enhance success, although some individuals raised many more young than others. Clearly, by considering only breeding birds in this study many opportunities for selection have already been overlooked (e.g. Price and Grant 1984). Birds surviving to maturity make up only a subset of the young fledged the previous year (and fledglings a subset of all eggs fertilised) and, if entry to the breeding population is itself dependent of individual status or phenotype, breeders then may not even be representative of all survivors (Grafen 1988). Daan *et al.* (1988), for example, have suggested that the reproductive value of European Kestrel chicks may decrease through the season since, even within survivors, late fledged chicks have reduced chances of breeding in their first year. Moreover, traits appearing beneficial at one point in the lifecycle, or under certain conditions, may be detrimental at other times (Bryant and Jones 1995; Price and Grant 1984; Smith 1988). Bryant and Jones (1995), for example, noted that large size enhanced reproductive success in male sand-martins, although over-winter mortality was greater for these birds during a period of drought. Within this population of dippers, Bryant and Newton (1996) showed that the annual survival of juvenile males was negatively related to their dominance the previous autumn, even though it seems likely that, for dominants, priority access to basic resources would confer some net fitness benefits over subordinates. If territory acquisition, status or other possible influences on LRS, are determined by attributes that have little to do with physical traits, correlations between breeding success and phenotype may not be evident. An obvious example may be the importance of the timing of post-fledgling settlement on subsequent survival or breeding success (e.g. Daan *et al.* 1988; Newton 1989a; Nilsson and Smith 1988).

Newton (1989, 1993) suggested that males in better autumn 'condition' (as judged from pectoral muscle thickness) may have been more likely to survive over-winter. However, he failed to identify any phenotypic traits influencing recruitment probabilities in a strong or consistent manner. Similarly, body mass, size and size adjusted mass (i.e. body condition) all appeared to be poor predictors of survival, dominance and reproductive success under normal conditions (Bryant and Newton 1994, 1996; Newton 1989a). As yet, it seems a clear understanding of the traits conferring 'fitness' to individual dippers is lacking at all stages of the lifecycle (Bryant and Newton 1994, 1996; Newton 1989a).

### 6.4.7. Site related determinants of lifetime reproductive success

Analyses of seasonal reproductive performance suggested that successful birds were likely to continue to be successful, while birds raising no chicks in one year were those most likely to be unsuccessful in the following season. Similarly, some territories tended to be repeatedly fledge young, while other were routinely unsuccessful, independently of the birds breeding within them (Chapter 5). In the absence of experimental manipulation, it is often difficult to separate the confounding influences of territory and individual quality as determinants of breeding success (Verhulst and Tinbergen 1991; Verhulst *et al.* 1995). Indeed, often they are not wholly independent (Hogstedt 1981; Newton 1989c), although the indications here were that the breeding site played an important role in determining reproductive success.

#### 6.4.7.1. Territory quality and site fidelity

Studies of a number of species have suggested that where consistent differences in territory quality exist in proximate habitats, where possible, birds will move from poor to good sites to enhance the prospects of reproductive success and/or survival (Baeyens 1981; Foppen and Reijnen 1994; Holmes *et al.* 1996; Hatchwell *et al.* 1996; Krebs 1971; Newton 1991). Newton (1989a) suggested that the seasonal altitudinal migrations undertaken by many upland birds within the Devon catchment would allow the occupancy of nearby lowland sites to be assessed and give upland breeders the opportunity to compete for vacancies should they arise. Tyler *et al.* (1990), however, found that less than 3.6% of dippers moved more than 2.5km between breeding attempts in upland Wales, and within this study there was no evidence of a significant directional movement of upland breeders towards lowland sites (See Chapter 4). Indeed, dippers that remained on the same breeding territories throughout their lifetimes had significantly higher LRS that those with comparable lifespans that changed sites between seasons. This was in spite of some birds remaining in apparently unproductive sites.

Although this result could be confounded by the fact that birds changing sites had to be a year older and hence more experienced following the territory shift, this appears unlikely to affect the outcome of the analyses. No age effects have been apparent in any measure of success between breeders (Chapter 5), and if experience was important, similarly enhanced success would be expected for all birds, including those remaining at the same sites in consecutive years. Indeed, if familiarity with a territory, for example in the distribution of secure roost or nesting sites, or of prey within and between riffles, could increase foraging efficiency, body condition, reproductive success or survival, birds remaining in a territory might be expected to show the greatest increase in production (Curio 1983). This was not the case.

Harvey *et al.* (1979) noted that females great tits were more likely to change breeding territories following the loss of a brood in the previous year, and Similar patterns have already been shown for dippers elsewhere, with Marzolin (in prep.) highlighting a strong positive relationship between site fidelity and breeding success in North-eastern France. In this study, as in Marzolin's, birds that moved were more likely to have been unsuccessful in the year prior to the territory shift, and, on average 24% of all unsuccessful breeders changing territories before the next season, compared to only 10% of successful birds. Birds in poor habitats may be unsuccessful breeders in one year, and also have the greatest scope to obtain better territories in subsequent seasons, yet the fact even some successful birds also moved between years (and that some unsuccessful birds didn't) suggests that movements were not initiated solely following years of poor breeding. Rather, studies of sage sparrows (Petersen and Best 1987) and red-winged blackbirds (Beletsky and Orians 1987) suggested birds changing territories between years appeared did so where opportunities to gain higher quality territories arose.

Blancher and Robertson (1985) have suggested that the decisions regarding territory movements should only be based on past reproductive success if it provides a reliable indicator of the potential outcome of future attempts. Yet, expectations for future success need not be based on the prior breeding experience *per se* if both current and subsequent success are determined by territory quality, which may be assessed at other times in the year. Dippers do appear to monitor the occupancy of surrounding sites during the non-breeding period and compete for vacancies should they arise (Newton 1989a). While reproductive success could then be increased by moving to a higher quality site, some birds remained in apparently unproductive sites. If the competitive exclusion of some birds to poor territories was important (Newton 1989a), those birds unable to move were likely to continue to have low probabilities of success, and with most breeders making few breeding attempts within a lifetime, low seasonal success was then ultimately reflected in a low lifetime production of young.

### 6.4.7.2. LRS of upland and lowland breeders

Within the Devon catchment, double-brooded pairs were entirely restricted to lowland rivers Consequently, in each season some lowland birds raised twice the number of broods of upland breeders. Although the most successful birds were all at 'double-brooded' lowland sites, and lowland birds of both sexes tended to lay more eggs, hatch more chicks and fledge more young, none of these differences was statistically significantly (Tables 6.9 and 6.10). This perhaps seems surprising given the *a priori* prediction that the broad upland/lowland habitat classification reflected the most distinct, and biologically meaningful difference in quality within the catchment, and evidence that some elements of seasonal success did differ with habitat type (Chapter 5). Possibly, differences in territory structure between habitats (Chapter 1) played little role in determining the reproductive success of the majority of breeding pairs, or alternatively, LRS measured only until fledgling did not fully represent reproductive success. The validity of fledgling production alone as an appropriate measure of LRS forms the basis of the following chapter.

# Chapter 7

# Factors influencing the post-fledging survival of dippers in the River Devon catchment

## 7.1. Introduction

Survival to fledging encompasses only a fraction of the potential lifespan of any individual, and for breeders, reproductive success is only achieved if the young they produce subsequently survive to raise offspring themselves (Clutton-Brock 1988; Newton 1989b). As such, the number of recruits to the breeding population, rather than the number of offspring fledged should be the primary measure of reproductive success (Grafen 1988; Lack 1956). In many field studies such a measure is often unavailable, however, due to an incomplete knowledge of dispersal and post-natal survival and typically, the total number of young raised to independence over a lifetime provides the most complete measure of individual success available (Clutton-Brock 1988; Newton 1989b). Because of this, many studies have sought to identify properties of nestlings that can be used to predict their likelihood of subsequent survival (Alatalo and Lundberg 1989; Hochachka and Smith 1991; Lack 1966; Linden *et al.* 1992; Tinbergen and Boerlijst 1990). In spite of parents playing little or no role in the lives of independent offspring, many elements determining the likelihood of entry to the breeding population, such as nestling size, nutritional state at fledgling and the timing of fledgling itself, will be determined by parental efforts prior to independence (e.g. Coulson and Porter 1985; Garnett 1981; Linden 1988; Magrath 1991, 1992; Nur 1984a; Smith *et al.* 1987; Tinbergen 1987; Verhulst *et al.* 1997).

Lack (1947) suggested that avian clutch size should correspond to the maximum number of nestlings that parents can adequately feed. Experimental studies have shown, however, that the most common clutch size within many populations is often smaller than most birds are capable of raising (e.g. Gustafsson and Sutherland 1988; Nur 1984a,b; Perrins 1966; Pettifor 1993). This has often been taken as evidence of a trade-off between chick quality and quantity. Where brood size is manipulated, nestling mass, post-fledgling survival and total brood productivity may all be influenced (Daan *et al.* 1990; Gustafsson and Sutherland 1988; Linden 1988; Nur 1984a, 1984b; Partridge 1989 for review; Pettifor *et al.* 1988; Pettifor 1993; Smith *et al.* 1987; Tinbergen 1987; although see Wheelwright *et al.* 1991). Positive mass/survival relationships have been seen within natural broods for many species (see Magrath 1991 for review). Hochachka and Smith (1991), for example, found increasing post-fledgling survival probabilities with mass for song sparrows whilst Magrath (1991) noted survival to be directly related to nestling mass in the blackbird for all stages until after independence. Krebs (1981), Perrins (1965) and Verhulst *et al.* (1997) noted that heavy great tit nestlings were more likely to recruit than light ones.

The balance between current and future reproductive success has been suggested as an alternative or additional determinant of avian clutch size (Charnov and Krebs 1974; Gustafsson and Part 1990; Gustafsson and Sutherland 1988; McCleery *et al.* 1996; Nur 1987; Smith *et al.* 1989; Williams 1966), although this trade-off, if important, should be evident in measurable differences in individual lifetime fledgling production (Clutton-Brock 1988, Newton 1989b). A measure of nestling 'quality' may be less obvious, although still a crucial component of LRS.

The timing of entry into the adult population (Krebs 1992; Newton 1989b; Nilsson and Smith 1988), the habitat a fledgling enters (Garnett 1981; Tinbergen and Boerlijst 1990), the demographic status of the population itself (in terms of growth or decline, for example) or a combination of any or all of these factors may all influence post-fledgling survival. Nilsson and Smith (1988) have shown that chicks fledged early were more likely to gain dominance in winter flocks of marsh tits, whilst Ormerod and Tyler (1993) suggested that dippers raised during the peak period of breeding had the greatest chances of recruitment. Newton (1989a) showed experimentally that, at least in the short-term, the juveniles arriving earliest on a river had the highest probabilities of becoming established.

If an individual pair raises their optimal number of young in terms of quality and quantity, based on current experience, body condition, or the prevailing environmental circumstances, then lifetime fledgling production would seem a likely correlate of breeding success (Coulson and Porter

1985; Lack 1954; Perrins and Moss 1974). Indeed, many studies have suggested that all fledglings may have approximately equal probabilities of survival (e.g. Dhondt 1989; Hotker 1989), and within this study, the lifetime production of fledglings and autumn survivors were strongly correlated (Chapter 6). However, where individual circumstances prior to, or at, fledging influence subsequent survival, the assumptions of independence and equality of the fate of all young may not hold (Coulson and Porter 1985; Garnett 1981; Linden 1988; Magrath 1991, 1992; Nur 1984a; Smith *et al.* 1987; Tinbergen 1987). The aims of this chapter were to assess the importance of two possible elements of 'quality' on chick survival. Nestling size and the timing of fledging are considered. Brood manipulations were undertaken in an attempt to influence chick growth and allow size/survival relations to be examined. Chick survival is considered in relation to time of fledgling from the census records between 1985 and 1993, within the program SURGE 4.1 (Lebreton *et al.* 1992).

## 7.2. Methods and results

### 7.2.1. Brood manipulations

In the years 1993-1995 inclusive, brood manipulations were undertaken at lowland nests within the Devon, Allan and Teith catchments. Nests were assigned to matched trios based on known dates of clutch completion with the two closest matched nests (usually hatching on the same day) being manipulated and the third acting as a control. Three treatments (i-iii below) were used with all transfers undertaken when the chicks were 3 days old;

i) A brood reduction by the transfer of one chick.
ii) A control with no change in brood size.
iii) A brood enlargement by the addition of one chick.

With the relative inaccessibility of many sites within the study areas and the limited time very young chicks could remain out of the nest, no attempt was made to randomise chicks between nests and account for genetic or pre-hatching developmental effects during manipulation (Magrath 1992), and following the chick transfers, introduced chicks could not be distinguished from those within the natural brood. However, to assess the best 'match', chicks from all nests, including controls, were weighed thereby standardising handling and disturbance effects. At three days of age the energetic demands of nestlings are low and no prior differences in chick growth would be expected between broods (Ormerod *et al.* 1986). All treatments were chosen to retain brood sizes within the natural range of this population.

Nests were revisited within two days of the manipulations to check that parents were still tending the broods, before returning to ring and measure all chicks at 18 days of age, immediately prior to fledging (Shaw 1978). At ringing, chicks were marked with a metal British Trust for Ornithology ring and tarsus length, wing length and chick mass recorded (see Chapter 2).

### 7.2.2. Analyses

Due to the inaccessibility of many sites, and the need to 'match' nests and to avoid breeders already included in the LRS analyses, in all years some manipulations were undertaken outwith the main study areas. All successfully manipulated nests are included in analyses assessing the effects of manipulation on chick body size at fledgling, although survival estimates are made only for chicks raised within the Devon catchment where post-fledgling survival could be followed.

Studies following natural brood reductions have suggested that following the deaths of siblings, nestlings can quickly gain mass with chicks fledging at masses approaching those of chicks from smaller broods (e.g. Martins and Wright 1993.) Consequently, broods where some chicks died before fledgling were not included in analyses of nestling size (n=9), although since chick mortality may be an important consequence of raising enlarged broods, all nests were retained in analyses of survival. Nests abandoned immediately following the manipulations, where experimental disturbance was suspected as causing failure (n=4), are excluded from all analyses.

To avoid pseudo-replication (Hulbert 1984), chicks were sexed using a discriminant function (see Chapter 2) and mean body measures for each sex within a brood were used in all body size analyses. However, following fledging the survival probabilities of all individuals were considered to be independent. The importance of this assumption is examined in a further chi-square contingency analysis simply looking at the proportions of nests producing at least one offspring surviving to autumn, to account for possible non-independence in 'quality' or dispersal distances within broods (Section 7.2.5.)

Combining data from all years, 62 manipulations were undertaken successfully, including 19 enlargements, 21 reductions and 22 control nests. Sample sizes for matched comparisons were often smaller however, if one or more nests within a trio failed and hence with limited sample sizes, data from all years have been pooled for analysis. This was justified because the results of previous analyses suggested that between-year variation in post-fledging survival rates may be only slight (Chapter 4). The total numbers of successful manipulations, together with the proportion of the Devon nests fledging at least one chick surviving to autumn and the proportion of all Devon fledglings surviving to this time are given in Table 7.1.

### 7.2.3. Nestlings biometrics

Male dippers are known to be larger than females at fledging and discriminant analyses can allow many chicks to be sexed at 18 days of age (Feltham 1987). However, although correctly sexing all females, the discriminant function used tended to classify some small males as female. A function constructed from data for all birds ringed at 18 days of age between 1993 and 1995 and subsequently recaptured and positively sexed, correctly sexed all females and 85% of male nestlings (n=34) ringed at a similar age and recaptured prior to 1993 (i.e. individuals not used in the calculation of the original function). The inability to correctly sex all chicks may have important implications within nestling condition experiments since, *a priori*, it seems likely that chicks from each manipulation treatment may not have the same chances of being classified correctly. For example, if brood enlargements do affect chick growth, small males in poor condition may be wrongly classified as healthy females. This approach then suffers from an unavoidable inter-dependence between a nestlings size and its predicted sex. However, since females were known to be smaller than males at 18 days of age and have been shown to have greater dispersal distances and hence lower local survival rates than males, each sex must be considered separately to avoid biased size/survival relations.

### 7.2.4. Nestling sex ratios

Before considering the influence of the brood manipulations, sex ratios were examined within each treatment group. An indication that small males were frequently classified as females might be given if the discriminant function predicted enlarged broods having sex ratios significantly biased towards females. Although this assumes 50/50 sex ratios in natural broods, and a sex bias could exist at hatching (c.f. Lessels *et al.* 1996), or occur if males suffered greater mortality in the nest, considering only broods where all chicks survived to fledging, overall the discriminant function classified 46.9% of nestlings as females and 53.1% as males (Table 7.2). Slightly more chicks were classified as females within the enlarged broods with slightly less than predicted within both unmanipulated and reduced nests (Table 7.2), although these differences were not statistically significant ($\chi^2_2=1.817$, p=0.403).

