Thesis
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RECRUITMENT DYNAMICS OF A RESIDENT PASSERINE: DIPPERS *Cinclus cinclus* IN SCOTLAND

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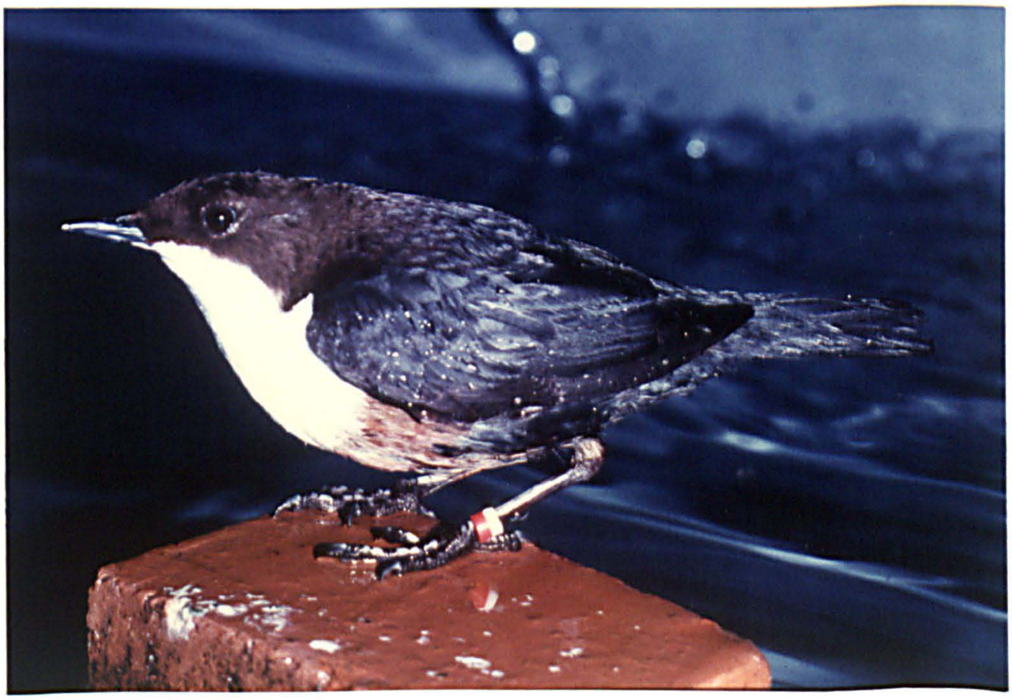
" Cottlestone, cottlestone, cottlestone pie,
why does a Dipper ?
I don't know why . . . . "



ABSTRACT

1. This thesis presents the results of a population ecology study of the Dipper *Cinclus cinclus* in the western Ochil Hills, Tayside and Central Regions, Scotland between April 1985 and May 1988.

2. Particular attention was given to factors affecting juvenile survival between fledging and recruitment to the breeding population. These included investigation of the variation and significance of body size, plumage colour, dispersal distance, home range acquisition, dominance status and autumn body condition.

3. Overwinter survival was higher in adults than juveniles. Juvenile females had a greater overwinter survival and recruitment rate than juvenile males. Few body size measures were consistently associated with overwinter survival, though juvenile females with longer wings and tarsi tended to survive better.

4. Males had higher plumage brightness scores than females and, within sexes, adults were brighter than juveniles. Overall, survival overwinter and recruitment were not related to plumage brightness.

5. A laboratory test arena was developed for assessing dominance relations in small groups of temporarily captive birds. Social status between age and sex classes was correlated with plumage brightness. Within age classes, plumage brightness was a significant predictor of status in adults, but body size was more important in juveniles.

6. Females settled farther from their natal sites than males; most of this dispersal was completed soon after independence. The relationship between dispersal and dominance is discussed and a model developed.

7. Autumn population density was manipulated locally in a series of experimental juvenile introductions. Numbers rapidly returned to initial levels, though earlier released individuals persisted for longer. About 20% of introduced birds recruited, mainly higher status males.

8. Body composition of a small sample of birds collected between September and April is described. Lipid stores were greatest in winter and least in spring. A method for measuring pectoralis muscle thickness was developed using an ultrasound-based technique.

9. Condition indices derived from "ultrasound" measurements on live birds were used to evaluate the importance of protein reserves in overwinter survival. Males in good condition in autumn were more likely to recruit but no trend was apparent in females.

10. Two periods of high juvenile losses were identified: post-independence and late autumn. Predation could only be implicated in the former. The agent of late autumn losses was not proven but probably involved territorial intolerance and the consequent exclusion of subordinates to fringe habitats. It is concluded that density-dependent changes in mortality, related to dominance and mediated *via* dispersal, caused Dipper numbers to be matched to available resources, principally food and breeding territories.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1. POPULATIONS, INDIVIDUALS & RECRUITS

The key reviews of wild bird populations by Lack (1954, 1966) have had a guiding influence on research in avian ecology. A central theme of Lack's (1966) studies was the evolution of reproductive rates by natural selection, whereby the number of surviving offspring per pair is maximised. They have also been concerned with the demographic consequences of variability in survival and mortality, dispersion, dispersal and immigration and the impact on populations of factors such as food supply, weather, predators, disease and habitat (Cody 1971, Ricklefs 1977a, 1977b, Stonehouse & Perrins 1977, Newton 1979, Klomp & Woldendorp 1980). More recently, the behavioural aspects of ecology have been a focus of attention, both illustrated and stimulated by Krebs and Davies (1978) review volume. The approach adopted here in the study of Dipper *Cinclus cinclus* involves elements of both population and behavioural ecology, specifically focussing on the significance of behavioural variability in its relationship to the fitness of individuals. Hassell & May (1985) and Smith & Sibly (1985) have stressed the need for contemporary studies to integrate these two themes to produce a more coherent synthesis of the importance of selection on individuals in overall population processes.

The role of individuals within populations (Lomnicki 1988) is now attracting more attention as researchers recognise individual variability within and amongst sex and age classes in their behavioural responses, body size and plumage characters. Clutton-Brock *et al.* (1982) pioneered this approach in treating the two sexes of their Red Deer *Cervus elaphus* population as two entities with markedly different life history strategies.

Interest in individuals has come to the fore with the publication of "Reproductive Success: studies of individual variation in contrasting breeding systems" (Clutton-Brock 1988), itself a benchmark in our understanding of the lifetime contribution of recruits by different individuals. In some species, the number of young fledged is a reliable indicator of the number of young subsequently recruiting to the breeding population (Newton 1985, Hötker 1988). However, such findings can only be generalised after long term studies of relatively sedentary resident species or those migratory species highly philopatric to breeding or wintering ranges (Tinbergen *et al.* 1987, avian contributions to "Reproductive Success", Clutton-Brock 1988, Pettifor *et al.* 1988). This focus on reproductive rates and recruits sometimes diverts attention from events between a young bird fledging and its eventual entry into the breeding population. Investigations of short-lived passerines, or other resident bird species that attempt to breed at the end of their first year, may give rapid insight into factors affecting recruitment as only two age classes exist: first year birds (or juveniles) and adults. Some of the key long-term population studies of temperate species that have followed events and processes during the "juvenile year" include the Mandarte Island, British Columbia, Song Sparrows *Melospiza melodia* (Smith *et al.* 1980, Arcese & Smith 1985, Arcese 1987, 1989), Great Tits *Parus major* in the Netherlands (Drent 1983, 1984), Sparrowhawks *Accipiter nisus* in the south of Scotland (Newton 1986), Nuthatches *Sitta europaea* in Sweden and Belgium (Enoksson & Nilsson 1983, Enoksson 1987, 1988, Matthysen 1986, 1987, Matthysen & Schmidt 1987) and Marsh Tits *Parus palustris* in Sweden (Nilsson & Smith 1985, 1988, Nilsson 1989). Although Magpies *Pica pica* do not always breed at the end of their first year, the population followed by Birkhead and colleagues in South Yorkshire provides an interesting comparison with the other studies, with some juveniles holding territories and recruiting in their first year whilst others spend most of their first two years in non-breeding flocks (Birkhead & Clarkson 1985, Birkhead *et al.* 1986, Eden 1987a, 1987b, 1989).

Within Britain and Europe, the Dipper has long proved popular as a study species (Robson 1956, Balat 1962, 1964, Hewson 1967, 1969, Shooter 1970, Shaw 1978, 1979a, 1979b). Some studies have involved recognition of individuals but most have either focussed on breeding biology at the population level or have been limited to a small area over a short time period. A long term study of Dippers in the River Wye catchment of South Wales was commenced around 1982 by Ormerod, Tyler and colleagues. This has focussed on feeding ecology throughout the annual cycle (Ormerod 1985, Ormerod & Tyler 1986) and the effect of stream acidity on breeding numbers, distribution and performance in their population (Ormerod *et al.* 1985a, 1985b, Tyler & Ormerod 1985, Ormerod *et al.* 1986).

Price & Bock (1983) first recognised the potential of Dippers (in their case, *Cinclus mexicanus*) for a large scale population study. They considered this avian genus suitable for study on the basis of the following criteria:

"1. individual organisms should be easily observed and censused;
2. social behaviour should be observable;
3. populations should be large enough that satisfactory quantitative data can be collected in reasonable time;
4. members of the population should be individually recognisable, or at least easily marked;
5. the species should have a well-delimited habitat so that an entire population can be studied;
6. major resources likely to influence the population should be quantifiable;
7. effects of interspecific competition and predation

should either be quantifiable or not significant;
8. the population should be sedentary or have quantifiable immigration and emigration"

Without exception, these criteria apply equally to British races of Dippers. The main topics covered by Price & Bock (1983) were movements, density and dispersion, and survival and productivity - but only in as far as they impinged on population processes. The role of individual variability was largely ignored. The present study forms part of a long-term investigation into the energetics and population ecology of the Dipper in central Scotland. The approach taken here has been to study individual juveniles rather than recruits and populations, and to attempt to integrate morphology and behaviour with overall survival and recruitment, concentrating on the period between late summer and spring. Thus, the relationships between largely inherited physical attributes (body size measures, plumage colouration), parental factors (hatching date, natal habitat) behaviourally mediated responses (dominance, dispersal), and autumn body condition are investigated and their relative importance in recruitment is assessed.

Initially it was envisaged that the majority of juveniles would be of known origin (ringed as nestlings) and parentage, and that some of the following questions would be addressed:

1. Are there sexual differences in dispersal distance and if so, what factors contribute to this?
2. How does the timing of arrival at a site relate to eventual performance?
3. Are there differences in juvenile sub-population density within and between years and how do they relate to breeding population density?
4. Is there any evidence for directional or stabilising selection on body size traits in juveniles?

5. Can body condition of live birds be assessed and used as a predictor of survival (without resorting to body mass manipulation)?
6. Does a dominance hierarchy exist at any level in a Dipper population and what are the consequences for juveniles of different status?
7. Are there any variable plumage characteristics that might be used to evaluate current ideas on status signalling and individual recognition?

As the study evolved, several of the questions were modified or set aside, though ultimately components of most were explored and the results are developed below.

1.2. THESIS ORGANISATION

The chapters of this thesis are largely self-contained. Chapter 2 is an exception and provides a general description of the study area and some aspects of Dipper biology not covered elsewhere.

The significance of body size variation is explored in Chapter 3, particularly with respect to overwinter survival, recruitment and autumn home range establishment. Chapter 4 documents the range of breast and belly plumage variability for Dippers in Scotland and then follows the approach of Chapter 3, evaluating the significance of plumage in survivorship. The role of intraspecific dominance relations is explored in Chapter 5. From an early stage, it was decided to assess dominance quantitatively in a neutral and constant environment, thereby reducing the bias inherent in field performance studies of dominance dependent on the bird's territorial status at the site of observation (i.e. as either transient, deliberate intruder/neighbour or resident).

Chapter 6 covers the post-fledging period when survival and dispersal from natal sites are hard to distinguish. In particular, I focus on differences between juveniles raised in upland hill burns and those from lowland sites along the main river. The effects of dominance, relative age and population density are explored experimentally in Chapter 7. Here, groups of five juvenile Dippers were released into new sites at varying times in the summer and autumn in an attempt to control for site-related factors.

Body composition and derived condition indices are given for a small sample of Dipper carcasses in Chapter 8. This chapter also introduces the potential of field-portable ultrasound flaw detectors to measure the thickness of pectoralis muscles in live birds. The influence of pectoralis protein, as a potential indicator of condition, in the overwinter survival and recruitment of free living Dippers is tested in Chapter 9. The final chapter (10) expands some of the points raised in the discussion sections of the "results" chapters and pulls together combinations of characters that may identify potential recruits in the autumn population. Lastly, I briefly review population regulation in the Dipper and compare life history tactics of Dippers in Scotland with other, well studied, resident temperate passerines.

CHAPTER TWO

STUDY AREA & SPECIES DEMOGRAPHY

2.1. INTRODUCTION

The present study was centred on the western Ochil Hills in east central Scotland (Figure 2.1). This chapter describes the physical characteristics of the study area and gives an outline of the annual cycle of the Dipper *Cinclus cinclus* in this area.

2.2. GEOLOGY & HYDROLOGY

The Ochil Hills form a detached upland massif on the northern flank of the Midland Valley, in part separating the major east flowing Forth and Tay catchments, and lying between the towns of Stirling, Perth and Kinross. Bedrock in the study area is wholly Palaeozoic in origin and mainly comprises Devonian Lower Old Red Sandstone volcanics with some sediments in the northern uplands and Carboniferous sediments in the lowlands to the south. These two units are separated by the Ochil Fault which has produced a dramatic southern scarp which runs due east from Stirling. The Ochil Hills predominantly comprise basic and intermediate lavas (basalt and andesite) with minor tuffs, agglomerates and intra-volcanic sediments. The Carboniferous rocks of the Devon Valley exhibit great variety with interbedded sandstones, siltstones, mudstones, shales, limestones, dolomitic cementstones and minor coal seams present. Rock outcrops are relatively uncommon away from watercourses and the Ochil Scarp and most parts of the study area are blanketed with considerable thicknesses of boulder clay and glacial drift. Limited areas of peat are present on the shoulders of some of the higher Ochil tops. A full description of the geology of the area is given by Francis *et al.* (1970).

Hill burns rising in the western Ochil Hills drain into two main rivers: the River Devon receives those from

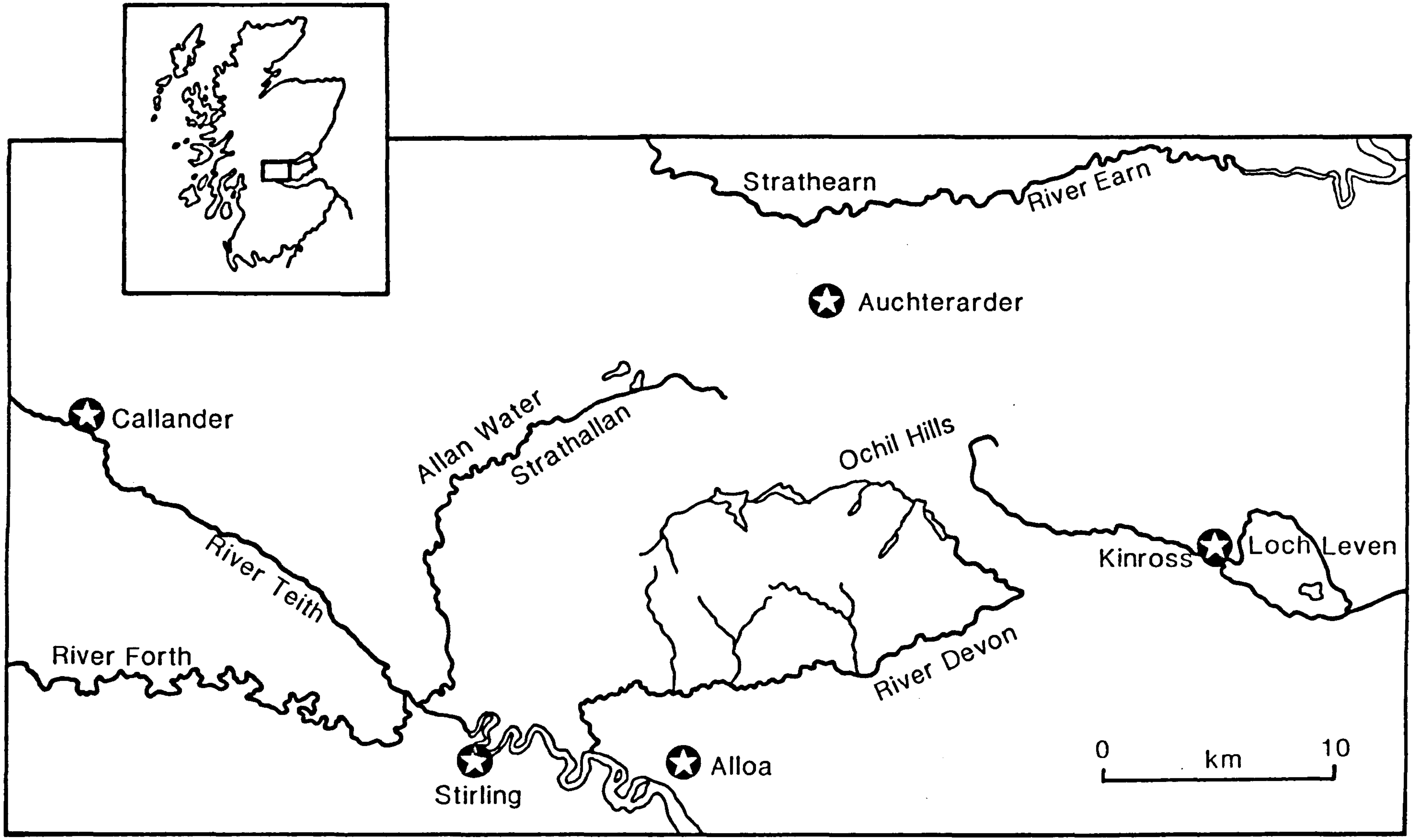


Fig. 2.1 Location of overall study within Central and Tayside Regions, Scotland.