### 7.2.5. Treatment groups and body measures

For males, at 18 days of age chicks from enlarged broods tended to be lighter (Matched pairs t=1.80, two-tailed p=0.096, n=14) and have shorter wings (Matched pairs t=1.83, two-tailed p=0.089, n=13) than chicks from brood reductions (Table 7.3a, Figure 7.1). No differences were apparent in tarsus length between manipulated broods (Matched pairs t=1.24, two-tailed p=0.243, n=10), or between control broods and either treatment group for any body measure (Matched pairs, two-tailed p>0.383 in all cases). Considering group means (unmatched nests), only the difference in mass between enlarged and reduced broods approached significance (independent t-test, t=1.80, n=35, two-tailed p=0.081).

For females, no differences between treatment groups approached significance for any of the body measure considered at 18 days of age, either using matched or independent comparisons (t-tests, p>0.190 in all cases; Table 7.3b, Figure 7.2).

### 7.2.6. Brood manipulations and chick survival

Nests subject to experimental reductions in brood size tended to be most likely to fledge at least one chick surviving to autumn. This was in spite of enlarged broods fledging at least two more chicks

**Table 7.1.** The numbers of manipulation experiments undertaken on dipper broods within the Devon catchment and elsewhere between 1993 and 1995 inclusive, and the subsequent survival of the fledglings raised. 'Successful' nests represent broods producing one or more chicks surviving at least until their first autumn (c.6 months). 'Surviving chicks' indicate the percentage of fledglings raised within the Devon catchment surviving at least 6 months.

| Treatment group | All catchments | Devon catchment | % successful Devon nests | % surviving Devon chicks |
|---|---|---|---|---|
| Enlarged | 19 | 14 | 50.0 | 13.7 (n=73) |
| Control | 22 | 13 | 46.2 | 20.8 (n=48) |
| Reduced | 21 | 9 | 66.6 | 26.7 (n=30) |

**Table 7.2.** Sex ratios predicted from discriminant analysis within experimental dipper broods between 1993 and 1995 inclusive.

| Count<br>*Expected* | Enlarged | Unmanipulated | Reduced | Row Total |
|---|---|---|---|---|
| Males | 53 | 66 | 28 | 147 (47.9%) |
| | *47.5* | *73.0* | *33.0* | 50.0% |
| Females | 42 | 80 | 38 | 160 (52.1%) |
| | *47.5* | *73.0* | *33.* | 50.0% |
| Column Total | 95 | 146 | 66 | 307 |
| | 30.9% | 47.6% | 21.5% | 100.0% |

than enlarged broods. Accordingly, the local survival probabilities (until autumn) of chicks from reduced broods were almost twice those for chicks from brood enlargements. Chicks from control broods had intermediate survival (Table 7.1). Although these results were in line with expectations if the manipulations had resulted in true differences in chick quality, neither the proportion of nests successfully fledgling at least one surviving chick ($\chi^2_2=2.507$, $p=0.285$) nor the overall survival rates of fledglings ($\chi^2_2=2.612$, $p=0.271$) differed significantly between groups. Reference to statistical power tables (Cohen, 1988) however, suggested that for the sample sizes available (n=108 chicks) a chi-squared contingency analysis had only slightly more than an "evens" chance (56%) of yielding statistically significant results at $p<0.05$ (Fleiss 1981). It was unclear, therefore, whether all birds had similar survival probabilities or if true survival differences simply remained undetected (Graves 1991).

### 7.2.7. Body size and chick survival

Logistic regression failed to identify any of the three biometric measures as significant predictors of post-fledgling survival (at $p<0.05$) for male nestlings. For nests fledging at least two male chicks, no differences in body measures were apparent between male survivors and the other male chicks within a brood (Matched t-test, n=15, $p\geq0.230$ in all cases). Too few survivors were recaptured to allow similar comparisons for females (n=5).

### 7.2.8. Natural variation in chick 'quality'

No significant relationships were evident between hatching date and any body measures considering only the broods included within the manipulation groups (Hatch-date was not significant as a co-variate in ANOVA analyses between treatment groups ($F<1.148$, 1df, $p\geq0.288$ for each sex); year not significant as a factor). Restricting the analyses to control and unmanipulated nests failed to identified any relationship between body measures (at 18 days) and hatch-date using either linear or quadratic regression ($r^2<0.04$, $p\geq0.265$ in all cases). No consistent differences in mean body measures were apparent between nestlings from upland and lowland habitats (independent t-tests, $t<1.16$, $p>0.25$, n=68 broods for males; $t<0.57$, $p>0.576$, n=62 broods for

**Table 7.3a.** Mean body measures (±S.D.) of male chicks within experimental dipper broods raised between 1993 and 1995 inclusive.

| | Mean mass | Mean tarsus | Mean wing |
|---|---|---|---|
| Enlarged | 56.99±4.90 | 30.14±0.66 | 67.02±2.60 |
| Control | 58.42±2.93 | 30.03±0.43 | 68.30±4.22 |
| Reduced | 59.61±3.31 | 29.97±0.63 | 69.06±4.67 |

**Table 7.3b.** Mean body measures (± S.D) of female chicks within experimental dipper broods raised between 1993 and 1995 inclusive.

| | Mean mass | Mean tarsus | Mean wing |
|---|---|---|---|
| Enlarged | 49.18±3.27 | 28.43±0.53 | 63.66±3.18 |
| Control | 51.26±1.96 | 28.30±0.48 | 66.01±5.48 |
| Reduced | 51.26±3.95 | 28.34±0.73 | 65.20±3.09 |

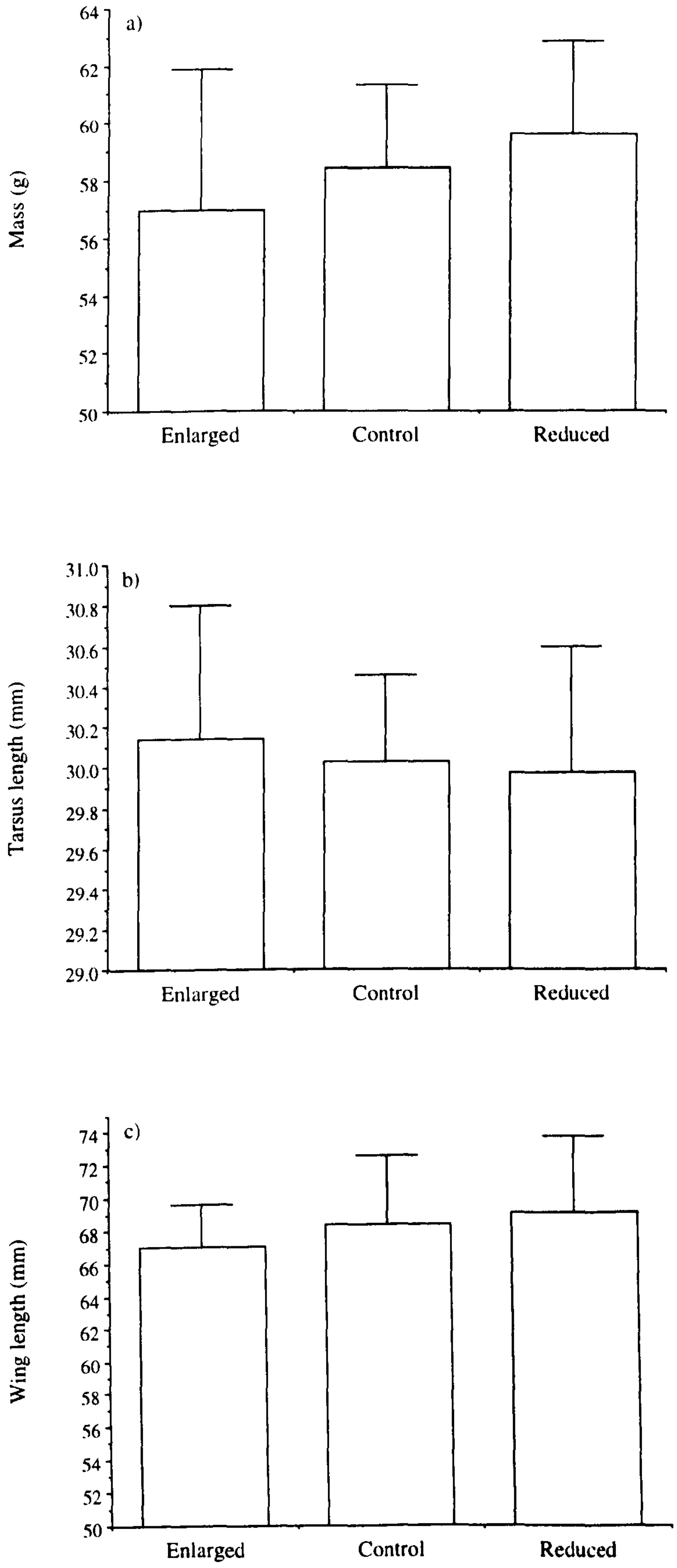


**Figure 7.1.** Mean measures (±S.D.) of a) mass, b) tarsus length and c) wing length for male chicks within experimental dipper broods raised between 1993 and 1995 inclusive.

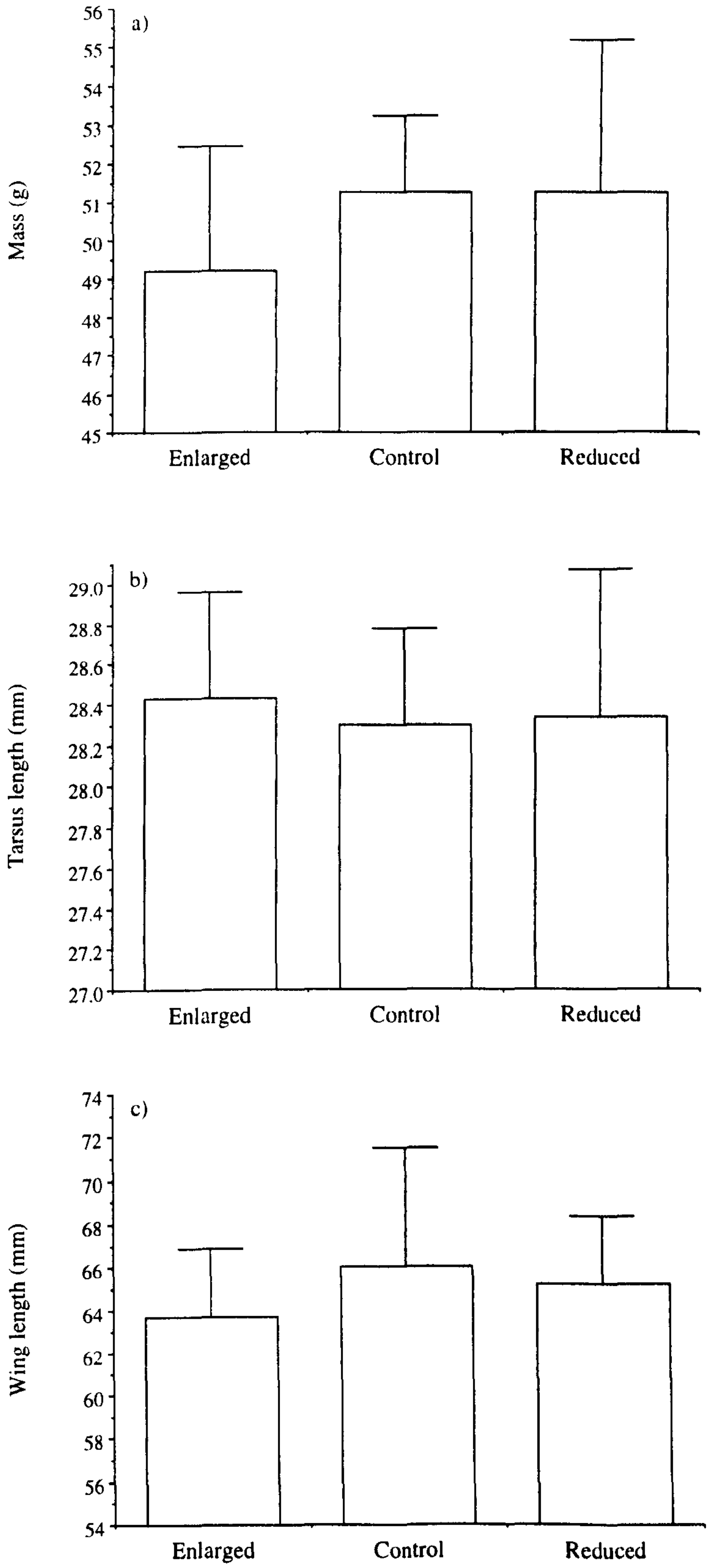


**Figure 7.2.** Mean measures (±S.D.) of a) mass, b) tarsus length and c) wing length for female chicks within experimental dipper broods raised between 1993 and 1995 inclusive.

females). Within natural broods, hatch-date and habitat type had no detectable influence of the size of offspring at fledging in either sex.

### 7.2.9. Hatching date and post-fledgling survival

Previous studies of dippers (Ormerod and Tyler 1993), and many other species (e.g. Perrins 1970; Cave 1968; Dow and Fredga 1984; Newton and Marquis 1984; Hochachka 1990) have demonstrated the importance of laying dates on chick survival. To assess these effects in the Devon catchment, within season trends were examined for chicks fledged between 1985 and 1993 using the program SURGE 4.1 (Lebreton *et al.* 1992).

For data-handling, the nestling census records were split to provide three data sets. 'Early' chicks included all fledglings hatching from clutches initiated before 1st April (n=373), prior to the peak of laying (see Chapter 4). 'Mid' season included all chicks initiated in the three week period from 2 April to 5 June (n=516) coinciding with the peak breeding period, with 'late' census records including all chicks hatched thereafter (n=234). Given the limited numbers of data sets handled by SURGE, sex differences in survival were not considered within these initial analyses, and models only calculate mean chick survival rates. Previous work however, has suggested that although different, the survival rates of males and females follow similar trends (no significant interaction terms, Chapter 4). Juvenile over-winter survival, adult survival and all recapture rates were estimated within the final model of Chapter 4 (see Table 4.6).

Table 7.4a displays the sequence of selection within SURGE, starting from an initial model with post-fledging survival dependent on hatching date within each year, and with equality in survival between years (as suggested in Chapter 4). The initial model (Model All.1), including all chicks fledged within the Devon catchment, predicted the highest survival probabilities from fledgling to autumn (± asymmetric 95% confidence limits) of 0.248 (0.191, 0.355) for early season chicks with survival estimated at 0.235 (0.187, 0.281) and 0.152 (0.112, 0.207) for mid season and late hatched birds respectively (Table 7.4b). However, a simplified model with equal survival probabilities for early and mid season chicks was selected with the lowest AIC of all the models fitted (Table 7.5, see Lebreton *et al.* 1992 for model selection). This model fitted the data as well as a fully time-dependent alternative (Model All.1 vs All.2, $\chi^2_1$=0.400, p=0.5271), and appeared to explain the data better than a model with equality in survival throughout the season, although this difference was not formally different at p<0.05 (Model All.2 vs All.5, $\chi^2_1$=3.22, two-tailed p=0.0693). The final model estimated post-fledgling survival probabilities of chicks hatched before or during the peak period of laying at 0.249 (0.222, 0.301) with late hatched fledglings showing reduced survival at 0.190 (0.147, 0.242)(Table 7.4 b, Figure 7.3).

### 7.2.10. Post-fledging survival and habitat type

Although significant trends in chick survival have been shown elsewhere (Ormerod and Tyler 1993), the initial analyses here do not demonstrate the existence of survival differences related to the timing of fledging. Importantly, 'early' nests are comprised almost entirely of lowland breeders, mid-season nests include both lowland and upland sites, with upland nests making up the majority of all 'late' broods. Clearly, the 'time' trends identified could simply reflect habitat or altitudinal effects. Indeed, SURGE models splitting the fledgling records only by habitat type showed significant differences in post-fledgling survival similar to those predicted from the time-dependent models (survival of upland fledglings 0.184 (0.145, 0.229), lowland fledglings 0.242 (0.188, 0.274)), with this model fitting the data significantly better than one with constant survival across all sites (Likelihood ratio test between models $\chi^2_1$=9.13, p=0.0025).

Evidence to support the importance of true time effects comes from analyses restricting post-fledgling survival estimates simply to lowland-raised chicks (Table 7.5a). As with the complete catchment records, an initial model (Model Low.1) was fitted, estimating survival rates separately for early, mid and late season fledglings. A simplified model with equal rates for early and mid season fledglings was then selected (Model Low.2) with the lowest AIC of all models fitted. This model fitted the data as well as the fully time-dependent alternative (Table 7.5a, Model Low.1 vs Low.2 $\chi^2_1$=0.08, p=0.777), and significantly better than one lacking time effects (Table 7.5a Model Low.2 vs Low.5 $\chi^2_1$=0.302, p=0.025). Late hatched chicks appeared to have reduced survival probabilities relative to those hatched early or at the peak of breeding, irrespective of their natal habitat (Table 7.5b; Figure 7.3).

**Table 7.4a.** Modelling post-fledgling rates for dippers (all chicks) raised within the Devon catchment between 1985 and 1993 inclusive. All models are fitted with juvenile over-winter survival dependent on lowland autumn population density and constant post-breeding and over-winter adult survival. Autumn recapture rates for all individuals, and spring recapture rates of known breeders are dependent on census effort only. The spring recapture rates of first year birds are dependent on the peak river flow ($m^3sec^{-1}$) during March (see Chapter 3). [a] np: number of identifiable parameters; Dev: relative deviance; AIC: Akaikes' Information Criterion. [b] Tests between models consider the relative fit of each model to the data. A significant result indicates that the more complex model provides a better description of the data and that the additional complexity of this model must be retained.

| Model | Fledgling survival rates | np[a] | DEV[a] | AIC[a] | Test between models[b] | |
|---|---|---|---|---|---|---|
| (1) All.1 | Time dependent within a season | 27 | 3577.12 | 3631.12 | (1) vs (2) $\chi^2_1$= 0.40, p=0.527 | Initial model |
| (2) All.2 | Equal for early and mid season chicks | 26 | 3576.72 | 3628.72 | (2) vs (5) $\chi^2_1$= 3.22, p=0.069 | Accepted |
| (3) All.3 | Equal for early and late season chicks | 26 | 3579.21 | 3631.21 | | Rejected |
| (4) All.4 | Equal for mid and late season chicks | 26 | 3578.77 | 3730.77 | | Rejected |
| (5) All.5 | Equal in all months | 25 | 3579.94 | 3629.94 | | Rejected |

**Table 7.4b.** Post-fledgling survival estimates (±asymmetric 95% confidence intervals) from selected models for dippers (all chicks) raised within the Devon catchment between 1985 and 1993 inclusive. Model codes refer to models fitted in Table 4a.

| Model | Early | Mid-season | Late |
|---|---|---|---|
| All.1 | 0.248 (0.191, 0.355) | 0.235 (0.187, 0.281) | 0.152 (0.112, 0.207) |
| All.2 | 0.240 (0.187, 0.252) | 0.245 (0.187, 0.252) | 0.152 (0.112, 0.207) |
| All.5 | 0.227 (0.198, 0.260) | 0.227 (0.198, 0.260) | 0.227 (0.198, 0.260) |

**Table 7.5a.** Modelling post-fledging survival for chicks raised on the lowland River Devon. All models are fitted with juvenile over-winter survival dependent on lowland autumn population density and constant post-breeding and over-winter adult survival. Autumn recapture rates for all individuals, and spring recapture rates of known breeders are dependent on census effort only. The spring recapture rates of first year birds are dependent on the peak river flow ($m^3sec^{-1}$) during March (See Chapter 3). [a] np: number of identifiable parameters; Dev: relative deviance; AIC: Akaikes' Information Criterion. [b] Tests between models consider the relative fit of each model to the data. A significant result indicates that the more complex model provides a better description of the data and that the additional complexity of this model must be retained.

| Model | Fledgling survival rates | np[a] | DEV[a] | AIC[a] | Test between models[b] | |
|---|---|---|---|---|---|---|
| (1) Low.1 | Time dependent within a season | 27 | 2934.61 | 2988.61 | (1) vs (2) $\chi^2_1$=0.08, p=0.777 | Initial model |
| (2) Low.2 | Equal for early and mid season chicks | 26 | 2934.69 | 2986.69 | | Final Model |
| (3) Low.3 | Equal for early and late season chicks | 26 | 2937.55 | 2989.55 | | Rejected |
| (4) Low.4 | Equal for mid and late season chicks | 26 | 2939.92 | 2991.92 | | Rejected |
| (5) Low.5 | Equal within a season | 25 | 2939.71 | 2989.71 | (2) vs (5) $\chi^2_1$=3.02, p=0.025 | Rejected |

**Table 7.5b.** Post-fledgling survival estimates (±asymmetric 95% confidence intervals) from selected models for dippers (lowland chicks only) raised within the Devon catchment between 1985 and 1993 inclusive. Model codes refer to models fitted in Table 5a.

| Model | Early | Mid-season | Late |
|---|---|---|---|
| Low.1 | 0.251 (0.201, 0.312) | 0.248 (0.198, 0.305) | 0.190 (0.144, 0.246) |
| Low.2 | 0.249 (0.222, 0.310) | 0.245 (0.222, 0.310) | 0.190 (0.144, 0.246) |
| Low.5 | 0.242 (0.201, 0.301) | 0.242 (0.201, 0.301) | 0.242 (0.201, 0.301) |

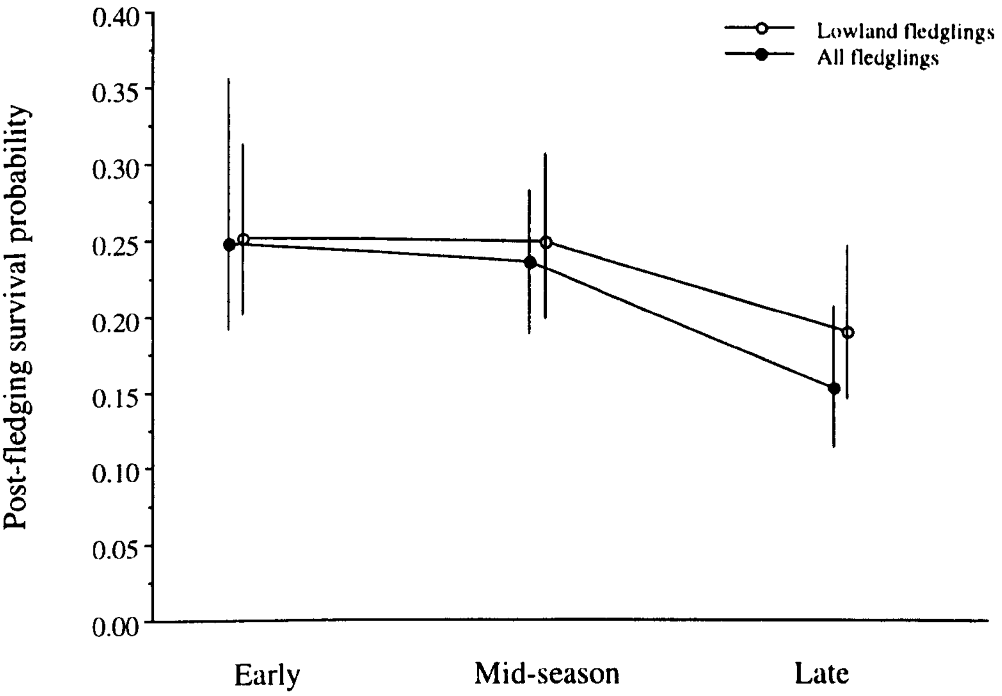


**Figure 7.3.** Estimates of post-fledging survival (± 95% asymmetric confidence intervals) in relation to fledgling date for dipper chicks raised within the Devon catchment between 1985 and 1993 inclusive (See text for model description)

## 7.3. Discussion

### 7.3.1. Brood manipulation and chick growth

Work on dippers within this catchment and elsewhere has suggested that factors associated with the timing of fledging may play an important role in determining subsequent survival (Newton 1989a; Ormerod and Tyler 1993; this study). However, the manipulation experiments described here were undertaken almost entirely during or before the peak of breeding, the periods when hatching date appears to play little role in influencing recruitment probabilities (Tables 7.4 and 7.5). Also, given the relative inaccessibility of most upland sites, manipulations were restricted to lowland rivers. It seems likely that any group differences in chick survival would, therefore, be due to the experimental treatments themselves rather than habitat or seasonal effects.

Male chicks from enlarged broods, tended to fledge at lower masses and with shorter wings than those from brood reductions (0.09>two-tailed p>0.05). Feltham (1987) showed tarsal growth to be complete by c.13 days for nestling dippers, whilst wing growth continued until fledgling, and mass peaked at approximately 18 days (Feltham 1987), the time when the final body measurements were taken in this study. If development was only impaired at the peak of energetic demand and then only after tarsus growth was complete (Feltham 1987), the trends in body size within this study would seem to be consistent with energetic stresses on males within enlarged broods during the latter stages of development. The lack of a detectable influence on tarsal growth may also reflect developmental priority being given to this trait to enhance the survival prospects of prematurely fledged young (Feltham 1987; Smith *et al.* 1989).

No differences in body measures were apparent for manipulated female dippers, although it remains impossible to determine whether the lower energetic demands of smaller females lead to a reduced impact of the manipulations themselves, or if the erroneous classification of some small males has distorted these results. If some male nestlings have been wrongly sexed, and small males were more frequently found in enlarged rather than control or reduced broods (as the results suggest, Table 7.2), their re-classification would strengthen difference between treatment groups for males. At present, wrongly sexing any birds would serve to obscure differences for females. Ideally, a molecular technique to reliably sex nestlings independently of body size would have been appropriate to remove this uncertainty (Lessells and Mateman 1996; Lessells *et al.* 1996; Madsen 1997).

### 7.3.2. Brood manipulation and chick survival

Overall, the survival of chicks from reduced broods was almost twice that of birds from brood enlargements, with control chicks showing intermediate survival. This difference was not statistically significant, although with the low power of this test (Fleiss 1981), it was unclear whether all birds had similar survival probabilities or if true differences simply remained undetected (Graves 1991).

It seems likely that large size could confer some advantages for fledgling dippers. For example, the period between fledging and nutritional independence is known to be critical (Sullivan 1989), and fledgling mass has been correlated with energy reserves for great tits (Perrins 1965). Garnett (1981) suggested that these reserves could be enough to last 'heavy' birds for approximately one day without food, or longer with restricted access to resources (Smith *et al.* 1989). Supporting the importance of size during this critical time, Magrath (1991) demonstrated that differences in fledging mass were only important until independence in blackbirds. Hochachka and Smith (1991), however, suggested that rapid growth was more important than the storage of nutrients. With the provision of supplementary food, nestling song sparrows grew larger and heavier, although they did not show a disproportionate increase in mass (Hochachka and Smith 1991). Possibly, more rapid growth early in life reduces the demands for self-feeding during the post-fledgling period when offspring may be inefficient at detecting and handling prey (Hochachka and Smith 1991; Sullivan 1989; Weathers and Sullivan 1989; Yoerg 1994).

Differences in size may also affect status and hence survival, with heavy males gaining dominance amongst juveniles during competition for territories. Drent (1983, cited in Tinbergen and Boerlijst 1990), for example, showed a relationship between male nestling mass in great tits and the probability of acquiring a territory. Yet, with Magrath (1991) showing that the advantages of fledgling size were only evident until independence, clearly the role of size as a determinant of social status was not of prime importance for his population of blackbirds. Similar results have been seen in other species, where post-fledging survival is strongly influenced by fledgling mass only in the first weeks after independence, or in populations where dominance status is independent of body size (e.g. Hochachka and Smith 1991; Nilsson and Smith 1988; Smith *et al.* 1989; Tinbergen and Boerlijst 1990). Dominance assessments within this population of dippers suggest that body size plays little role in determining status or over-winter survival in either sex (Bryant and Newton 1996). In this study, with few nestlings ever recaptured later, its role immediately post-fledging remains unclear.

### 7.3.3. The timing of fledgling and chick survival

Post-fledgling survival is known to show a seasonal decline in many bird species (Cave 1968; Dow and Fredga 1984; Hochachka 1990; Newton and Marquis 1984; Ormerod and Tyler 1993; Perrins 1970). Recent experimental studies attempting to separate the contributions of parental or territory quality and date *per se*, suggest that the timing of breeding itself may be causally involved in this relationship, with parental quality appearing insufficient to account fully for many of the patterns recorded (Brinkhof *et al.* 1993; Norris 1993; Verhulst and Tinbergen 1991; Verhulst *et al.* 1995).

Within the Devon catchment, nestlings raised late in the season had significantly lower survival probabilities than those raised early or at the peak of breeding (Tables 7.4a and 7.5a). Upland fledglings had significantly lower survival probabilities than lowland raised young. Yet, problems in interpretation arise within these results since survival probabilities represent only local estimates. Chicks from upland nests, raised on the fringes of the catchment have only short distances to fly to cross-watersheds and move outwith the study area. Consequently, the trends identified may represent differences in emigration rather than survival.

Inter-catchment movements generally result where birds follow water courses towards their source then fly up over ridges to cross to adjacent rivers (Price and Bock 1983; Schmid 1985). With the main upland streams in the Devon catchment flowing from both the north and south slopes of the same hills, the most obvious 'exits' for the catchment simply lead to alternative sections of the River Devon (Figure 2.1b). Also, the rivers to the immediate south and east of the Devon catchment are either largely unsuitable for dippers or included as additional sites within this study, where emigrant birds might be likely to be captured (see Chapter 2). Consequently, habitat determined differences in dispersal appear unlikely to account for the results presented. This is supported by the identification of significant time trends when considering only lowland chicks, all of which were raised within the core study area.

Newton (1989a) suggested that late fledged birds may disperse over greater distances within the Devon catchment, and this general pattern has been seen in a number of other passerine species (Dhondt and Huble 1968; Dhondt and Olearts 1981; Pienkowski 1965; Van Balen and Hage 1989). Too few dippers ringed as nestlings in this study have ever been captured elsewhere to determine in emigration rates were strongly influenced by hatching date. Tyler *et al.* (1990), however, found no evidence of differences in emigration rates with seasonal progression in a more extensive study of dipper dispersal in upland Wales. Sufficient data on seasonal trends in emigration and survival are available for few species of passerines, although national ringing recoveries of great tits in Belgium suggest that seasonal patterns in the survival still hold after accounting for post-natal dispersal (Dhondt and Olearts 1981). Indeed, Verhulst *et al.* (1997) have recently shown that hatching date has little effect on the dispersal of the great tits raised in and around Wytham wood, Oxford.

### 7.3.4. Causes of seasonal patterns in survival

The lower survival of late fledged birds may reflect differences within the environment with seasonal progression. For example, it has been suggested that the seasonal declines in fledging success in the coot and clutch size in the great tit were causally related to patterns of food availability (Brinkhof *et al.* 1993; Perrins 1965). Similar trends may be important for dippers, with prey abundance known to decline significantly with the emergence of many aquatic insects (Hynes 1970). However, no seasonal trends in chick size at fledgling were evident within this study. Indeed, in natural situations, even with variation in individual, territory or environmental quality, differences in nestling growth need not be expected if the seasonal decline in clutch size (see Chapter 5) is tied to the ability of parents to raise young (Coulson and Porter 1985; Hogstedt 1980; Perrins and Moss 1975; Pettifor 1993). In many species, the timing of fledging itself, rather than its correlates, may be important (Brinkhof *et al.* 1993; Norris 1993; Verhulst and Tinbergen 1991; Verhulst *et al.* 1995).

Using experimental introductions into this population, Newton (1989a) has shown that, at least in the short term, the first juvenile dippers to settle on a river have the highest chance of becoming established, whilst Perrins (1965) noted early fledgling to be beneficial to great tits, even when accounting for fledgling mass. In situations where occupancy of vacant habitat is an important determinant of status, or a prerequisite for territory acquisition, the date of fledgling itself may be crucial (Arcese and Smith 1985; Drent 1983; Garnett 1981; Nilsson and Smith 1985, 1988). Nilsson and Smith (1989) have shown that for marsh tits fledging date and the date of territory acquisition were strongly correlated and the two most important components determining juvenile survival. In great tits, early fledgling is important for the acquisition of a high quality territory (Linden et al. 1992) and although a seasonal decline in survival occurs (Perrins 1966; Tinbergen and Boerlijst 1990; Linden et al. 1990), removal experiments have suggested that late fledged young are equally capable of surviving as earlier fledged chicks when given access to vacant habitat (Kluyver 1971).

Linden *et al.* (1992) highlighted the differences in the relative importance of fledging mass and timing of fledging in a study of great tits and collared flycatchers. In the migratory flycatcher, body mass appeared a strong predictor of survival in six out of seven years, whereas in the great tit, where the acquisition of an autumn territory was required for over-winter survival (Smith *et al.* 1989), hatching date rather than fledgling mass was critical, with mass only predicting survival in one of five years. The authors suggested that although attaining a high mass may have a positive influence on survival, it may mean deferred fledgling. For migratory species, such a delay may result in little cost since the timing of independence may be of low importance. Great tits, on the other hand, may have to trade mass against early fledging (Linden *et al.* 1992).

Studies of dippers in Wales (Ormerod and Tyler 1993) and other species elsewhere (e.g. Norris 1993; Tinbergen and Boerlijst 1990), have shown that early raised chicks may have lower survival prospects than those raised at the peak of breeding. Clearly, if only date itself is important, rather than any influences associated with the seasonal progression, a continued decrease in post-fledgling survival might be expected (Norris 1993). As yet, the additional processes involved remain unclear. The aquatic prey taken by dippers does not appear to show a strong mid-season peak, for example, although with the early breeding of dippers, constraints on food acquisition rates, such as high river flows and short active days, may be important early in the season.

### 7.3.5. Territory quality and chick survival

An initial aim of these analyses was not only to examine if development within the nest affected subsequent survival, but if consistent differences in nestling growth or survival, tied to territory quality, existed within the catchment. Ormerod and Tyler (1991), for example, have suggested that a seasonal decline may occur in the growth rates of nestling dippers, and that on acidic streams, where food availability is known to be reduced, chicks aged between 6-13 days have slower growth relative to nestlings on circum-neutral rivers. They did not, however consider difference in body size at fledging. Egg size may be a indicator of 'quality' and smaller eggs have been shown to have reduced hatching success and produced smaller chicks with lower survival probabilities that larger eggs (Bryant 1978; Davis 1975; Lundberg and Vaisanen 1979; Moss *et al.* 1981; Schifferli 1973). Ward (1992) however, failed to identify differences in egg size between upland and lowland breeders.