the interior and southern part of the hills whilst the western and northern flanks drain into the Allan Water. The eastern section of the Ochil Hills mostly drains into the River Earn to the north or directly into Loch Leven (south and east). The core study area comprises the River Devon and all its tributary hill burns. The river is unusual in that it flanks both sides of the major watershed linking the highest summits in the western part of the major hills: flowing eastwards from its source on Ben Cleuch (721m) through Glendevon until it crosses the Ochil Fault in the Muckhart/Crook of Devon area where it doubles back to flow westwards until it enters the Forth estuary at Cambus. Thus both northward and southward flowing hill burns often rise on the same "mosses" within one kilometre of one another (Figure 2.2). Geomorphology and hydrology are well covered by T.N.George and K.Smith in Timms (1974). Lennon (1988) gives considerable detail on the physico-chemical characteristics of the River Devon. The river flows over basic rocks for much of its course, and with little upland afforestation, except for a small area in Glensherup, the pH lies in the range 6.7 to 7.0 for all parts regularly inhabited by Dippers. Percentage oxygen saturation is marginally higher in the upland areas (100.0 - 102.8) falling to 92.3 in the lower middle reaches near Dollar, partly as a result of lower gradients and increasing organic inputs from fish farms, sewage treatment plants and septic tanks.

2.3 SUMMARY OF METEOROLOGICAL OBSERVATIONS, 1985-88

The University of Stirling maintains two weather stations: one near sea level on the main campus (Parkhead, NS8196) close to both the south-west corner of the Ochil Hills and the lower reaches of the River Devon and an automated recording station situated in the hills at Carim (NN8606) eight kilometres to the north-east at approximately 300m. A summary of some temperature and precipitation statistics for spring 1985 to spring 1988 is given in Table 2.1. Seasons are

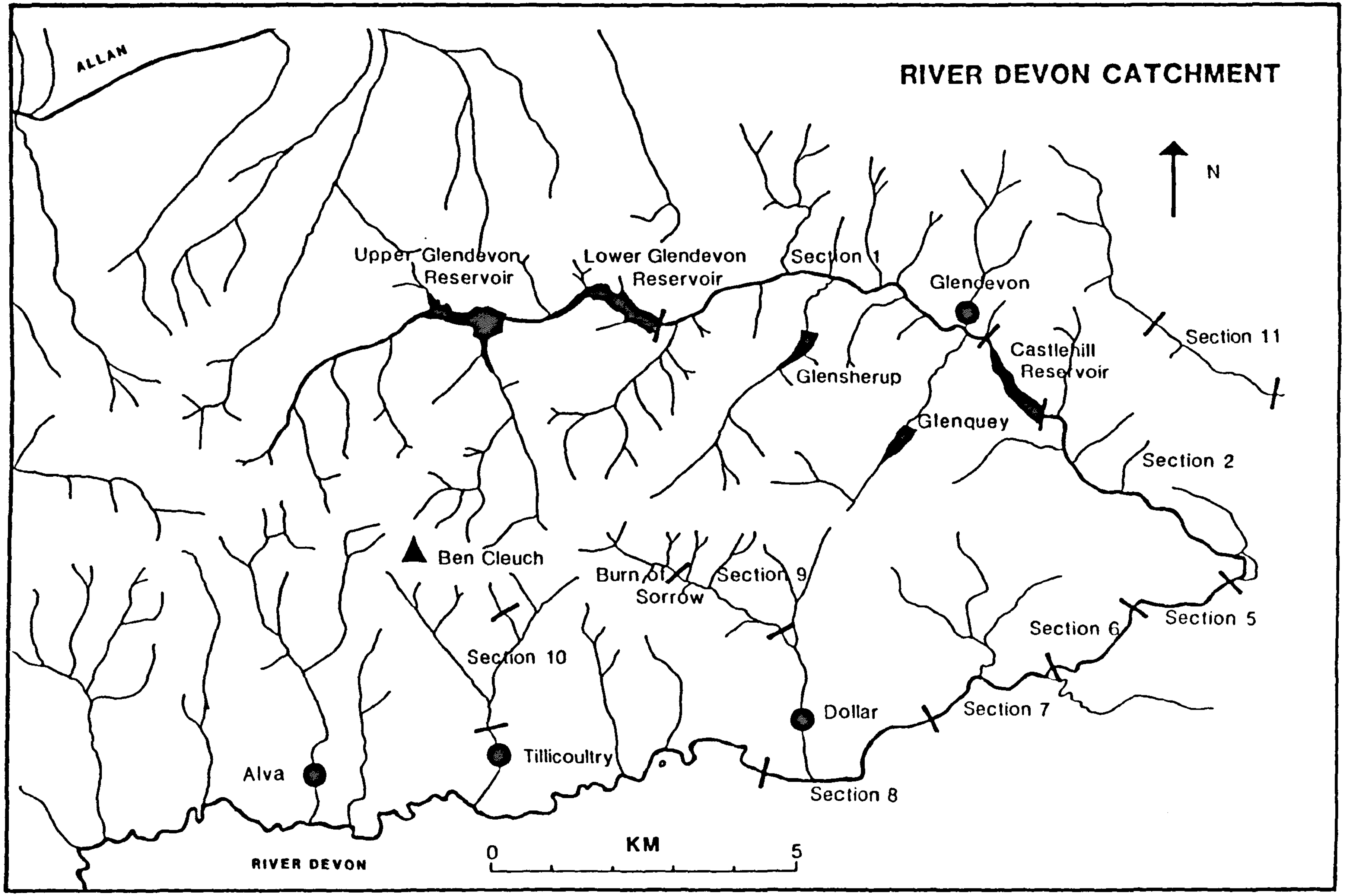


Fig. 2.2 Western Ochil Hills/River Devon Catchment core study area with localities and river sections mentioned in text.

Table 2.1. Meteorological data (1985-88) from two weather stations situated at the University of Stirling (30m asl) and in the western Ochil Hills (300m asl).

Season	Year	No.days <0^{o}C **		Total precipitation (mm)		No.days with precipitation	No.days with ≥ 5mm precipitation
		Stirling	Ochil Hills	Stirling	Ochil Hills	Stirling	Stirling
Spring	1985	14	22	174.8	284.9	52	15
	1986	18	41	290.0	528.3	68	25
	1987	16	20	187.1	404.5	42	11
	1988	8	22	221.0	340.0	57	13
Summer	1985	0	0	388.8	605.5	69	25
	1986	0	0	148.6	212.3	35	10
	1987	0	0	249.4	324.8	52	19
Autumn	1985	19	22	312.8	468.9	48	15
	1986	11	13	294.9	496.6	60	18
	1987	9	3	247.7	384.4	55	19
Winter	1985/86	49	64	263.9	474.2	64	20
	1986/87	55	58	307.5	476.8	55	21
	1987/88	20	45	301.5	506.0	60	25

Note: ** Number of days with minimum air temperature recorded below 0^{o}C.

defined as follows: spring is March to May, summer June to August, autumn September to November and winter December to February (all inclusive).

The spring of 1986 was noticeably colder and wetter than those of the remaining three years. Summer 1985 was one of the wettest ever recorded in the Stirling district with exceptionally high rainfall in July and August and continuing into September. Otherwise there has been a trend towards wetter summers overall. Autumn rainfall was similar in all years with autumn 1987 marginally the mildest of the three under consideration. Winter snowfall has not been a significant feature of recent winters, though snow lay longest in late winter 1985/1986 with lowest temperatures being recorded in the short cold snap of January 1987. The winter of 1987/88 was exceptionally mild, though overall precipitation was little different to the preceding two years. The most distinctive climatological feature of the three years was the lack of seasonality in precipitation: summer was barely distinguishable from spring and autumn in terms of total rainfall.

Although the upper reaches of the River Devon and its tributaries have been dammed for water abstraction at five localities, gross manipulation of river levels by the Fife and Kinross Water Board are rare and consequently river flow is usually reflective of current precipitation and run-off. River flow and depth data are continuously monitored by the Forth River Purification Board at their Fossoway (NO0101) gauging station just below the Castlehill Reservoir Dam. Mean monthly flow rates and river depths are given in Table 2.2. These compare favourably with overall precipitation data from the weather statistics. August and September 1985 stand out with high flow rates, normally only recorded in December. The low flow rate of February 1986 was perhaps due to the prolonged snow

Table 2.2. Monthly mean flow rates and depths for the middle reaches of the River Devon, 1985-88.

Month	1985		1986		1987		1988		15 year mean flow
	mean flow	mean depth	mean flow	mean depth	mean flow	mean depth	mean flow	mean depth	
January			4231 (15)	0.414	3026 (10)	0.350	4716.5 (22)	0.444	3182
February			836 (0)	0.208 [43%]	1828 (6)	0.278 [46%]	3824.2 (23)	0.406 [56%]	2270
March			3590 (22)	0.383	2462 (6)	0.326	1827.4 (8)	0.282	2442
April	2597 (16)	0.329	1500 (9)	0.246	2095 (19)	0.307	1797.2 (9)	0.277	1557
May	653 (0)	0.187 [26%]	4970 (31)	0.451 [67%]	637.4 (0)	0.185 [27%]	782.1 (1)	0.203 [20%]	1268
June	606 (0)	0.182	1326 (26)	0.253	1225.9 (20)	0.238	475.2 (0)	0.162	836
July	1167 (18)	0.221	513 (7)	0.168	478.0 (1)	0.163			558
August	5096 (31)	0.444 [53%]	725 (4)	0.196 [40%]	556.5 (3)	0.173 [26%]			889
September	5624 (28)	0.452	523 (0)	0.170	1510.4 (11)	0.263			1395
October	2958 (14)	0.324	915 (5)	0.195	1881.7 (14)	0.292			1757
November	894 (0)	0.211 [46%]	3982 (13)	0.392 [20%]	1964.4 (7)	0.295 [35%]			2950
December	5282 (24)	0.459	5489 (25)	0.471	1889.5 (6)	0.270			3055

Notes:

1. Mean flow (litres per second) and depth (m) are recorded at an automatic monitoring station situated on River Devon Section 2.

2. Numbers in parentheses refer to the number of days in that month with flow rates higher than the 15 year mean for that month.

   Those given quarterly [in square brackets] refer to the % of days with flow rates higher than the 15 year mean for that season.

cover that month but flow rates and depths for March and May were well above their respective 15 year means.

2.4. DISTRIBUTION OF NON-BREEDING DIPPERS IN THE RIVER DEVON CATCHMENT

During autumn and winter the majority of the Dippers on the River Devon catchment were found on the upper middle reaches of the main river. The Devon is 50.08km long from source to Forth estuary, including three reservoirs, and the part referred to occurs between 9.10 and 32.33km from the source. For the purpose of regular censusing this length was sub-divided into six sections listed in Table 2.3. and illustrated in Figure 2.2. Outside these sections, numbers were generally much reduced, both on the main river and especially on the adjacent hill burns. However, non-breeding Dippers were present intermittently on the Devon to its mouth, where some individuals were seen feeding on intertidal mud and rocks. Tables 2.4a, b and c give the age and sex composition of Dippers using the main river sections 1 to 8 for all or part of three autumn/winter periods. Birds may arrive or disappear from these sectional sub-populations at any time during the course of the autumn/winter though the greatest flux is usually in September and October.

Neither age structure nor sex ratios differed from unity (50:50, X^2 tests) when all sections were combined, though in some years different age groups or sexes may predominate on particular sections. Numbers have remained approximately constant both within sections and overall; slightly lower numbers in autumn 1986 were probably due to reduced census effort later in the season, particularly on sections 1 and 7. Autumn and winter censuses of upland birds failed to locate any males (Table 2.5). The majority of males were presumed to be altitudinal migrants, overwintering on the main river.

Table 2.3. Subdivision of core study area: River Devon section lengths and autumn densities of non-breeding Dippers, 1985-87.

Section no.	From/to	Section length (km)	Mean birds/km for 3 autumns
1	Frandy - Castlehill Reservoir (head)	6.5	3.6
2	Castlehead Reservoir Dam - Crook of Devon	5.4	5.6
5	Crook of Devon - Rumbling Bridge	2.3	5.5
6	Rumbling Bridge - Cauldron Linn	1.6	7.5
7	Cauldron Linn - Vicars Bridge	2.6	9.0
8	Vicars Bridge - Dollar Village	3.2	3.8
	Total length; overall density	21.6	5.3
9	Burn of Sorrow, Dollar	2.0	1.0
10	Gannel Burn, Tillicoultry	2.0	0.8
11	South Queich, Carnbo	2.0	1.0

Notes:

1. Sections 1 to 8 comprise the middle reaches of the main River Devon.
2. Sections 9 to 11 are parts of adjacent hill burns.
3. Sections 3 and 4 are located on rivers elsewhere.

Table 2.4.(a). Population structure, lowland reaches of the River Devon, autumn 1985.

Age/sex	River section						Total	Totals (age/sex)
	1	2	5	6	7	8		
Adult male	5	8	2	2	10	4	31	Adult 63
Adult female	7	6	5	3	9	2	32	Juvenile 61
Juvenile male	7	11	0	6	9	5	38	Male 69
Juvenile female	7	4	4	2	6	0	23	Female 55
Total	26	29	11	13	34	11	124	% Juveniles 49.2

Table 2.4.(b). Population structure, lowland reaches the River Devon, autumn 1986.

Age/sex	River section						Total	Totals (age/sex)
	1	2	5	6	7	8		
Adult male	0	7	6	3	5	2	23	Adult 53
Adult female	4	7	7	4	7	1	30	Juvenile 44
Juvenile male	7	10	1	2	1	1	22	Male 45
Juvenile female	1	5	5	3	3	5	22	Female 52
Total	12	29	19	12	16	9	97	% Juveniles 45.4

Table 2.4.(c) Population structure, lowland reaches of the River Devon, autumn 1987.

Age/sex	River section						Total	Totals (age/sex)
	1	2	5	6	7	8		
Adult male	5	8	2	3	9	6	33	Adult 59
Adult female	7	8	2	3	5	1	26	Juvenile 61
Juvenile male	8	10	1	3	2	7	31	Male 64
Juvenile female	12	7	3	2	4	2	30	Female 56
Total	32	33	8	11	20	16	120	% Juveniles 50.8

Table 2.5. Population structure of three Ochil upland burns, autumns 1985 and 1987.

	Burn of Sorrow Dollar (9)		Gannel Burn Tillicoultry(10)		South Queich Carnbo (11)
	1985	1987	1985	1987	1985
Adult male	0	0	0	0	0
Adult female	1	0	1	0	1
Juvenile male	0	0	0	0	0
Juvenile female	1	2	1	1	1

2.5. ALTITUDINAL MIGRATION & BREEDING DISTRIBUTION

From March onwards, potential breeding pairs begin to explore nest locations on lowland sections of river with suitable features (cliffs, waterfalls, bridges, dams, etc.). Some sections are almost devoid of suitable nest sites (e.g. 8) and the majority of winter inhabitants move up adjacent hill burns that offer a wide variety of potential nest sites in gorges, waterfalls or bridges and other man-made features within the Hillfoots villages. Some typical spring altitudinal migrations are given in Figure 2.3; most of the winter residents of section 8 breed on the Burn of Sorrow above Dollar village. A small scale nest box experiment was carried out on sections 7 and 8. The former usually has nine or ten pairs of breeding Dippers whilst the latter never more than two. Ten nest boxes were erected on apparently suitable trees, cliffs and man-made features (viaduct "legs") on both sections during February 1987. None was utilised by Dippers in the 1987 breeding season, but a pair occupied one of the centrally located nest boxes on section 8 and successfully reared a brood in 1988 (Figure 2.4). A pair of Grey Wagtails *Motacilla cinerea* used one of the other nest boxes on section 8 in both years. No boxes on section 7 were utilised in either year.

Breeding territories are categorised as either upland or lowland primarily on the basis of this spring altitudinal migration. The lowland sites are predominantly on or close to the main river and were occupied year-round. In instances where the nest is located on a side burn, the adults continue to forage and defend their main river territory. Upland sites are not necessarily occupied throughout the year by either members of a pair and such birds do not utilise main rivers in spring and summer. Furthermore, successful double brooding is restricted to lowland breeding territories.