Acknowledging the limitations of the analyses here and the uncertainty in sexing some nestlings, no significant differences between upland and lowland raised chicks were found for either sex in any measure of body size. However, if growth is most affected in situations of stress or food shortage, possibly, by excluding upland and late hatched chicks from the manipulation experiments, the birds most likely to suffer low food availability have not been considered within these analyses. Moreover, post-fledgling survival may be reduced for birds entering poor habitats irrespective of nestling mass (Tinbergen and Boerlijst 1990).

Although the difference in mean survival between upland and lowland fledglings may principally reflect the timing of breeding rather than habitat trends, an indication that post-fledging survival was lower in the uplands comes from a comparison of the mean survival probabilities for all chicks (Table 7.4b) and for lowland chicks only (Table 7.5b). In all time periods, the post-fledging survival probabilities of lowland birds exceeded the population mean, indicating that the inclusion of upland breeders had depressed the overall population survival rates. As the season progressed and the contribution of upland nests to the total number of breeding attempt within each group increased, these differences became more pronounced (see Figure 7.3). It has been suggested that dippers fledging on acidic rather than circum-neutral streams may have reduced survival prospects due to the low prey availability (Tyler and Ormerod 1994). Fledgling dippers are known to be inefficient at detecting and handling prey and it seems likely that the more dispersed food within upland streams may limit self-feeding immediately following independence (Yoerg 1993). No significant differences in the age of breeders were evident between habitat classes (Chapter 5), suggesting that this was not a component of the subsequent survival of fledglings (c.f. Wilson 1996), although the importance of emigration in determining these trends remains unclear (Newton 1989a; although see Tyler *et al.* 1990; Verhulst *et al.* 1996).

# Chapter 8

# General Discussion

## 8.1. Introduction

Dippers have been studied within the Devon catchment since the mid-seventies (Shaw 1978, 1979) and the entire population has been monitored since 1985. The likely role of some intrinsic factors such as population density and social behaviours (Chapter 4; Newton 1989a), some stochastic and abiotic influences including river flows, stream acidity and river structure (Logie *et al.* 1996; Chapters 3, 4, 5 and 6) and the role of individual traits including age, status and phenotype in determining survival, recruitment, breeding probabilities and/or reproductive success have been considered at many stages within the life cycle (Bryant and Newton 1994, 1996; Newton 1989a, 1993; Chapters 4, 5, 6 and 7). Although some demographic parameters, principally immigration and emigration rates, remain poorly understood, with the information now available it is possible to outline the processes likely to determine dippers numbers within the Devon catchment, and influence the patterns of individual lifetime reproductive success.

## 8.2. Factors likely to determine population size

Lack (1966) suggested that external factors, such as food, nest-sites, predators or parasites regulated populations, and in particular, that territoriality did not regulate numbers, but merely determined which individuals were able to breed. Importantly, he argued that influences on mortality and recruitment outwith the breeding season and primarily tied to food shortage, rather than effects on fecundity, determined population size. This view has found much support from field studies on birds (e.g. Dhondt *et al.* 1990; Ekman *et al.* 1981; Ekman 1984; Krebs 1970; Lack 1966; Tinbergen *et al.* 1985; Perrins 1991 and Sinclair 1989 for reviews), and for many species there is strong evidence of the importance of critical resources throughout the year and/or territorial behaviours related to access to these resources in determining survival, reproductive success and the size of breeding populations (Arcese *et al*, 1992; Brown 1969; Dhondt *et al.* 1990; Klomp 1972; Krebs 1970; Lack 1954, 1966; McCleery and Perrins, 1985; Newton 1980, 1991, 1992 for reviews; Nilsson, 1987; Southern 1970; Tinbergen *et al.* 1985; Village 1983).

### 8.2.1. The role of food abundance in determining population size

Evidence that food supplies influence bird numbers come from observations that differences in density often correlate with variations in food availability, either between sites or over time, and that experimental manipulations of food supply are often followed by predictable changes in population size (See Boutin 1990, Martin 1987 and Newton 1980 for reviews). In dippers, the strong and consistent relationships between autumn population densities and prey abundance or its correlates (Figures 3.2, 8.1; Logie *et al.* 1996; Ormerod *et al.* 1988), provide strong evidence that, to some extent, population size is already matched to food availability prior to this time. The decline in reproductive success with increasing acidity seems likely to confound assessments of the role of prey abundance in determining population densities, because potentially, breeders on acid streams may produce few young to fill vacant habitats. However, support that the relationship between population size and prey density is casual come from findings that acidic streams often occur well within the dispersal distance of dippers from circum-neutral rivers, even within otherwise 'circum-neutral catchments (Bryant *et al.* unpubl.; Logie 1995; Tyler and Ormerod 1993), and that the post-fledging period coincides with the moult of adults, a time of minimal territorial defence (Hewson 1969; Marzolin in prep.; Newton 1989; Tyler *et al.* 1991) when juveniles seem able to disperse throughout vacant habitat, yet acid streams hold reduced dipper densities throughout the year relative to circum-neutral rivers. During breeding, the negative relationship between the size of the defended home-range and stream acidity, suggests that the spacing of pairs reflects resource (prey) abundance, and not simply the number of potential breeders (Ormerod and Tyler 1987; Vickery 1991; Vickery and Ormerod 1991). Moreover, in circum-neutral catchments at least, population size is known not to be limited by the number of potential recruits, and entry to summer and early autumn populations appear to involve competitive processes.

### 8.2.2. Evidence that entry to autumn populations involves competitive processes.

A significant seasonal decline in post-fledging survival probabilities was identified in this study (Chapter 7), and Newton (1989a) has shown experimentally that this is likely to reflect the importance of the timing of settlement, with the first dippers to occupy a site excluding others. Although the results of the brood manipulations within this study were equivocal, chicks raised in reduced broods were heavier, had longer wings and were almost twice as likely to recruit into autumn populations as those raised in enlarged broods (Chapter 7). Newton (1989a) has shown that smaller dippers disperse over greater distances, most likely reflecting their poorer competitive status, although recently Verhulst *et al.* (1997) have shown that relationships between local survival and nestling mass reflect true mortality rather than dispersal in a population of great tits. In great tits, large birds dominate smaller individuals (Drent 1983; Garnett 1981), and heavier nestlings are more likely to emigrate into prime woodland from surrounding sites than light ones (Verhulst *et al.* 1997). Although, potentially, the poor survival of small or late-season fledglings, could reflect poor developmental condition or seasonal changes in habitat suitability, and confer low survival probabilities to these birds even in the absence of competitive effects, the findings from Newton's (1989) experimental manipulations, provide strong evidence that juveniles are not able to settle freely within and between sites, and that differences in individual status, linked to early settlement and some aspects of dominance and/or body size are important in determining an individuals' chances of entering the autumn population (Chapter 7, Newton 1989a).

Laboratory studies have confirmed that, in a neutral setting, individual dippers do differ in their ability to hold resources (e.g. a single perch in a pool of water, Bryant and Newton 1994), and although in natural situations most dippers do not maintain exclusive territories in autumn, territorial aggression escalates at this time with some birds gaining, and defending, sole access to river sections (Bryant and Tatner 1988; Hewson 1969; Newton 1989a). This competition not only separates those individuals that gain access to resources from those that do not, but determines the quality of the home-range for survivors (Fretwell and Lucas 1970; Jenkins *et al.* 1963; Krebs *et al.* 1991; Smith *et al.* 1995; Watson and Jenkins 1968). Subordinates may be excluded entirely, or forced to remain as non-territorial floaters on, or between, defended sites, or to occupy fringe habitats where competition is less intense, although where food is likely to be poor or where predation risk is high (Jenkins *et al.* 1957, 1963; Krebs *et al.* 1991; Newton 1989a; Smith *et al.* 1995; Watson and Jenkins 1968). The competitive exclusion of low quality individuals appears a general pattern in passerine species, where birds occupying poor habitats are likely to be young, inexperienced and/or of low social status (e.g. Dias *et al.* 1996; Hatchwell *et al.* 1996; Holmes *et al.* 1996; Newton 1991). Monkkonen (1990), for example, showed that the experimental removal of territory holders in a number of passerine species resulted in rapid replacement by smaller sized individuals. Alatalo *et al.* (1985) found that male Pied flycatchers in the preferred deciduous woods were larger and heavier than those in coniferous woods, whilst in southern France, males blue tits breeding in 'sink' habitats are smaller and lighter than those in 'sources', apparently reflecting their lower quality and social status (Dias *et al.* 1996). As suggested by Newton (1989a) and supported by the relationships that were established within this study between juvenile over-winter survival and population density, and between population density and stream acidity, territorial intolerance and density-dependent changes in mortality, related to dominance and mediated though dispersal and competitive exclusions from preferred sites, seem likely to cause dipper numbers to be matched to available resources, principally food, roost sites and ultimately breeding territories.

### 8.2.3. The role of density-independent mortality in determining population size

Newton (1989a) showed that within the Devon catchment the period of peak juvenile over-winter mortality did not coincide with the worst of the winter weather, and analyses within this study failed to highlight any influence of environmental conditions on the survival of juveniles or adults. Marzolin (in prep.) and Clobert *et al.* (1990), however, report evidence of the direct impact of extreme river flows on adult survival, and Tyler and Ormerod (1994), Price and Bock (1983) and Wilson (1996) provide anecdotal support for the role of floods in determining nestling, post-fledgling, juvenile and adult over-winter survival, and both breeding success and/or breeding probabilities. Many dippers are unable to feed during spates (Da Prato and Langslow 1981), and Bryant and Tatner (1988) have shown that in winter, the rates of food gain needed to maintain energy balance exceed those required during breeding, due to a combination of increased foraging

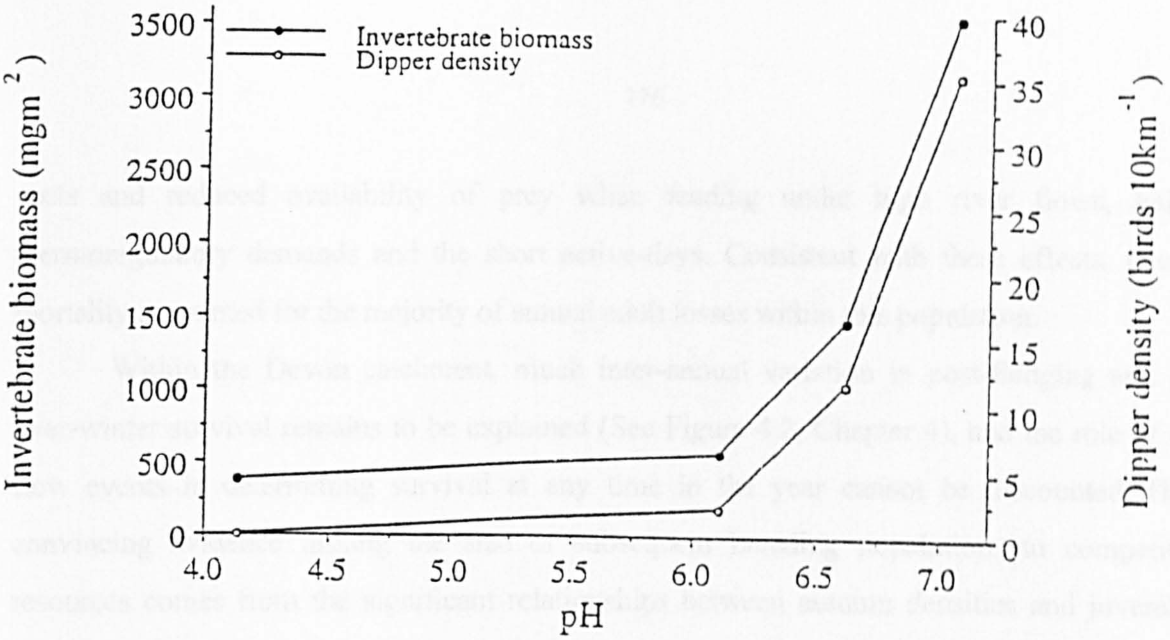


**Figure 8.1.** Dipper densities and invertebrate biomass for four rivers in central Scotland (from Logie 1995). Biomass figures represent mean dry weights derived from 15 samples (5 sites), dipper densities from two census counts.

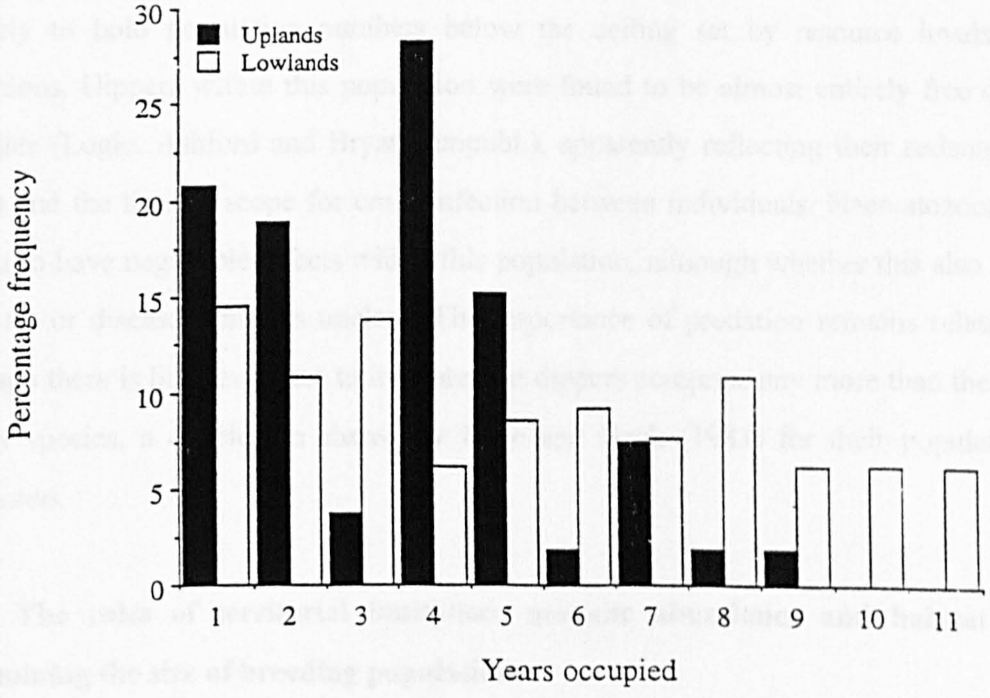


**Figure 8.2.** Patterns of territory occupancy for upland and lowland site within the Devon catchment between 1985 and 1995 inclusive (only sites occupied in at least one year are included). The difference in occupancy rates is significant (Chi-square$_{1,10}$=30.748, p=0.001, n=53 upland sites and 65 lowland sites)

costs and reduced availability of prey when feeding under high river flows, heightened thermoregulatory demands and the short active-days. Consistent with these effects, over-winter mortality accounted for the majority of annual adult losses within this population.

Within the Devon catchment, much inter-annual variation in post-fledging and juvenile over-winter survival remains to be explained (See Figure 4.2, Chapter 4), and the role of extreme flow events in determining survival at any time in the year cannot be discounted. However, convincing evidence linking the size of subsequent breeding populations to competition for resources comes from the significant relationships between autumn densities and juvenile over-winter survival (but not between juvenile survival and autumn or winter weather conditions) (Figure 4.2, Chapter 4) considered above, and between juvenile breeding probabilities and adult mortality elsewhere (i.e. the number of available breeding 'gaps' (Marzolin in prep.)). These relationships indicate that intrinsic processes, linked to resource abundance, primarily determine population size and set a ceiling on the potential number of breeders (Chapter 4). Moreover, they imply that additional factors such as environmental extremes, predators, parasites or disease are unlikely to hold population numbers below the ceiling set by resource levels under normal conditions. Dippers within this population were found to be almost entirely free of haematozoon parasites (Logie, Ashford and Bryant, unpubl.), apparently reflecting their sedentary and solitary habits and the limited scope for cross-infection between individuals. Haematozoon parasites thus appear to have negligible effects within this population, although whether this also applies to other parasites or diseases remains unclear. The importance of predation remains relatively unknown, although there is little evidence to indicate that dippers comprise any more than the incidental prey of any species, a conclusion shared by Price and Bock (1983) for their population of *Cinclus mexicanus*.