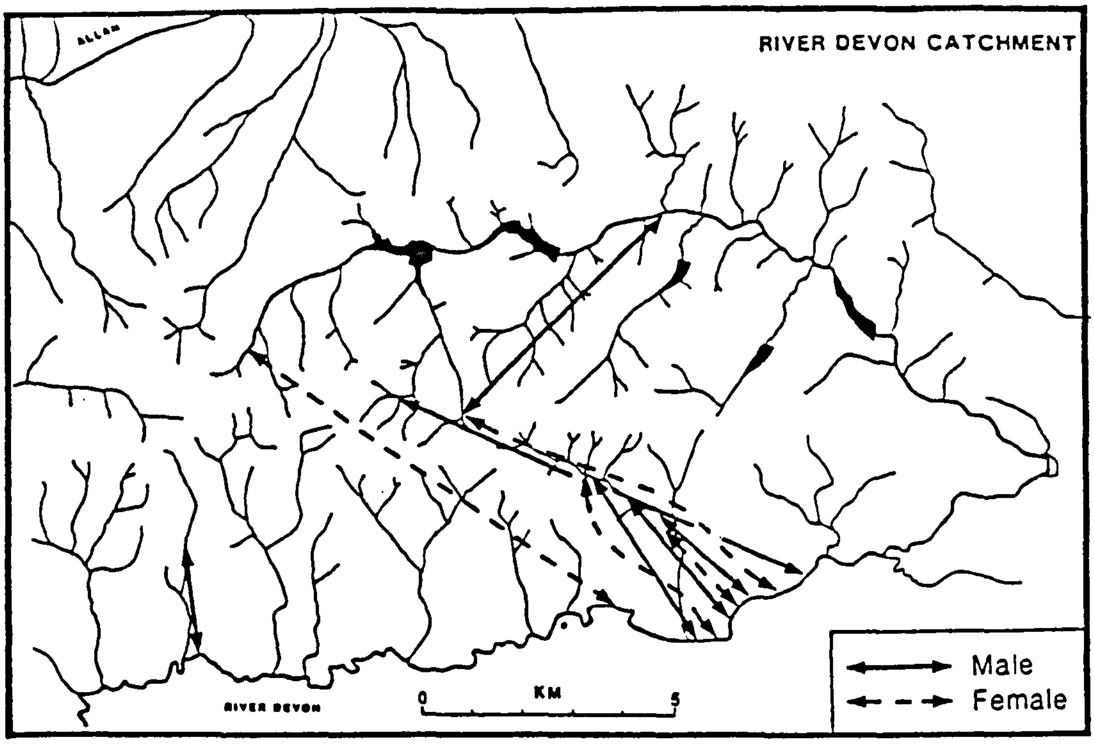


Fig. 2.3 Spring altitudinal migration of Dippers between main river autumn/winter home ranges and upland breeding territories.

Fig. 2.4 An occupied Dipper nest box on river section 8.

On suitable stretches of lowland river, nest sites may be as little as 200m apart though between 500m and 700m would be more typical (Figure 2.5). High nest densities tended to occur around natural features such as the Rumbling Bridge gorge which provided many suitable sites (sections 5/6). Upland nests were more regularly spaced, often about 1.0 to 1.5km apart, though again clumping may occur in gorges where south flowing burns cut through the Ochil scarp. In 1985 (Figure 2.5a) only three upland burn systems were searched for nests: Burn of Sorrow and Burn of Care, Dollar; Mill, Gannel and Whum Burns, Tillicoultry and the South Queich. In the following three springs (1986-88) the whole of the River Devon catchment was covered together with several burns flowing northwards into the Allan Water (Figure 2.5b).

2.6. COMPOSITION OF THE BREEDING POPULATION

Due to the continual, slow influx of birds into the study area from surrounding catchments, it proved impossible to keep the population 100% ringed. Thus, the data on age and sex composition of the breeding population presented in Table 2.6. are based on samples. Nonetheless, it usually remained at greater than 90% ringed. Two methods were used: firstly, only pairs where both members were of known age were considered, and secondly a sample including the former and the known birds of a mixed ringed/unringed pair were analysed (i.e. all ringed birds in the population). The two methods produced statistically indistinguishable results (X^2 tests): juveniles consistently formed a little over one third of the breeding population (34-40%) and there were no significant differences between years. This implied higher mortality of juvenile between autumn and spring as adults and juveniles formed equal proportions of the early autumn population.

There were no significant differences in the proportion of juveniles between upland and lowland breeding

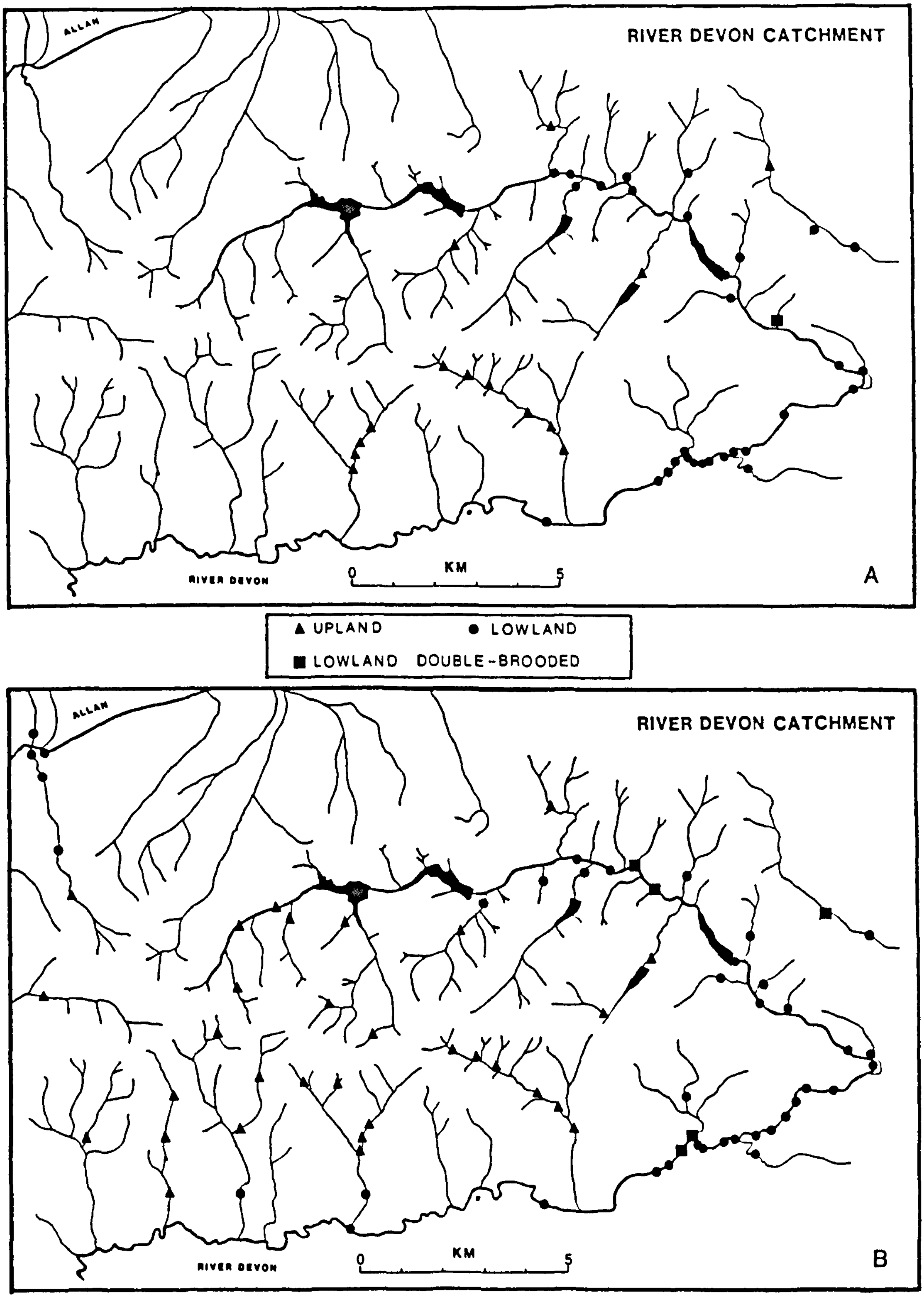


Fig. 2.5 Location of nest sites on the River Devon Catchment in 1985 (A) and 1986 (B).

subpopulations (Table 2.7). In two out of three years, juveniles were more prevalent at lowland nesting territories. Thus, it would be unwise to conclude that those birds undertaking a spring altitudinal migration had been excluded from lowland breeding territories by more experienced conspecifics.

2.7. COMPARATIVE BREEDING BIOLOGY 1985-87

The breeding biology of Dippers in the study area is summarised in Tables 2.8 to 2.11. Altitude appeared to have little effect on breeding performance in terms of clutch and brood size in most years, though the day of the first egg (or hatchday) was correlated with altitude (Table 2.8). There was a difference of around two to three weeks in the timing of breeding between the highest nests at 400m and typical lowland sites below 100m asl.

Approximately one third to one quarter of all nesting attempts failed to fledge young (Table 2.9). Most loses occurred at early stages prior to hatching. Breeding success was lowest in 1986; heavier rainfall than usual

Table 2.6. Age and sex composition of breeding populations of Dippers on the Rivers Devon, Teith and Allan, 1986-88.

	Number of birds		
	1986	1987	1988
Adult males	25 (22)	25 (22)	28 (24)
Adult females	34 (21)	29 (18)	38 (17)
Juvenile males	17 (13)	12 (10)	9 (8)
Juvenile females	23 (14)	21 (14)	25 (23)
Total	99 (70)	87 (64)	100 (72)
% Juveniles	40.4 (38.6)	37.9 (37.5)	34.0 (35.9)

Note: Numbers in parentheses refer to members of a pair where both individuals were of known age; otherwise the data include some birds with mates of unknown age (unringed).

Table 2.7. Age and sex composition of upland and lowland breeding Dippers, 1986-88.

	1986		1987		1988	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
Lowland nests	44	34(43.6)	44	26(37.1)	47	26(35.6)
Upland nests	15	6(28.6)	10	7(41.2)	19	8(29.6)
Total	59	40	54	33	66	34
X^2 (1 d.f.)	1.55 n.s.		0.10 n.s.		0.32 n.s.	

Note: Numbers in parentheses are percentages of juveniles in the samples from the upland and lowland breeding sub-populations.

Table 2.8. Dipper breeding biology: correlations (Pearson coefficients) between breeding parameters and nest altitude on the River Devon and its tributaries, 1985-87.

	1985	1986	1987
Clutch size	n.s.	n.s.	n.s.
Brood size	n.s.	n.s.	0.270 $p<0.05$
Fledged brood size	n.s.	n.s.	n.s.
Hatch day	0.427 $p<0.05$	0.633 $p<0.001$	0.718 $p<0.001$

Table 2.9. Dipper breeding biology: overall breeding success and nest histories, 1985-87.

	1985	1986	1987
Number of occupied territories monitored	41	86	78
% with no breeding attempt (single birds)	0	0	6.4
% failing at nest building or at egg stage	14.6	20.9	15.4
% failing at nestling stage	7.3	7.0	5.1
% failing for unknown reasons or stages	4.9	3.5	0
Overall % failing to fledge young	26.8	31.4	26.9
% attempting second broods	N.R.	7.6	6.4

Abbreviation: N.R. = not recorded.

Table 2.10. Dipper breeding biology: losses of eggs and young at various stages of the nesting cycle, 1985-87.

	1985	1986	1987
Total number of eggs laid	146	302	260
% eggs laid infertile/failed to hatch	4.8	3.3	3.1
% eggs laid deserted/predated	8.9	19.5	8.8
% eggs laid and very small nestlings "lost"	0.0	4.6	4.2
% "natural" nestling mortality	10.3	9.6	3.8
% human influenced nestling mortality	1.4	1.0	1.2
Overall % eggs failing to produce potential fledged young	25.4	38.0	21.1

Table 2.11. Dipper breeding biology: mean clutch and brood sizes, 1985-87.

	1985	1986	1987
Mean clutch size (± S.D., n) including early replacements	4.61 (0.72,31)	4.56 (0.66,66)	4.56 (0.63,57)
Mean brood size (n)	4.34(29)	3.96(54)	4.25(52)
Mean fledged brood size (n)	4.07(28)	3.80(49)	4.02(51)
Mean clutch size, second broods (n)	Not recorded	3.83 (6)	3.75 (4)
Mean second brood size (n)	Not recorded	3.50 (6)	3.25 (4)

caused prolonged spates that either flooded many early lowland nests or otherwise led to clutch desertions. The incidence of true second broods (rather than replacements) following successful fledging of first broods was low (less than 8% of occupied territories) and in most cases involved the re-use of the original nest.

The fate of eggs laid, as opposed to overall nest histories, is given in Table 2.10. Losses at each of the stages identified in Table 2.10. were relatively constant between years with the exception of a higher clutch desertion during 1986. Natural nestling mortality included the death of runts by starvation whereas human-influenced losses included premature fledging (see Shaw 1978) or accidental spillage of individuals during their resettlement after ringing and replacement in nests. Completed clutch sizes ranged from three to six with a modal value of five. Mean clutch sizes are given Table 2.11. Second clutches and broods were usually less than the overall population means and were reduced relative to the first brood of the same breeding pair.

2.8. SUMMARY

During the course of this study there have been no major demographic pertubations in the Dipper population of the western Ochil Hills or River Devon catchment in particular. Autumn/winter numbers and the age and sex composition have been relatively constant. Breeding density and productivity has also changed little. Although variable spring weather and river conditions limit the breeding success of early lowland pairs, their shortfall may enable later fledging juveniles from upland sites more opportunity to recruit into the autumn population.

Further background information on the feeding ecology, roosting habits and moult of Dippers in central Scotland can be found in Shaw (1979a,b) and Galbraith *et al.* (1981). Bryant *et al.* (1985) and Bryant & Tatner (1988) have investigated the energetics of the annual cycle of River Devon Dippers.

CHAPTER THREE

OVERWINTER SURVIVAL & RECRUITMENT OF JUVENILE DIPPERS IN RELATION TO BODY SIZE

3.1. INTRODUCTION

The main aim of this chapter is to describe body size variation in the juvenile Dipper *Cinclus cinclus* population in autumn and to explore the overwinter survival prospects of individuals of differing size. Data are presented for three cohorts of autumn caught juveniles (1985 to 1987) and their performance is compared to that of established adults over the same time period. The birds in this study were all individually identifiable by means of unique colour ring combinations and assessment of survivorship was thus by direct observation and was not reliant on recapture. Between September and the beginning of the breeding season (March) most Dippers in the study population were relatively sedentary, and movements such as the spring altitudinal migration of some birds were mostly restricted to the study area. Thus the disappearance of a colour marked bird was likely to be due to death rather than emigration.

Previous work on survivorship and mortality in Eurasian races of the Dipper has been confined to approximate estimates of annual mortality (e.g. 64%, Robson 1956) and studies of ring recovery rates. Galbraith & Tyler (1982) analysed British recovery data: only 1.4% of 10,000 plus birds have been recovered. Such a low recovery rate is unlikely to yield representative seasonal mortality patterns in a local population. However, Galbraith & Tyler (1982) were able to calculate annual mortality rates of 59% for first year birds and 46% for adults. These are similar to those given by Price & Bock (1983) for their colour marked population of American Dippers *Cinclus mexicanus* (67-77% for juveniles and 48-61% for adults).

Dippers are sexually size dimorphic and an extensive literature on body size variation and seasonal changes within sex and age cohorts is available (Andersson & Wester 1971, 1972, Bryant & Tatner 1988, Galbraith & Broadly 1980, Ormerod *et al.* 1986, Rockenbauch 1985, Schmid & Spitznagel 1985). However, none of these studies has related body size variation to survival or breeding success, though Schmid & Spitznagel (1985) hinted at the fitness consequences of size variation when they reported that pairs comprising larger males and smaller females had higher reproductive success.

3.2. METHODS

3.2.1. Study Area & Field Methods

Birds were captured by daytime mist-netting and by hand at night roosts between 1 September and 30 November 1985, 1986 and 1987. In each autumn, catch effort was concentrated on a 23km length of the middle reaches of the River Devon between the Lower Glendevon Reservoir and the village of Dollar, known to hold the highest concentration of non-breeding Dippers in the western Ochil Hills study area. An attempt was made to capture all birds on the river, though a small proportion (probably less than 5%) evaded capture or moved into the area very late in the autumn. Seven measurements were made on each bird:

1. Body mass: measured to 0.1g with 100g Pesola balance.
2. Wing length (maximum chord): to nearest mm with a stopped rule, wing flattened and straightened (Evans 1986, and preferred method of Spencer, 1984).
3. Keel length: to 0.1mm using blunt dividers and rule, from anterior notch to posterior end of sternum.
4. Tarsus length: to 0.1mm using vernier dial-reading callipers, diagonal length of tarso-metatarsus bone (Spencer 1984).

5. Head and bill length: to 0.1mm using dial-reading callipers, maximum length from back of skull to tip of bill.
6. Bill length: to 0.1mm using dial-reading callipers, bill tip to feathering along top surface of upper mandible.
7. Bill depth: to 0.01mm using dial-reading callipers, measured vertically upwards from edge of feathering on undersurface of lower mandible (line of measurement passes through anterior point of the nares).

Birds were sexed on size difference criteria established for birds of known sex (incubating females, copulating males, etc.). A combination of mass and wing length or keel length was sufficient to separate the majority of individuals. Outside the breeding season, females have masses below 60g and wing lengths and keel lengths less than or equal to 92.0mm and 30.0mm respectively. Males typically have masses greater than 65g and wing and keel lengths exceed 94.0mm and 30.0mm respectively. The criteria are very similar to those used by Andersson & Wester (1971, 1972, 1973), Galbraith & Broadly (1980) and Svensson (1984). First-year birds, hereafter referred to as juveniles, were easily separable from adults by the presence of white-tipped primary and greater wing coverts. Up to 30% of juveniles had been ringed earlier as nestlings. All birds were fitted with unique combinations of celluloid colour rings in addition to B.T.O. metals. Many birds were caught on more than one occasion and in these instances, mean measurements were used for analyses. All adults had completed their annual moult by the time of first capture and first-year birds had also completed their post-juvenile moult. There was no evidence for the continued growth of wing feathers or skeletal measures during the course of each autumn in juvenile birds.