### 8.2.4. The roles of territorial limitation, nest-site abundance and habitat suitability in determining the size of breeding populations

Territorial limitation during breeding is implied if, in situations where resources such as food, breeding sites and mates are not limited, individuals capable of breeding fail to do so through the

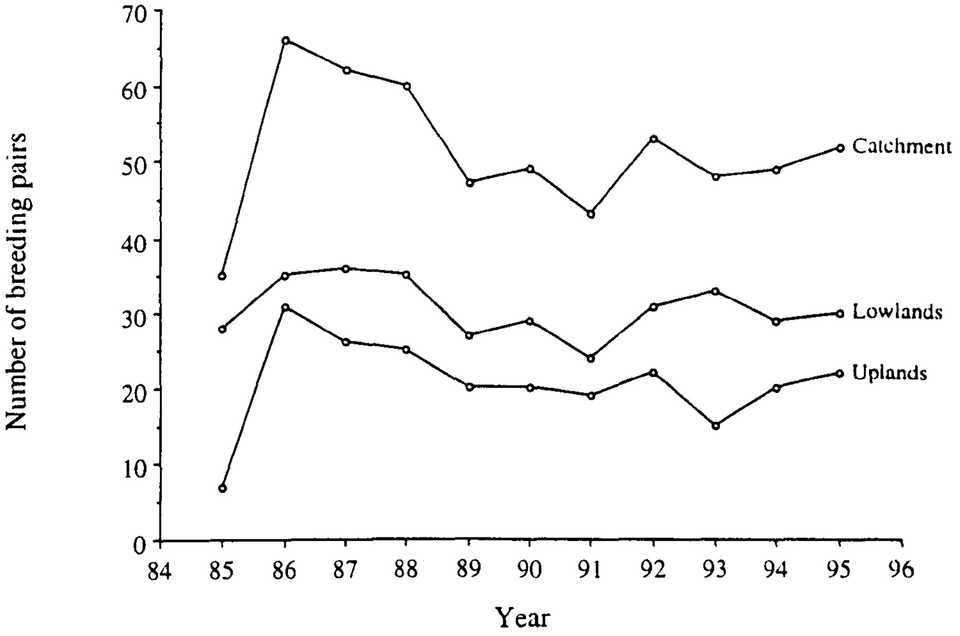


**Figure 8.3.** Patterns of breeding density within the Devon catchment between 1985 and 1995 inclusive.

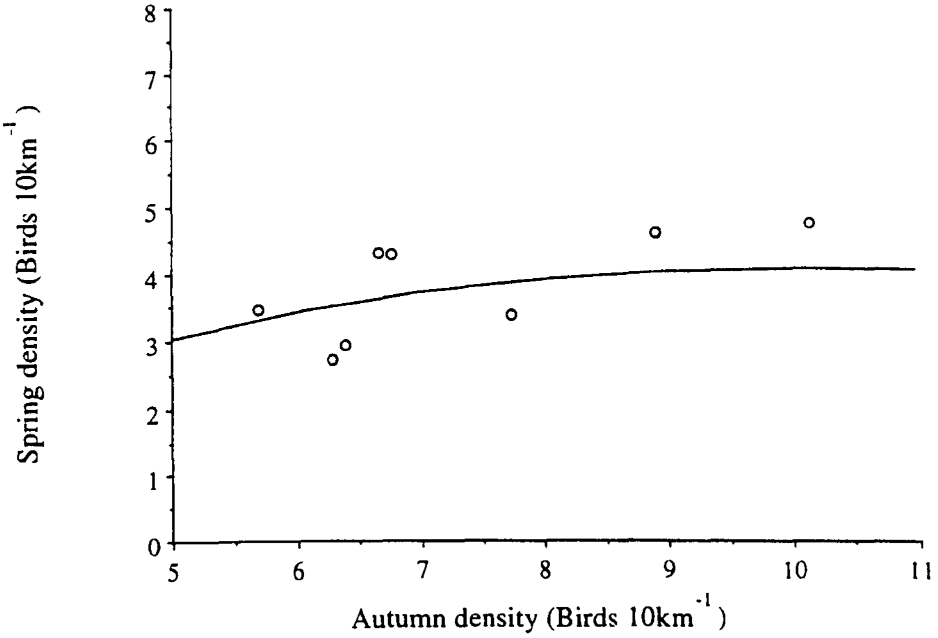


**Figure 8.4.** Relationship between autumn and spring population densities for dippers within the River Devon catchment (See Figure 4.2 and Chapter 4 for explanation and calculations)

territorial intolerance of others (Newton 1992; Smith *et al.* 1991; Watson and Moss 1970). In many species with specialised nest-site requirements, the provision of excess artificial sites (usually nest-boxes) have led to increased breeding densities, suggesting that the availability of suitable nest-sites is often important (See Newton 1994 for review). Within the Devon catchment some river sections which were used extensively by non-breeding birds, and appeared to provide sufficient prey, at least for self-maintenance, were routinely vacant during the breeding season. Incidental 'manipulations' of site availability following the repair of bridges or culverts and the loss of nest holes at some lowland sites led to previously occupied territories remaining vacant for several years, whilst subsequent deterioration in the masonry or the provision of nest-boxes saw these sites immediately reoccupied (Bryant *et al.* unpubl.). The indications were that these sites at least, remained vacant due to the lack of suitable nesting places. However, in many other areas in the Devon catchment several alternative nests sites were known to be available to dippers within each territory (and were used over the years of this study) implying that nest-site abundance *per se* was not a limiting factor.

In all years more birds of both sexes were alive than actually bred, and overall an estimated 16% of all individuals surviving to maturity failed to initiate a breeding attempt (Chapter 6). It remains unclear within this population whether all 'non-breeders' were excluded by the presence of others, or if some birds failed or abandoned early, or lost or were unable to locate (or obtain) a mate. Nevertheless, the presence of apparent non-breeders even though vacancies were available among potential nesting places, implies that some form of constraint was inhibiting the growth of the breeding population. The continuous (or near continuous) occupation of prime lowland territories and the infrequent use of many upland sites, suggested that this constraint largely reflected habitat suitability, and that the places remaining vacant were deficient in some elements required for successful breeding. The steep, rugged nature of many upland streams apparently provided suitable waterfalls, rock-faces and undercut river-banks for nest sites, indicating that this was unlikely to be the limiting factor in most situations. Rather, the availability of food and foraging sites will be important if it influences survival, prevents birds from laying eggs, or causes them to abandon, or leave eggs and chicks unguarded in favour of foraging (Bakacincka *et al.* 1996;

Drent 1975; Lijjeld and Slagsvold 1986; Newton 1986, 1991; Zicus *et al.* 1995). Indications that many upland territories were of poor quality not only comes from the territory occupancy rates (Figure 8.2), but evidence that the birds within them birds maintained larger, and not just longer, territories (Lennon 1988), and that the delayed laying at many upland sites was inconsistent with optimising post-fledgling survival and more likely to reflect some resource scarcity (Daan *et al.* 1990; Drent and Daan 1980; Martin 1987 for review; Perrins 1965, 1970; Tyler and Ormerod 1991). At least for first year recruits, the quality of the territories had much to do with how severely flow regimes affected their early breeding success.

### 8.2.5. Density-dependent influences on breeding success

Important density-dependent influences on the success of breeders have been identified in passerine populations elsewhere, with changes in clutch size, brood size, fledging success or the incidence of second broods being related to population size (e.g. Alatalo and Lundberg 1984; Arcese and Smith 1988; Ekman 1984; Kluyver 1951; Krebs 1970; Lack 1966; Moller 1989; Nilsson 1987; Sinclair 1989; Stenning *et al.* 1988; Tinbergen *et al.* 1985). Some authors have suggested that density-dependent changes in production are unlikely to be important for dippers, citing evidence that breeding success is often greatest where population densities are high i.e. on lowland, circum-neutral streams (Tyler and Ormerod 1994). This reasoning is in error, however, as it fails to consider the relationship between breeding densities and resource abundance (Da Prato and Langslow 1976; Ormerod and Tyler 1987; Price and Bock 1983; Vickery 1991; Vickery and Ormerod 1991; Wilson 1996), and territorial intrusions, interference and/or predation may all be more frequent where nests are closely spaced (Arcese *et al.* 1991; McCleery and Perrins 1985; Potts and Aebischer 1991; Tinbergen *et al.* 1985).

Territory boundaries were not recorded during the course of this study, although the consistency in both breeding densities and nest-site selection within territories suggested that any variation in the size of spring populations did not result in territory compression, or increased densities in already occupied sites. Removal of territory holders may provide a means of detecting experimentally whether birds are truly being excluded from breeding, although within the context of LRS studies and the need to follow breeders under natural conditions, this was not considered appropriate within this study. Similarly, in the absence of experimental intervention, the relative stability in breeding densities between years (Figure 8.3) precluded the investigation of density effects on the success of established lowland birds (i.e. the use of key-factor analysis).

In years of high total population size, mean success could potentially be reduced as an increasing proportion of the birds were forced into poor quality territories (e.g. Dhondt *et al.* 1992; Nilsson 1987; Van Balen 1982), and the lack of second broods in upland territories is an illustration of sub-maximal reproduction in this habitat. However, at current levels of occupation, with little evidence of habitat effects on the size of first clutches and less than 10% of all pairs attempting to make a second breeding attempt each year, the exclusion of some birds to poor sites will have little influence on the mean success of the population as a whole (Figure 8.6), unless an increasing proportion of birds die, are forced to remain as non-breeders, or have little probability of breeding successfully. In practice, evidence of territorial exclusions and density-dependent juvenile over-winter survival, of non-breeders in all years and the relationship between first-year breeding probabilities and river flows apparently tied to differences in territory quality, provide support for all of these possible processes (Newton 1989a; Chapter 4).

Using key-factor analysis (Varley and Gradwell 1960) on the great tit data from Wytham Wood, Krebs (1970) and later McCleery and Perrins (1985, 1991) confirmed Lack's (1966) suggestion that variation in fecundity or breeding success was of relatively little importance in determining the size of subsequent breeding populations compared to non-breeding mortality. Under normal conditions, this also seems likely for dippers in the Devon catchment. Although the majority of all the losses of independent young occurred during the first months (possibly weeks) after fledging (Newton 1989a; Chapter 4), between 1985 and 1995 juvenile over-winter survival was the only population parameter significantly related to population density. Restricting consideration to the range of densities recorded within this and other dipper populations, this relationship alone appears sufficient to regulate the population (Figure 8.4). These findings, coupled with the relationships between stream acidity and dipper densities throughout the year, closely match Lack's (1966) contention that mortality and recruitment outwith the breeding season, and principally tied to resource abundance, rather than influences on fecundity, determine population size. Between 1985 and 1996, clutch size, brood size, mean fledgling numbers, egg to fledging survival, mean post-fledging survival, adult survival and adult breeding probabilities did not show any relationship with density or differ significantly between years (Figures 4.1, 5.6, Chapters 4 and 5), and therefore were not directly involved in population regulation.

### 8.3. Processes likely to determine population size within the Devon catchment

Figure 8.5 shows a graphical representations of the distribution of breeders between two habitats in relation to territory quality, based on the assumptions that the best available territories are occupied preferentially and that the presence of territory holders deters further birds from settling (the processes suggested as important within this population). These predictions correspond to the ideal 'despotic' or 'pre-emptive' models of Fretwell and Lucas (1970) and Pulliam and Danielson (1991), where the initial settlers occupy the best territories in order of suitability, forcing additional birds into lower quality sites. If the lowlands and uplands represent 'good' and 'poor' habitats respectively within the Devon catchment, initial settlers would be predicted to occupy lowland sites preferentially before excluding further birds upland streams, although variations in laying dates and the LRS of breeders within each habitat suggest that, some overlap in quality between the upland and lowlands would be expected (Chapter 5, 6 and 7)..

Based on this model, and the findings from previous chapters and work elsewhere (Newton 1989a; Marzolin in prep.; Chapters 3, 4, 5, 6 and 7), Figures 8.6, 8.7, and 8.8 display representations of how population birth and death rates might be matched to available resources within the Devon catchment, depending on the distribution of individuals between sites and possible relationships between population size, site quality, survival and breeding success. At the lowest densities on lowland rivers (densities below $D_1$, Figure 8.6) all individuals gain access to 'prime' lowland sites and have the potential for double brooding. Later settlers lay only a single clutch each year and mean lowland production per pair tends towards the rate of single-brooded (upland) pairs. From Figure 8.5, only a limited number of suitable breeding territories are available and once these are filled (at densities greater that $D_2$ and $D_3$ for lowland and upland habitats

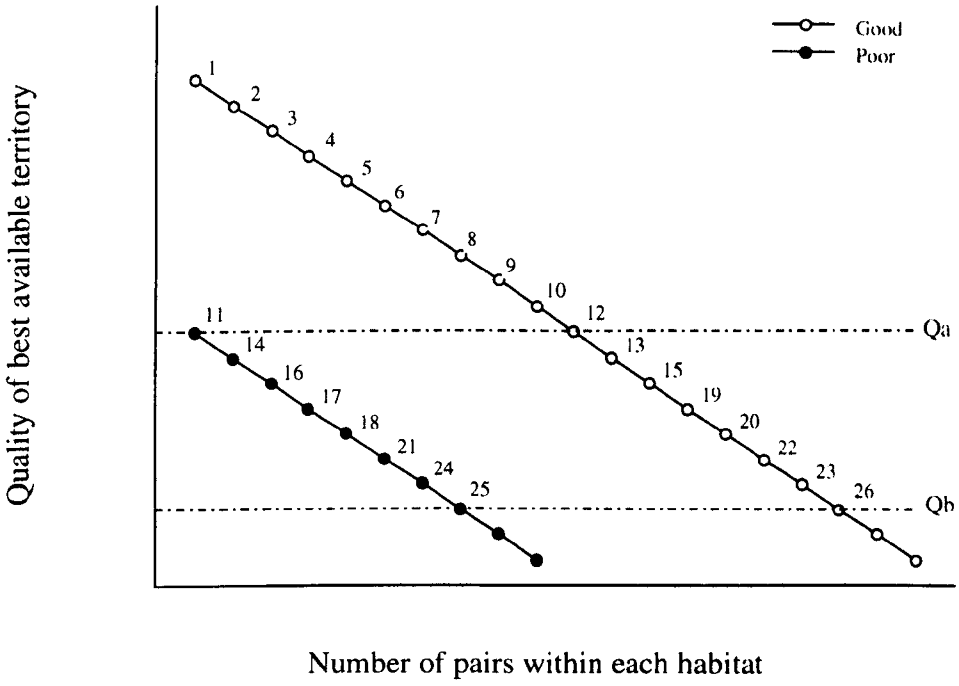


**Figure 8.5.** Patterns of individual distribution and sequence of territory occupancy (labelled) in good and poor habitats, following an ideal despotic or pre-emptive distribution (after Fretwell and Lucas 1970; Fretwell 1972; Pulliam and Danielson 1991). Initial settlers occupy the best territories in order of suitability, forcing additional birds into sites of lower quality. At the point where the best available site in the good habitat is of equal or lower quality than the best site in the poor habitat (Qa), birds will begin to settle both habitats, depending on the suitability of the best available site. Mean territory quality for the population declines with additional numbers of settlers, due to the occupation of increasingly poor sites, although the fitness of established birds remains unchanged. The model assumes a minimum quality threshold (Qb) and thus a finite number of suitable sites. Sites below the threshold may be suitable for self-maintenance, although not for breeding and hold non-breeding birds, or may be wholly unsuitable, where birds will be lost from the population through death or emigration.

respectively, Figure 8.6), additional birds are forced to remain as non-breeders or to occupy sites where the probability of successful breeding is low (Chapter 4). The mean success of lowland breeders is always higher than for upland breeders due to the inclusion of some double-brooded pairs, although under current conditions this difference is not significant. Significance differences in mean production may still exist, however, if the proportion of non-breeders differs between habitats. These predictions assume no habitat influences on the size of first clutches and that the potential for raising two broods within a season is primarily a function of territory, rather than individual, quality (See Chapter 5).

The relationships between population density and riffle area/river width in both autumn and spring (Chapter 3; Lennon 1988; Logie and Bryant 1995; Newton 1989), suggest that although upland sites may hold a comparable number of breeders to the lowlands (Figure 8.3), they will only persist at significantly reduced densities, and that this will then be reflected in the population levels found before birds are forced into unsuitable sites, where they may be unlikely to survive (Figure 8.7) or reproduce (Figure 8.6).