A small number of birds was caught in upland habitats:

the definition of upland and lowland river sections is given in the preceding chapter. Dippers are generally scarce on upland hill burns during autumn and winter months. The presence or absence of marked birds was checked at approximately monthly intervals during autumn and winter censuses. During a census, up to 6km of river bank was walked slowly each day: Dippers were located using 10x40 binoculars and were identified by means of their colour rings with a 22-60x telescope. Their positions were marked on 1:10,000 maps. During the breeding season, late March to mid June, censuses were conducted more frequently and included searches for nest sites and the determination of pairings. These were conducted on both the main River Devon and all adjacent hill burns in the Western Ochil Hills area. The outcome of nesting attempts was monitored as completely as possible, though the size of the field area to be covered permitted only weekly visits to particular river sections.

3.2.2. Data Handling and Analysis

Each autumn caught bird was allocated to one of six survival/recruitment classes:

1. Died or emigrated between capture and the end of February.
2. Survived overwinter, sighted in March but not again.
3. Survived to the breeding season, but nest locality and outcome unknown; also includes some unmated birds.
4. Made a breeding attempt within the study area but failed to fledge young.
5. Made a breeding attempt that was presumed successful (inaccessible nests, etc.).
6. Successful breeder.

In most analyses these were regrouped as overwinter mortality (1 + 2), failed recruits (3 + 4) and successful recruits (5 + 6). Individuals were also ranked as to their time of disappearance from the population: a bird with a score of 1 was last seen in September whereas one with a score of 7 was last seen in March. All recruits were given a score of 8 (i.e. 8 months after August). The degree of fidelity to a stretch of river, approximating to a settled autumn home range, was assessed as follows: birds seen at least twice during daylight hours, less than one kilometre apart, but over a minimum time span of 30 days, were assumed to be settled. However, if one of the two sightings was a roost observation, then the permissible distance was increased to two kilometres. Finally, a bird recorded only once in autumn or winter but next seen breeding within one kilometre of the same location in spring was also afforded settled status. The remaining birds were inferred to be transients, territorial birds which had been ousted, or were excluded from home range analyses if there was any doubt over their true status (birds from upland sites only visited once).

Three body size-adjusted masses were also used in the analyses: SIZE1 = mass/wing length; SIZE2 = mass/keel length and SIZE3 = mass/head + bill length. Other authors (e.g. Slagsvold 1982) often refer to the former as a "condition index".

Body mass, size-adjusted masses, and biometrics were normally distributed and thus relationships between these measurements and survival, breeding success and autumn home range status were investigated using one way analyses of variance (ANOVAs). These were performed separately for juvenile females and juvenile males in each year and for all years combined. Some of the autumn pool of juveniles in 1986 and 1987 originated from density manipulation introductions carried out earlier in the summer or autumn and for these years analyses were duplicated to include and exclude introduced birds.

3.3. RESULTS

3.3.1. Comparative Overwinter Survival and Recruitment of Juveniles and Adults

Overwinter mortality averaged 52% in juvenile females and 60% in juvenile males (Tables 3.1 & 3.2., introduced birds included). Within sexes, there were no significant differences between years, nor between sexes in the same year (X^2 tests, $p>0.05$). Approximately one quarter of the autumn population of juvenile females made successful nesting attempts whereas only one fifth of males were successful recruits (Tables 3.1. & 3.2). The overwinter mortality of adults was lower than that of juveniles and adult males survived marginally better than females (Tables 3.3 & 3.4). However, there were no significant differences between years, within the same sex, or between sexes in the same year (X^2 tests, $p>0.05$).

Differences between age cohorts are given in Table 3.5. Juvenile male mortality was significantly higher than that of adults during winter 1985/86, 1987/88 and all years combined whereas juvenile and adult females showed no such differences. When sexes were pooled, overall juvenile mortality was higher than that of adults in winters 1985/86, 1987/88 and all for years combined.

3.3.2. Time of Disappearance of Juveniles From the Autumn/Winter Population

The greater proportion of non-recruiting juveniles disappeared from the autumn population in October and November (Table 3.6). Losses in September, winter and early spring (December through March) were relatively few. Patterns for males and females appear very similar and inclusion of introduced birds, released into the study area in autumns, 1986 and 1987, did not alter these trends (Figure 3.1a, b, c.). These data may slightly distort the true picture as they are based on the date of the last sighting: birds could have lived up to one month longer and thus the actual peak of

Table 3.1. Overwinter mortality and recruitment of autumn caught juvenile female Dippers.

	Numbers caught			
Survival/recruitment class	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
1	10	13	18	41
2	2	0	0	2
3	2	3	1	6
4	4	2	6	12
5	4	1	3	8
6	6	4	4	14
Total caught	28	23	32	83
% overwinter mortality (1+2)	42.9	56.5	56.3	51.8
% recruits (3+4+5+6)	57.1	43.5	43.7	48.2
% successful recruits (5+6)	35.7	21.7	21.9	26.5

Explanation of survival/recruitment classes:

1. Dies between September and the end of February.
2. Survives to March but dies before breeding attempt.
3. Survives to breeding season, but no nest history.
4. Attempts to breed, fails.
5. Probably nests successfully.
6. Successful breeder.

Table 3.2. Overwinter mortality and recruitment of autumn caught juvenile male Dippers.

	Numbers caught			
Survival/recruitment class	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
1	20	12	16	48
2	0	0	0	0
3	5	3	0	8
4	3	3	2	8
5	1	0	3	4
6	6	3	3	12
Total caught	35	21	24	80
% overwinter mortality	57.1	57.1	66.7	60.0
% recruits	42.9	42.9	33.3	37.5
% successful recruits	20.0	14.3	25.0	20.0

Explanation of survival/recruitment classes:

1. Dies between September and the end of February.
2. Survives to March but dies before breeding attempt.
3. Survives to breeding season, but no nest history.
4. Attempts to breed, fails.
5. Probably nests successfully.
6. Successful breeder.

Table 3.3. Overwinter mortality of autumn caught adult female Dippers.

	Numbers caught			
Survival/recruitment class	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
1	9	7	11	27
2	1	3	0	4
3+4+5+6	23	12	14	49
Total caught	33	22	25**	80
% overwinter mortality	30.3	45.5	44.0	38.8
% survivors	69.7	54.5	56.0	61.2

Note ** includes a single introduced bird.

Explanation of survival/recruitment classes:

1. Dies between September and the end of February.
2. Survives to March but dies before breeding attempt.
3. Survives to breeding season, but no nest history.
4. Attempts to breed, fails.
5. Probably nests successfully.
6. Successful breeder.

Table 3.4. Overwinter mortality of autumn caught adult male Dippers.

	Numbers caught			
Survival/recruitment class	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
1	6	5	11	22
2	1	0	0	1
3+4+5+6	17	10	19	46
Total caught	24	15	30	69
% overwinter mortality	29.2	33.3	36.7	33.3
% survivors	70.8	66.7	63.3	66.7

Explanation of survival/recruitment classes:

1. Dies between September and the end of February.
2. Survives to March but dies before breeding attempt.
3. Survives to breeding season, but no nest history.
4. Attempts to breed, fails.
5. Probably nests successfully.
6. Successful breeder.

Table 3.5. Differences in overwinter survival between adult and juvenile Dippers.

Autumn	1985	1986	1987	All years combined
Females: adults v. juveniles	1.04 n.s.	0.55 n.s.	0.84 n.s.	2.80 n.s.
Males: adults v. juveniles	4.49 *	1.99 n.s.	4.80 *	10.56 **
Sexes combined: adults v. juveniles	5.45 *	2.13 n.s.	4.76 *	12.01 ***

Note: Values are X^2 statistic; n.s. = not significant, * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$; 1 degree of freedom.

Table 3.6. Timing of the disappearance of juvenile Dippers from the autumn/winter population.

Month of death or disappearance	1985/86		1986/87		1987/88		All years combined		
	M	F	M	F	M	F	M	F	M&F
September	2	1	0 (0)	0 (0)	1 (1)	4 (2)	3 (3)	5 (3)	8 (6)
October	6	4	6 (4)	8 (6)	8 (7)	5 (4)	20 (17)	17 (14)	37 (31)
November	9	3	3 (2)	3 (3)	7 (5)	8 (8)	19 (16)	14 (14)	33 (30)
December	1	1	3 (3)	1 (1)	0 (0)	0 (0)	4 (4)	2 (2)	6 (6)
January	0	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
February	2	1	0 (0)	1 (1)	0 (0)	1 (1)	2 (2)	3 (3)	5 (5)
March	0	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (2)	2 (2)
Number of recruits	15	16	9 (4)	10 (10)	8 (8)	14 (12)	32 (27)	40 (38)	72 (65)
Initial autumn population	35	28	21 (13)	23 (21)	24 (21)	32 (27)	80 (69)	83 (76)	163 (145)

Note: Numbers in parentheses exclude introduced birds.