The processes likely to determine the size if breeding populations of dippers, and described above, are summarised in Figures 8.8 and 8.9. The size of autumn populations represents the numbers of survivors from previous years, and juvenile recruits, and in circum-neutral catchments this appears to be set by the availability of critical resource, principally food and roost sites. Territorial intolerance and density-dependent changes in mortality, related to dominance and mediated though dispersal and competitive exclusions from preferred sites, seem likely to match numbers to available resources over the late autumn and winter, and determine the size of the potential breeding population. The number of surviving birds that then breed is determined by the availability of suitable breeding territories, through territorial defence, and the interactions of individual and territory quality, and river flows. Additional effects identified in dipper populations elsewhere are represented by dashed lines on Figure 8.9. River flows are likely to be important throughout the year, influencing mortality (Clobert *et al.* 1990; Marzolin in prep.; Price and Bock 1983; Tyler and Ormerod 1994; Wilson 1996), and possibly also breeding probabilities through the

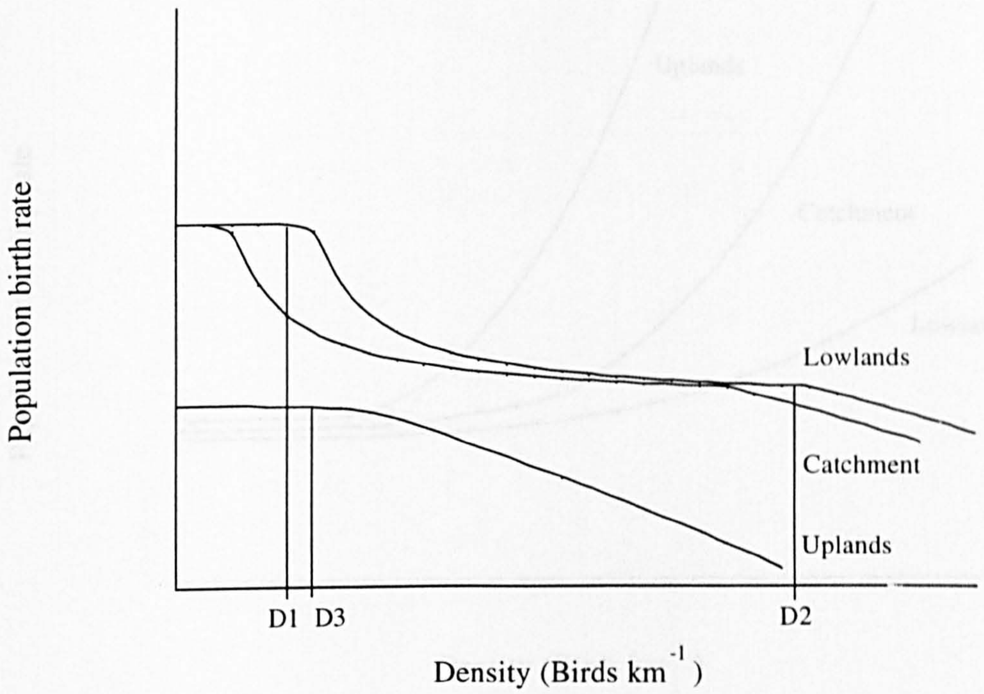


**Figure 8.6.** The influence of population size on mean breeding success within the Devon catchment. On lowland rivers at the lowest densities (densities below $D_1$) all individuals gain access to 'prime' sites and have the potential for double brooding. Later settlers lay only a single clutch each year and mean lowland production per pair tends towards the rate of single-brooded (upland) pairs. When all suitable breeding territories are filled (at densities above $D_2$ and $D_3$ for lowland and upland habitats respectively), additional birds are forced to remain as non-breeders or to occupy sites where the probability of successful breeding is low, reducing the mean population success. The relationships between population density and riffle area/river width in both autumn and spring (Chapter 3; Lennon 1988; Logie and Bryant 1995; Newton 1989), suggest that uplands sites will only support reduced densities compared to the lowlands before birds are forced into unsuitable sites.

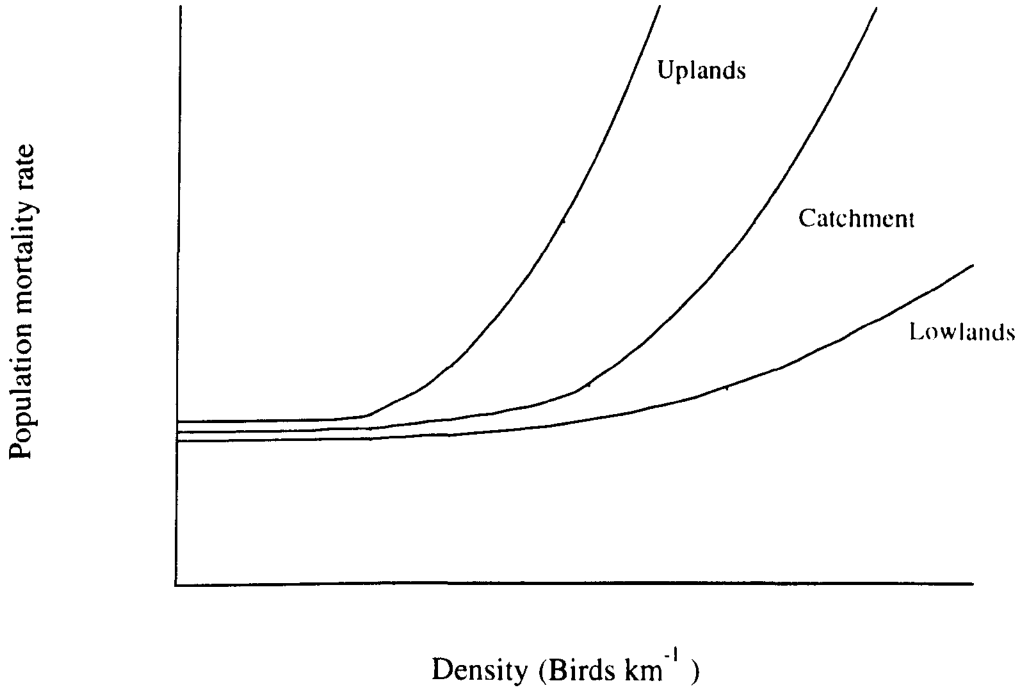


**Figure 8.7.** The influence of population size on mean population mortality within the Devon catchment. The relationships between population density and riffle area/river width in both autumn and spring (Chapter 3; Lennon 1988; Logie and Bryant 1995), and evidence that over-winter mortality is density-dependent and related to resource abundance (Chapter 4), suggest that upland sites will only support significantly reduced densities relative to lowland sites, and that this will be reflected in the strength of density-dependent mortality within each habitat.

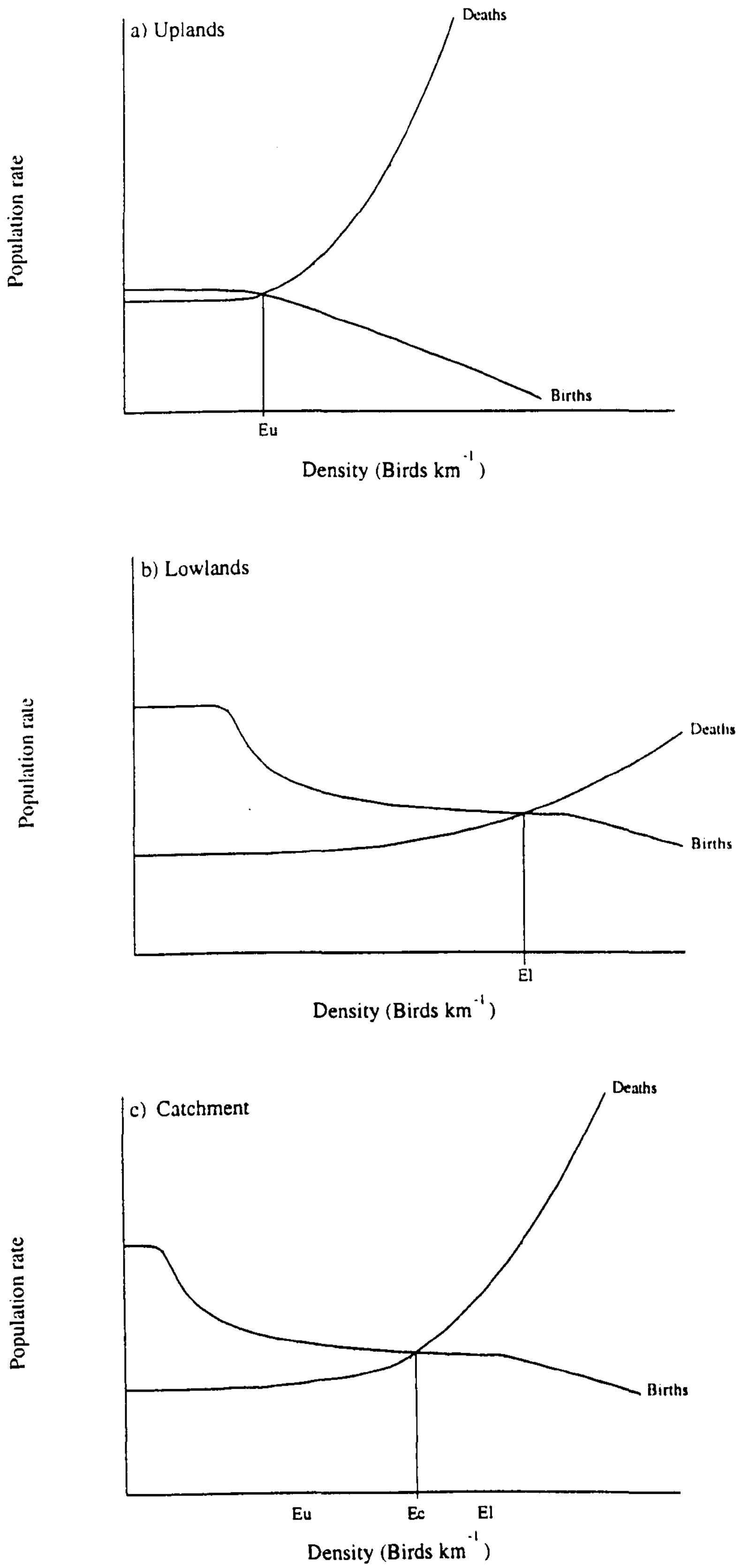


**Figure 8.8.** Likely processes determining the population size of dippers for a) upland sites, b) lowland sites and c) the Devon catchment, based on the balance between population mortality and reproductive rates (See Figures 8.6 and 8.7 for explanation). $E_U$, $E_L$ and $E_C$ predict the equilibrium population sizes for the uplands, lowlands and whole catchment respectively.

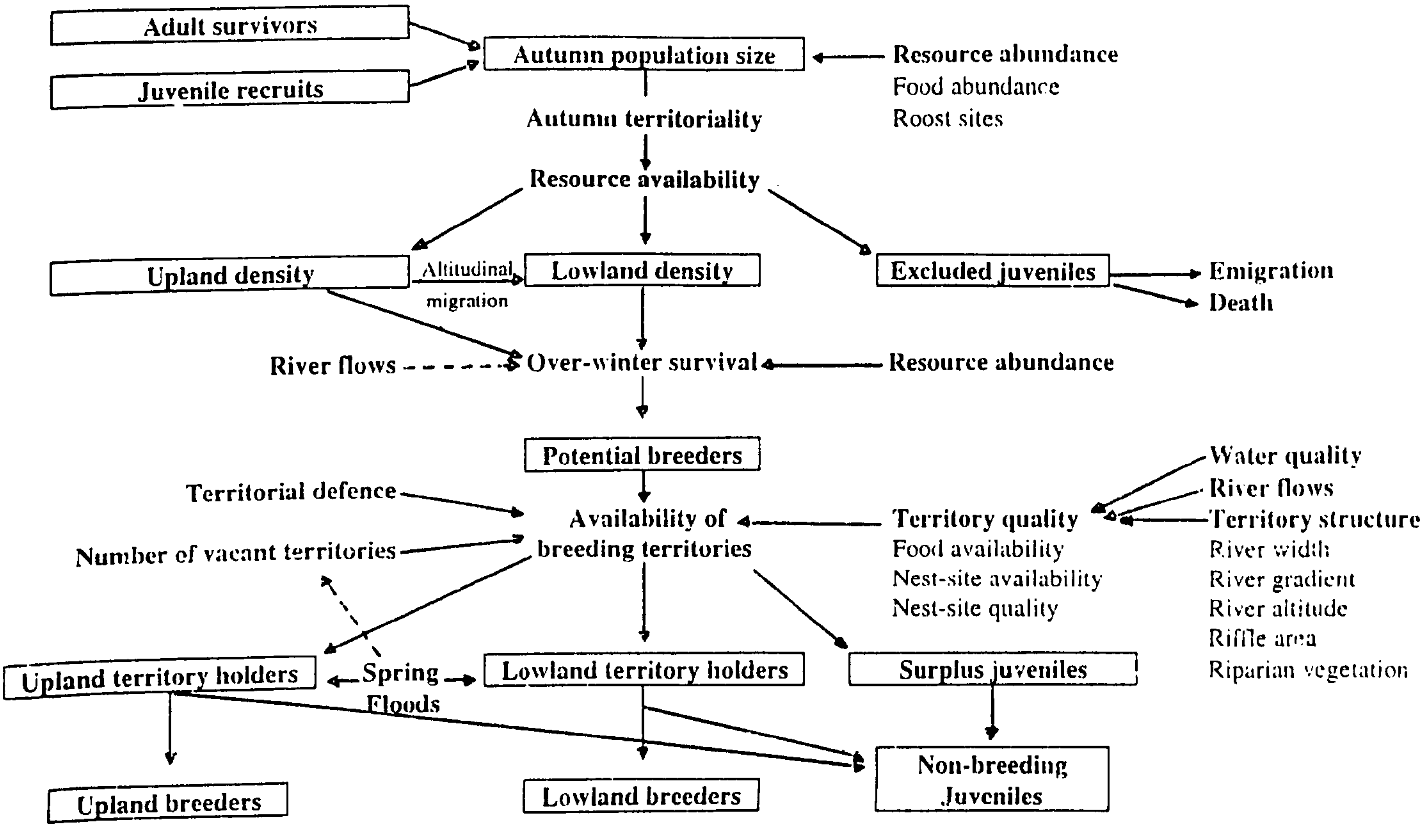


**Figure 8.9.** Summary of the likely processes determining the size of breeding populations in dippers.

death of territory holders and the creation of breeding 'gaps' (Clobert *et al.* 1990; Marzolin in prep.; Price and Bock 1983).

## 8.4. Likely determinants of habitat quality for dippers

The mechanism proposed above to regulate population size necessarily implies variation in habitat quality. The minimum requirements of any site are that it provides access to sufficient resources for self-maintenance, whilst a breeding territory must provide a suitable nest site and satisfy the energetic and nutritional requirements of breeders and their young. For dippers, variation in territory quality appears to be related to water chemistry, riffle area (governed by river gradient and width) and altitude through their influence on prey (and in the case of stream acidity, possibly nutrient) abundance, nest or roost site suitability, and the character of the riparian zone to supply and retain detritus for stream invertebrates and possibly also for the direct input of terrestrial prey (Dobson and Hildrew 1992; Martin 1987 for review; Price and Bock 1983; Ormerod *et al.* 1985, 1986; Richardson 1991; Vickery 1991, 1992; Chapters 3, 5, 6 and 7).

### 8.4.1. Territory structure as a measure of habitat quality within the Devon catchment

Differences in territory structure were apparently reflected in the probability of surviving to maturity via competitive exclusions from suitable habitats (Newton 1989a), of breeding (or breeding successfully) as a juvenile (Chapter 4), and for those birds raising young, in the timing of laying though the likelihood of initiating a second brood within a season (Chapter 5) and the post-fledging survival prospects of the young reared (Chapter 7). Within the Devon catchment, the date of laying was strongly related to river width, altitude and gradient (Chapter 5). Late-fledged young had significantly reduced post-fledging prospects and, although habitat differences in mean fecundity were slight, between 1985 and 1995, lowland-raised chicks accounted for c.57% of all fledglings ringed, but c.76% of autumn recaptures.

Pulliam (1996) and Sutherland (1996) suggest that, generally, habitat quality can be considered equivalent to the average fitness of the individuals occupying any site. The birds raising the most young each year all bred at lowland sites, yet this 'success' need not be reflected in greater fitness (and hence assumed habitat quality), if over a lifetime, upland birds recruit a similar number of young as breeders elsewhere, or the differences between adult mortality and juvenile recruitment (the rates of population growth) are the same.

There may be a trade-off between the benefits for reproductive success of maintaining a high quality lowland territory against a higher energetic demand and possibly reduced survival (Bryant and Newton 1994, 1996; Bryant and Tatner 1988; Newton 1989a), or between 'double-brooded' or 'single-brooded' strategies. Many experimental studies, for example, have demonstrated reproductive costs, showing that raising additional chicks can reduce the survival or reproductive success of both adults and young (e.g. Bryant 1979, 1991; Ekman and Askenmo 1986; Gustafsson and Sutherland 1988; Nur 1988 see Partridge 1989 for review). In natural situations, however, if the number of young raised reflects some aspects of individual or territory quality, it need not reflect the effort expended rearing young or the costs incurred in doing so, and results from correlative (non-manipulative) studies examining the relationships between brood size and reproductive costs have been equivocal (Hogstedt 1980; Partridge and Harvey 1985, 1988; Perrins and Moss 1975; Pettifor *et al.* 1988; van Noordwijk and de Jong 1986; see Partridge 1989 for review). Additionally, large size and high social status may be important in territory acquisition and/or survival (Arcese and Smith 1985; Ekman 1990; Hogstad 1989; Kikkawa 1980), although previous work within this populations has shown energy expenditure to be related positively to both dominance and body size (Bryant and Tatner 1988; Bryant and Newton 1994), and, other factors equal, maintaining lower levels of energy expenditure seems likely to have benefits for fitness (Bryant 1979, 1991; Daan *et al.* 1996; Ekman and Askenmo 1986; McCleery 1996; Nilsson 1994). Tyler and Ormerod (1985) even suggest that lowland birds may gain an energetic advantage by only having a small territory to defend. The relationships between habitat, population densities and 'fitness' thus remain unclear, and these cannot be examined adequately in cross-sectional studies because, generally, variation in individual performance relates closely to lifespan (Newton 1989b for review). In this sense lifetime studies of known individuals are required to examine possible trade-offs, allowing alternative strategies to be considered against a common goal, namely raising the maximum number of offspring over a lifetime that subsequently recruit to breed themselves.

### 8.4.2. Evidence of differences in habitat quality within the Devon catchment

Although variation in survival in relation to habitat quality remains an area requiring further investigation within this population, there was no indication that upland breeders survived longer than those in the lowlands (Chapter 6), in a way that might compensate for their lower seasonal reproductive success. Indeed, in the Devon catchment, the most successful breeders, both within a season and over a lifetime, all bred at ‘double-brooded’ lowland sites. Although differences in mean seasonal fecundity were slight, the indications were that lowland breeders did, on average, recruit more offspring than those breeding in the uplands, due in some cases to a greater seasonal production of young, although more usually, to the enhanced recruitment prospects of their young (Chapter 7). In contrast, in Northern France, Marzolin (in prep.) has shown that adult dippers occupying brooks (equivalent to upland streams in this study) have significantly reduced survival prospects relative to birds breeding on wide (lowland) rivers. These findings suggest that the upland/lowland distinction does represent a biologically appropriate classification of habitat quality at the broad scale. They are consistent with an ideal despotic or pre-emptive distribution of individuals between habitats suggested above (Fretwell and Lucas 1970; Pulliam and Danielson 1991), with the individuals occupying 'prime' sites gaining fitness benefits over those settling elsewhere.

The effects of competition are unlikely to fall equally among all members of a population, and Sibly and Smith (1985) and more recently Sutherland (1996) have highlighted the need to integrate population dynamics and individual behaviour. Identifying the processes determining where individuals settle and assessing the influence of habitat quality on production and mortality are central to understanding population regulation and dynamics, and explaining the patterns of lifetime reproductive success observed within populations (Bernstein *et al.* 1991; Pulliam and Danielson 1991; Newton 1989b).

## 8.5. The components of individual 'fitness'

Newton (1989b), in his synthesis, drew three main generalisations from the 23 studies of avian lifetime reproductive success within his book, namely that a large fraction (if not the majority) of fledglings fail to reach reproductive age, that not all individuals surviving to maturity (and not all breeders) subsequently produce offspring, and that successful individuals vary greatly in productivity. These generalisations apply equally to the dippers within this study (see Chapter 6), and the challenge remains to explain what factors determine the overall patterns of LRS within a population, and what attributes of the individual, in terms of genetic make-up or non-inherited features determined during development, influence how an it performs under the prevailing conditions (Grafen 1988; Newton 1994).

### 8.5.1. First-year survival

Consistent with many previous studies (e.g. Catterall *et al.* 1989; Hatchwell *et al.* 1996; Loery *et al.* 1987; Chapters in Newton 1989b; Newton 1989b for review), post-fledgling mortality accounted for the greatest losses at any stage within the lifecycle, apparently reflecting elements of inexperience including poor foraging abilities (Desrochers 1992; Greig-Smith 1985; Sullivan 1989; Yoerg 1994) low social status (Arcese and Smith 1985; Bryant and Newton 1994; Ekman 1984, 1990; Koivula and Orell 1988) and possibly incompetence with predators. Since entry into the breeding population is viewed as a competitive process, the proportion of young failing to recruit was apparently determined by the number of breeding gaps created through adult mortality, and this general pattern of LRS reflected the prevailing population mortality and reproductive rates. As considered above, the probability of entering summer and early autumn populations reflected differences in individual status, linked to early settlement and some aspects of dominance and/or body size (Chapter 7, Newton 1989a). Newton (1993) has suggested that juvenile males in better condition (as judged by pectoral muscle thickness) were more likely to survive over-winter, although beyond the first autumn, the attributes determining which individuals within the population were most likely to survive or raise young appeared unclear (Bryant and Newton 1994, 1996; Newton 1989a).

### 8.5.2. Age effects and lifetime reproductive success

McNamara and Houston (1996) considered that an individual's ability to survive and reproduce should best be represented by its current 'state', a measure combining territory or environmental quality, with attributes of the individual animal, such as body size, experience, social status and current physiological or nutritional condition. Conventionally, many of the differences between individuals have been considered mainly with reference to age, often a correlate of some elements of 'quality', with older animals generally more successful than juveniles (e.g. Bryant 1979, 1989; Coulson and Thomas 1985; Daan *et al.* 1990; Desrochers 1992; Nol and Smith 1987; Perrins and McCleery 1985, 1989; Thompson 1992; see Curio 1983 and Saether 1990 for reviews).

Lifetime studies provide the most appropriate method for examining age-related trends in survival and breeding performance yet, in contrast to many other studies (e.g. Bryant 1979, 1989; Coulson and Thomas 1985; Daan *et al.* 1990; Desrochers 1992; Chapters in Newton 1989; Nol and Smith 1987; Perrins and McCleery 1985, 1989; Thompson 1992; see Curio 1983 and Saether 1990 for reviews), no age effects were apparent in dippers in any measure of production until fledging, and age had no detectable influence on lifetime production that was not attributable to breeding lifespan (Chapter 6; Clutton-Brock 1988, Newton 1989b for reviews). Within the Devon catchment, previous work has shown that older females are able to adopt more efficient incubation regimes (Bryan 1996; Ward 1992) and maintain lower levels of energy expenditure during brood-provisioning (Bryant and Tatner 1988) than younger birds, both of which seem likely to have benefits for fitness (Bryant 1979, 1991; Daan *et al.* 1996; Ekman and Askenmo 1986; Nilsson 1994; Tinbergen *et al.* 1985). Daan *et al.* (1996), for example, have shown for kestrels that post-breeding mortality increases with higher levels of daily energy expenditure during breeding.

Seasonal declines in recruitment probabilities are well documented in birds (e.g. Brinkhof *et al.* 1993; Cave 1968; Dow and Fredga 1984; Hochachka 1990; Newton and Marquis 1984; Norris 1993; Ormerod and Tyler 1993; Perrins 1970; Perrins and McCleery 1991; Verhulst and Tinbergen 1991; Verhulst 1995), and individual females did lay, on average, more than 5 days earlier as adults than they had done as juveniles (Chapter 5). Yet the significance of only a few days advancement in laying remains unclear, particularly given the broad groupings used to examine the seasonal trends in survival within this study (Chapter 7). Perrins and McCleery (1991), however, showed that the numbers of surviving great tits declined by up to 10% for each days' delay in fledging, with an average of 3.7% per day over 37 years of study. Clearly, with such a strong seasonal decline in the 'value' of fledglings, any advancement in laying date is likely to represent an important means of enhancing seasonal and lifetime reproductive success. However, perhaps more importantly, all surviving birds appeared to gain breeding territories by their second year. Indications that non-breeding juveniles could not compensate later for their 'lost' first year production in this and many other species (e.g. Dhondt 1989; Newton 1991; Sternberg 1989; Chapter 6), and that, within the Devon catchment, birds excluded to 'fringe' sites appeared to have significantly lower lifetime production of autumn recruits, provide further support for the view that, even amongst those birds surviving to maturity, social behaviour actively excluded some individuals from adopting the most successful lifetime reproductive strategies (Chapters 6 and 7). The relationship between river flow and first-year breeding probabilities suggests that this may be of greater importance for some cohorts than others, and even for recruits, chance may be an important component of LRS (Figure 6.6; Bryant 1989; Korpimaki 1992; Thomson *et al.* 1992).

### 8.5.3 Phenotype and lifetime reproductive success

The role of phenotype in determining LRS is still poorly understood, even though the mechanism proposed to match population size to available resources necessarily implies individual differences in status, competitive ability and responses to competition. Analyses failed to identify any phenotypic traits that appeared to confer 'fitness' or enhance the success of individual breeders. Similarly, in previous studies within this population, although social status was closely related to both age and sex, body size, mass and size adjusted mass (often referred to as body condition) all appeared to be poor predictors of survival and dominance (Bryant and Newton 1994, 1996; Newton 1989a). Possibly, because recruits represent only a subset of young fledged the previous year, and the post-fledging period not only accounts for the greatest losses at any stage in the life-cycle but appears to be linked with competitive interactions, much of the selective mortality may have already occurred by the first autumn. Additionally, dominance may be critical for the establishment of juveniles within a population, yet once established site-related factors may take precedence over status (Dearborn and Wiley 1993). The significant seasonal decline in post-fledging survival within this population suggests that site-related factors, such as early settlement, and not necessarily tied to phenotypic differences, may be important in the initial establishment of dominance relations (Chapter 7; Choe 1994; Davies 1978; Krebs 1982).

### 8.5.4. Interactions between individual and habitat quality in determining seasonal and lifetime reproductive success

Within the Devon catchment the quality of the habitat a bird occupied was critical in determining lifetime reproductive success (Chapters 5, 6 and 7). Breeders were more successful in the lowlands than uplands, and laying date, which influenced post-fledging survival and the probabilities of double-brooding, varied greatly with habitat structure but much less so between age-classes (Chapters 5, 6 and 7). Evidence that movements of breeders within habitats could increase seasonal reproductive success (Chapter 6), and that river flows appeared to have a strong influence on the breeding success of first-year, although not adult, birds (Chapter 4) suggests some interaction between individual and territory quality, with these effects likely to be additive. Age specific patterns in survival, breeding probabilities (Chapter 4), dominance (Bryant and Newton 1994, 1996; Newton 1989a), female laying date (Chapter 5) and evidence of the role of individual status is determining settlement patterns (Newton 1989; Chapter 7) confirm that individual traits did influence performance. Newton (1991) has suggested that similar patterns may be important in sparrowhawks, showing that when given access to breeding sites following the experimental removal of territory holders, 'surplus' birds were less successful than average, apparently reflecting their low competence in some aspects of breeding. What is clear is that lifetime fledgling production varies greatly even for those individuals surviving to maturity, and seasonal patterns in post-fledging survival which are strongly tied to habitat structure, seem likely only to accentuate this skew.

### 8.6. Habitat heterogeneity, and population and meta-population processes

To date, the inability to link population densities to demographic processes has been a major shortcoming when considering the decline in dippers on many acidified rivers. For conservation and management it is important to identify source habitats (Pulliam 1988), particularly if they represent only a small proportion of the landscape, because they are critical for population maintenance. Thus, a principal aim of this work was to consider the role of reproductive success in the population and meta-population dynamics of dippers.

Assessments of meta-population dynamics, where demography is considered across a set of local populations linked by dispersal, requires data on survival, reproduction and dispersal at several neighbouring sites. Source and sink habitats have often been classified in the absence of reliable data on habitat specific recruitment rates (Blondel *et al.* 1992; Foppen and Reijnen 1994a, b; Hatchwell *et al.* 1996; Holmes *et al.* 1996; Newton 1991; Pulliam 1996 for review; Smith *et al.* 1996), a problem equally pertinent within this study. At least for breeding dippers, however, reliable estimates of survival are now available from this population, and the strong and consistent relationships between stream acidity and reproductive success (Ormerod and Tyler 1987; Ormerod *et al.*1991; Vickery 1992; Vickery and Ormerod 1991) suggests that pooling data from this study and others is likely to yield valuable insights into population processes, and allow predictions to be made about the status of populations elsewhere based on likely demographic limits.

#### 8.6.1. Source and sink habitats

Pulliam (1988) describes a 'source' as a population in which births exceed deaths and emigration exceeds immigration, and a 'sink' as a population where deaths exceed births and immigration exceeds immigration. A graphical separation of source and sink populations based on mean seasonal production of fledglings and pre-breeding survival rates is shown on Figure 8.10.a. The pre-breeding survival required to match all adult losses is represented as a reciprocal function; a simple example being that with 50% adult survival, and one recruit needed from each pair each season to balance breeder mortality requires pre-breeding survival rates of 1/2, 1/3, 1/4 and 1/5 for mean clutch sizes of 2, 3, 4 and 5 respectively. All populations where the combination of mean first

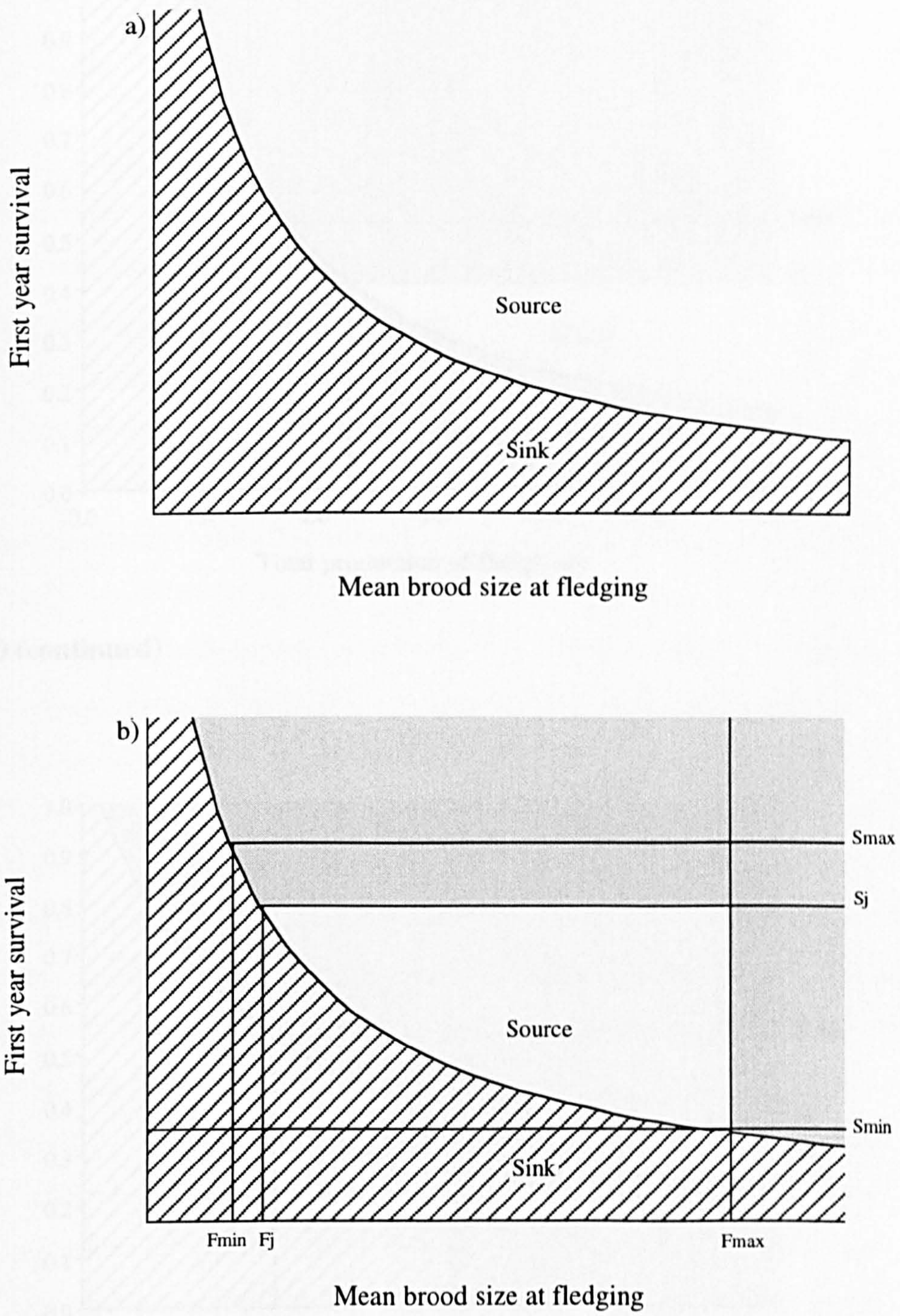


**Figure 8.10.** Graphical separation of **a)** sink and potential source populations, and **b)** sink and realised source populations, based on mean seasonal production of fledglings, mean first-year (pre-breeding) survival rates, and species demographic limits (See text for explanation). Within populations a maximum survival rate (Smax) and associated minimum fecundity for persistence (Fmin) is likely to exist, even under optimal conditions. Maximum pre-breeding survival rates (Sj) are likely to be somewhat lower, however, increasing the minimum required fecundity (Fj), due to elements of juvenile naivety, inefficiency and inexperience. Minimum rates of pre-breeding survival are also likely to exist (Smin), determined by constraints on the ability of parents to produce and raise young (Fmax). **c)** Likely separation of source and sink populations for dippers, based on current knowledge. With Smax at 53.2% (this study), a minimum mean seasonal production (Fmin) of 1.76 fledglings pair is required for population persistence. Fj is 2.60 with pre-breeding survival at 36% (Galbraith and Tyler 1982).

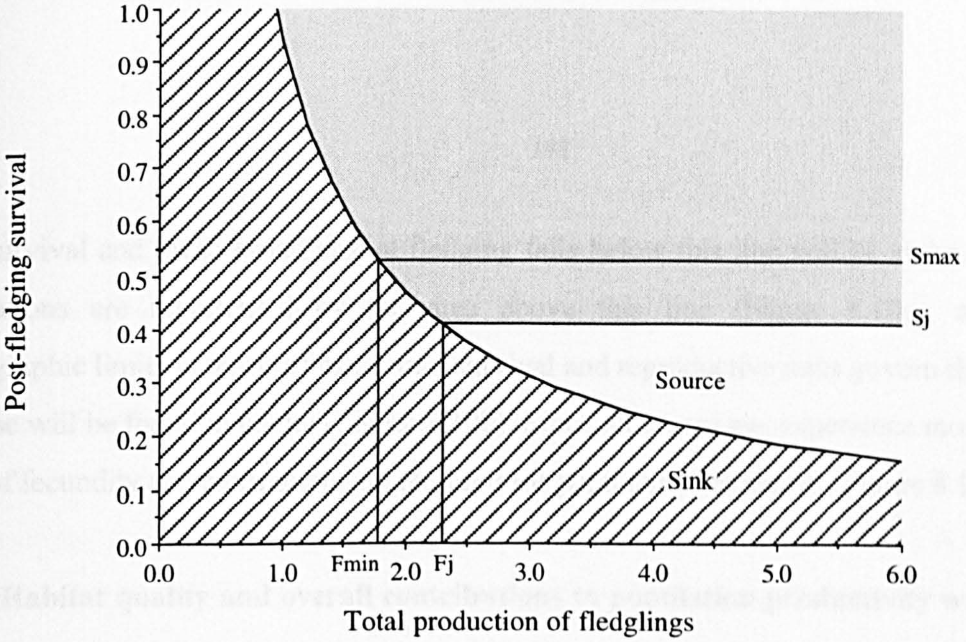


**Figure 8.10 (continued)**

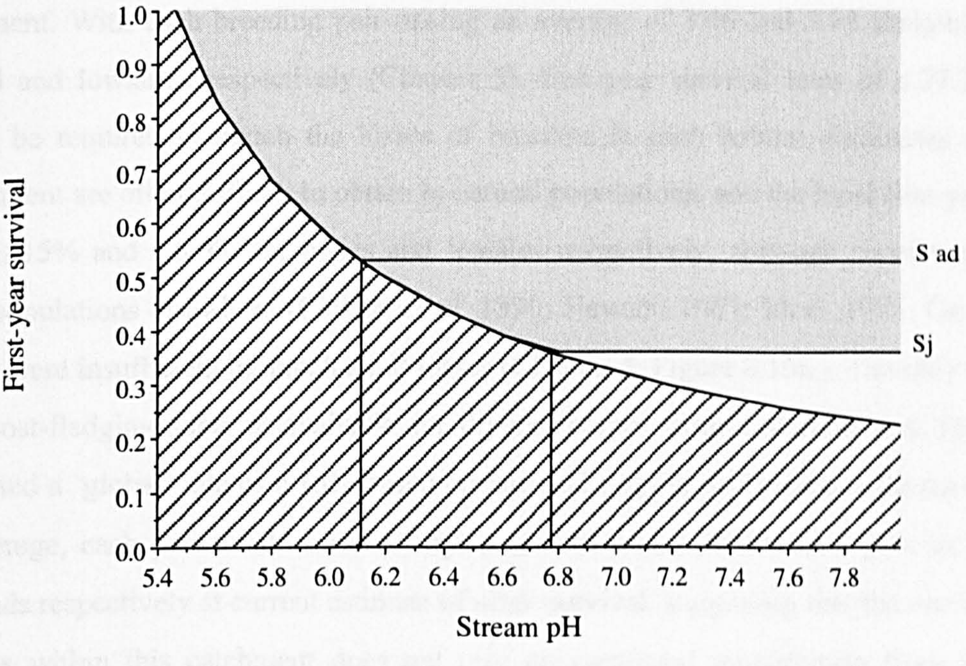


**Figure 8.11.** Likely separation of source and sink habitats for dippers, based on current knowledge. The figures are calculated with Brood size=-7.91+1.68*pH* (successful nests only, after Vickery 1992) and assuming nest success at a national mean of 75% (calculated as the mean from this study, Ormerod *et al.* 1991, Shaw 1979 and Vickery 1992), adult survival (S ad) at 53.2%, (this study) and pre-breeding survival (Sj) at 36% (Galbraith and Tyler 1982).

year survival and mean brood size at fledging falls below this line will be sinks. Potential source populations are represented by the area above this line (Figure 8.10a), although species demographic limits in terms of maximum survival and reproductive rates govern that only a portion of these will be found in nature (Figure 8.10b). Since all organisms experience mortality, minimum rates of fecundity and recruitment are required for populations to persist (Figure 8.10b).

### 8.6.2. Habitat quality and overall contributions to population productivity within the Devon catchment

Figure 8.10.c shows the likely separation of source and sink populations for dippers, based on the relationship between mean seasonal fledgling production and the minimum first-year survival required to replace adult losses at the 53.2% annual adult survival estimated for the Devon catchment. With each breeding pair raising an average of 3.46 and 3.88 fledglings a year in the upland and lowlands respectively (Chapter 5), first year survival rates of c.27.2% and c.24.2% would be required to match the losses of breeders in each habitat. Estimates of dispersal and recruitment are often difficult to obtain in natural populations, and the local first-year survival rates of c.10-15% and c.6-9% for males and females respectively, although consistent with estimates from populations elsewhere (Clobert *et al.* 1990; Hewson 1967; Moss 1975; Ormerod and Tyler 1994), were insufficient to match adult losses (Chapter 4; Figure 8.10a.). The only estimate of first-year post-fledging survival available for dippers comes from Galbraith and Tyler (1982), who estimated a 'global' rate of c.36% based on national ringing recoveries. With survival at this rate, on average, each pair would raise a surplus of 0.82 and 1.20 chicks a year in the uplands and lowlands respectively at current estimate of adult survival, suggesting that the occupation of upland streams within this catchment does not rely on continued immigration from more productive lowland sites. Rather, as noted previously, competitive interactions appear to limit the local recruitment of upland-raised young (Chapter 7; Newton 1989a). The process proposed to match population size to resource abundance, however, necessarily implies that a proportion of the total population will occupy marginal (usually upland) habitats, where they fail to survive or reproduce.

This is likely to reflect competitive exclusions at high densities and does not indicate the unsuitability of all upland habitats.

### 8.6.3. Stream acidity and population persistence

Figure 8.11. displays the relationship shown in Figure 8.10.c. but with production replaced by pH, known to be a principal determinant of clutch and brood sizes (Ormerod and Tyler 1987; Ormerod *et al.* 1991; Vickery 1992; Vickery and Ormerod 1991). Even if the first-year survival could match the adult rate of 53% (and assuming no acidity effects on adult survival), Figure 8.11. suggests that rivers with pH less than 6.1 would not be able to support breeding populations in the absence of immigration, whilst with survival at the rate of 36% predicted by Galbraith and Tyler (1982), populations on streams with acidity greater than pH 6.75 appear unlikely to persist (Figure 8.11). This is unlikely to be the full story, however, since the calculations are based on first broods only, and thus take no account of second-breeding attempts. Moreover, Vickery (1992) acknowledges that an apparent divide exists at pH 6.5, above which stream acidity has no influence on breeding production, and the fitted (straight) line is unlikely to adequately describe the relationship between reproductive success and stream acidity. In particular, the apparent consistency in reproductive success above pH 6.5 acts to reduce the slope of a single fitted regression line, and Vickery's (1992) equation seems likely to under-estimate the impacts of acidity on breeding success for acid streams (pH<6.5). Unfortunately, the data presented do not allow the fit of alternative curves to be assessed, although as stated by Vickery (1992), and evident from data presented elsewhere for both Welsh and Scottish sites (Vickery and Ormerod 1991), a sigmoidal fit would seem to be more appropriate. Evidence that current (linear) relationships are inadequate biologically, comes from a comparison of the relationships presented between acidity and brood size (first broods only) and total production (first and second broods combined) (Vickery 1992). The fitted lines predict that second broods increase seasonal production most markedly on the acid streams (where they are entirely absent), and yet have little influence on the success of birds on circum-neutral rivers. These inferences conflict with the data on which they are based.

In spite of the large body of literature detailing the breeding biology of dippers (See Tyler and Ormerod 1985, 1994 and Wilson 1996 for reviews), only three British studies (this study, Vickery 1992; Ormerod *et al.* 1991) and Price and Bock (1983) estimate total seasonal success, or provide the necessary information on the frequency, success and size of first and second broods needed for its calculation. Table 8.1. displays the estimates of total fledgling production from these studies and the post-fledgling survival rates required to replace all adult losses assuming 53.2% adult survival. With reference to Figure 8.10.c., the data provided by Vickery (1992) and Ormerod *et al.* (1991) predict that dipper populations occupying acid streams in South-west Scotland are unable to produce enough young to replace adult losses.

In upland Wales, Ormerod *et al.* (1985) recorded few breeding dippers on streams with pH <6.0, although Vickery (1991, 1992) recorded dippers breeding in south-west Scotland at pH 4.5. If as suggested within Chapter 3 the current UK critical load exceedance estimates do represent a biologically appropriate classification of river 'quality' on a broad scale, consistent with Pulliam's (1988) source-sink model, many of Britain upland rivers, currently occupied by breeding dippers (Battarbee 1992, 1993; Gibbons *et al.* 1993), appear unlikely to produce enough offspring to match adult mortality in some, or possibly all, years (Table 8.1), and are only likely to persist with continued immigration from more productive (circum-neutral) catchments elsewhere.

### 8.6.4. Species demography, and reproductive success as a measure of population 'status'

An important caveat of the approach used here is that relatively little is known about the variability of species demography in passerines. For example, Kluyver (1970), reported that the removal of 60% nestling great tits resulted in a doubling in adult survival, whilst Blondel (1985) found that blue tits and coal tits *Parus ater* in southern France reared almost three times as many young as those on Corsica, although both populations were apparently stable. Relationships within the Devon catchment (Figure 4.2) suggest that in situations of low relative population size a greater proportion of the juveniles may survive to fill vacant territories (See also Clobert *et al.* 1990), and possibly, adult survival may also be higher in situations with reduced competition from juveniles (Kluyver 1970).

**Table 8.1.** Comparison of total seasonal production of fledglings (first and second broods combined±standard deviation where available) and the post-fledgling survival rates required to replace all adult losses at 53.2% adult survival, in relation to habitat type.

| Habitat type | Seasonal production | First-year survival | Reference |
|---|---|---|---|
| Acidic (pH<6.0) | 2.52 | 37.1 | Ormerod *et al.* (1991) |
| Circum-neutral (pH>6.0) | 3.75 | 25.0 | Ormerod *et al.* (1991) |
| Acid (pH<6.5) | 2.08±1.37 | 45.0 | Vickery (1992) |
| Non-acid (pH>6.5) | 4.40±1.79 | 21.3 | Vickery (1992) |
| Circum-neutral | 3.0 | 31.2 | Price and Bock (1983) |
| Upland circum-neutral | 3.46±1.85 | 27.1 | this study |
| Lowland circum-neutral | 3.88±2.44 | 24.1 | this study |

Most probably, chance losses, predation and environmental stresses all remove a fraction of the population independently of other processes, and the pre-breeding survival rates of naive and inexperienced juveniles are unlikely to match the adult survival rate under any conditions (Galbraith and Tyler 1982; Perrins 1991). Further, young entering poor habitats may be likely to show reduced survival if opportunities for self-feeding are limited, or growth is incomplete at the time of fledgling (Hochachka and Smith 1991; Nilsson and Smith; Smith *et al.* 1989; Tinbergen and Boerlijst 1990). Moller (1995), for example, not only showed that young blackbirds raised in poor habitats were of lower quality (as judged by fluctuating asymmetry), but suffered greater mortality than those raised elsewhere.

The delayed laying, reduced chick growth and lower egg to fledgling survival recorded on some acid streams are inconsistent with any optimisation of post-fledging survival, instead appearing to reflecting resource scarcity and poor habitat quality (Ormerod *et al.* 1991; Ormerod and Tyler 1991, 1993; Vickery 1992; Chapter 7). Rate of energy gain may be a valuable correlate of habitat quality if the time devoted to foraging conflicts with other, possibly fitness-enhancing behaviours, such as vigilance, territorial defence, mate guarding, incubation and/or the provisioning or guarding of young (e.g. Drent 1975; Gosler *et al.* 1995; Hogstad 1988; Lijjeld and Slagsvold 1986; Lima and Dill 1990; Newton 1991; Zicus *et al.* 1995), and O'Halloran *et al.* 1990 have shown that although dippers on acid streams do not have significantly greater daily energetic demands, they are required to devote a significantly greater proportion of the active day to foraging activities (see also Logie 1995). Consistent with this being indicative of poor habitat quality, Tyler and Ormerod (1994) suggest that both breeding and juvenile dippers may have reduced survival prospects on acidic relative to circum-neutral streams, albeit in the absence of formal analyses. Perrins (1991) suggests that factors reducing production, such as acidity, will also decrease the survival of both adults and young in parallel, and if so, it seems that the range of conditions predicted as source habitats (Figure 8.11.) represent 'best case' estimates.

## 8.7. Population size and habitat quality in dippers: Conservation implications and conclusions

Practical considerations often necessitate directing conservation efforts towards small portions of a habitat, thus for effective conservation a means of reliably assessing the 'value' of sites is crucial. The strength and consistency of the relationships between population densities, reproductive success and stream acidities, suggest that the status of dipper populations can be adequately and reliably assessed from external correlates, such as stream acidity (Vickery and Ormerod 1991; Logie *et al.* 1996). Yet, this cannot be inferred without a knowledge of the links between habitat, species distribution and demography, and although correlations between population distributions or densities and environmental conditions may highlight some features of habitat suitability, a knowledge of the conditions for individual survival or successful breeding alone is often insufficient to reveal the status (in terms or growth or decline) or 'health' of populations. In this respect, the relative balance between recruitment and mortality is paramount, and for long-term viability populations must, on average, be able to raise sufficient young to match all adult losses. In this context, a comparison of the upland Devon catchment with acidic streams elsewhere is illustrative. Both represent sub-optimal habitat and are occupied, and apparently persist, at reduced densities relative to lowland, circum-neutral rivers (Logie 1995, Logie *et al.* 1996; Newton 1989a; Ormerod *et al.* 1985, 1986). Upland populations, however, appear able to maintain a positive balance between juvenile recruitment and breeder mortality as illustrated by the (potential) levels of surplus production within the upland Devon catchment. This is not the case for dippers on acid streams (Table 8.1; Figure 8.10c).

Generally, populations cannot be considered in isolation and continued occupation need not reflect habitat suitability if an exchange of individuals is likely between sites (Pulliam 1988). 'Despotic' distributions seem common in territorial species (See Parker and Sutherland 1986 for review), and where competitive interactions interfere with habitat choice individuals may be forced to emigrate or to live and breed in marginal habitats. The processes suggested to match dipper population size to available resources within the Devon catchment necessarily implies this, and provide a mechanism likely to drive the non-random dispersal of individuals from source to sink habitats. Individuals in 'prime' habitats will contribute disproportionately to total production, not only within populations, with implications for individual fitness and gene flows, but across sites influencing species distributions. In the case of dippers, the loss or degradation of 'prime' circum-neutral lowland habitat may be of particular concern because this is where recruitment exceeds mortality to the greatest extent, although the surplus proportion at similar upland sites may still be crucial in population maintenance if, as is the case in many catchments, they are abundant relative to optimal lowland sites (Bernstein *et al.* 1991).

Although this study has highlighted that dipper populations on acid streams are unlikely to persist based on current levels of production alone, it has not shown that the observed population levels on these streams are limited by recruitment. Work on dippers within the Devon catchment and elsewhere (Chapters 3, 4; Clobert *et al.* 1990; Marzolin in prep; Price and Bock 1983) and many other species, shows that external limiting factors are often important in determining population size (Arcese *et al*, 1992; Brown 1969; Klomp 1972; Lack 1954, 1966; McCleery and Perrins, 1985; Newton 1991, 1980, 1992 for review; Nilsson, 1987; Southern 1970; Tinbergen

1957; Tinbergen *et al.* 1985; Village 1983). The strong consistency of autumn densities with stream acidity between remote sites suggests that, for dippers, food availability is crucial (Logie 1995; Logie *et al.* 1996; Vickery 1991; Ormerod *et al.* 1985, 1988; Ormerod and Tyler 1987), and on circum-neutral streams, territorial intolerance and density-dependent changes in mortality, related to dominance and mediated though dispersal and competitive exclusions from preferred sites, seem likely to match numbers to available resources over the late autumn and winter. If suitable habitat is available on acid streams although it remains unoccupied it would suggest that resource availability is not limiting, focusing attention back on the role of recruitment, either in terms of local breeding success or juvenile dispersal.

As yet, it remains unclear whether the observed patterns of population density reflect local reproductive success, resource abundance, or a combination of these, coupled with reduced immigration and enhanced emigration rates. Extensive studies in Wales, for example, have shown that the exchange of dispersing juveniles usually only occurs between neighbouring catchments, and remote assessments of water quality predicts that acidic catchments are likely to be clumped (Battarbee 1992, 1993). Thus distributions may reflect both habitat selection and dispersal ability, and although dispersal appears central in population regulation and the continued occupation of some fringe sites (Gadgil 1971; Levin 1976; Lidicker 1962), the processes by which birds find and settle in new habitats remains relatively poorly known in dippers (Newton 1989a; Tyler *et al.* 1990), and passerines in general (Greenwood 1980; Greenwood and Harvey 1982; Pusey 1987). Tyler and Ormerod (1994) suggest that to some extent, all of these processes may be important, and possibly experimental manipulation may provide the most appropriate means of considering the relative importance of each. Manipulation has been shown to of value in unravelling causality in the processes leading to declines in grey partridges, for example (Potts and Aebischer 1991; Rands 1985), and previously Newton (1989a) has shown that summer manipulations of population density are feasible with juvenile dippers. Whether manipulation of food availability at the river or catchment scale is achievable or appropriate remains unclear.

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