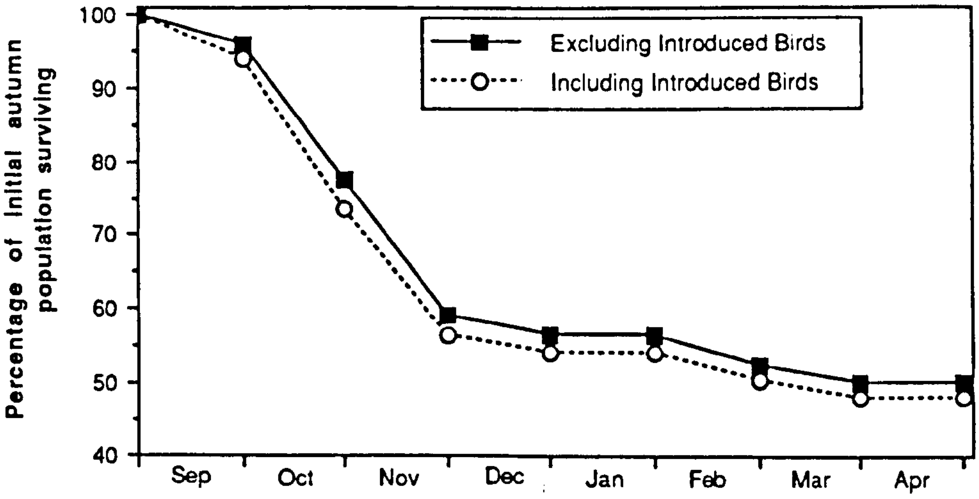


Fig. 3.1a Survivorship curve for juvenile female Dippers over the winter.

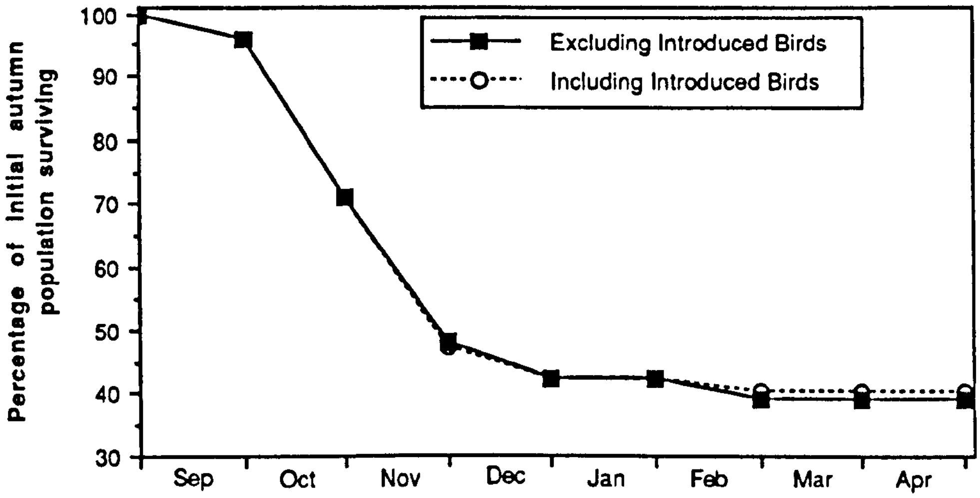


Fig. 3.1b Survivorship curve for juvenile male Dippers over the winter.

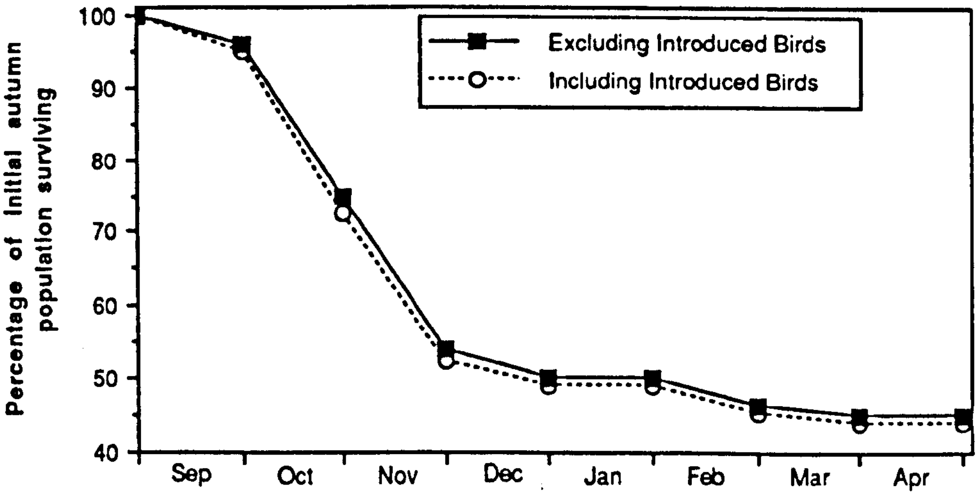


Fig. 3.1c Survivorship curve for juvenile Dippers over the winter (sexes combined).

mortality may have occurred a little later in the autumn and early winter.

3.3.3. Variation in Body Size of Juvenile Dippers Between Years and Comparisons with Adults

Mean body size measures for autumn caught female and male Dippers are given in Tables 3.7 and 3.8. Within sex differences between age groups for all three autumns combined are given in Table 3.9. Juvenile females had significantly lower body masses, shorter wings and smaller head and bill measurements than adult females. Juvenile males similarly differed from adult males in these measurements but also had shorter keels and less deep bills (Table 3.9). Differences between autumns, within sexes were relatively slight with the following exceptions. Autumn 1985 juvenile females were significantly larger billed than those caught in 1986 ($t = 3.00$, 45 d.f., $p<0.01$) and 1987 ($t = 3.53$, 56 d.f, $p=0.001$). Their bills were also significantly deeper (1986: $t = 4.98$, 45 d.f., $p<0.001$; 1987: $t = 6.47$, 56 d.f., $p<0.001$). There were no significant differences in body size measures or size-adjusted masses (SIZE1-3) between juvenile females caught in autumn 1986 and 1987.

Juvenile males caught in autumn 1985 were larger winged than those of 1986 ($t_{54} = 2.91$, $p<0.01$) and 1987 ($t_{60} = 3.80$, $p<0.001$). Bill lengths of 1985 males were greater than those of 1986 ($t_{46} = 3.37$, $p<0.01$) and 1987 birds ($t_{52} = 3.23$, $p<0.01$) as were bill depths (1986: $t_{46} = 5.07$, $p<0.001$; 1987: $t_{52} = 5.46$, $p<0.001$). Autumn caught samples of juvenile males in 1986 and 1987 showed no significant differences in any body size measures or size-adjusted masses.

3.3.4. The Consequences of Within-year Variation in Body Size

3.3.4.1. Body Size & Overwinter Survival of Juveniles

There were few significant differences in body size between recruiting and non-recruiting juveniles in the

Table 3.7. Body size measures of autumn caught female Dippers.

Adult females	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
Mass (g)	58.73 ± 2.77 (33)	57.89 ± 3.93 (22)	58.45 ± 2.69 (26)	58.41 ± 3.08 (81)
Wing length (mm)	90.64 ± 1.52 (33)	90.95 ± 1.66 (21)	90.44 ± 1.75 (23)	90.66 ± 1.62 (77)
Keel length (mm)	27.40 ± 0.89 (33)	27.45 ± 0.88 (19)	27.79 ± 0.77 (23)	27.53 ± 0.86 (75)
Tarsus length (mm)	27.70 ± 0.76 (33)	28.02 ± 0.87 (19)	27.68 ± 0.60 (23)	27.78 ± 0.75 (75)
Head & bill (mm)	45.75 ± 0.63 (28)	45.96 ± 0.51 (19)	46.05 ± 0.67 (23)	45.91 ± 0.62 (70)
Bill length (mm)	15.93 ± 0.63 (28)	15.52 ± 0.38 (19)	15.70 ± 0.43 (23)	15.74 ± 0.53 (70)
Bill depth (mm)	4.52 ± 0.20 (28)	4.28 ± 0.20 (19)	4.27 ± 0.12 (23)	4.37 ± 0.21 (70)
Size1	0.65 ± 0.03 (33)	0.64 ± 0.04 (21)	0.65 ± 0.03 (23)	0.65 ± 0.03 (77)
Size2	2.15 ± 0.13 (33)	2.11 ± 0.16 (19)	2.11 ± 0.10 (23)	2.13 ± 0.13 (75)
Size3	1.28 ± 0.06 (28)	1.26 ± 0.09 (19)	1.27 ± 0.06 (23)	1.27 ± 0.07 (70)
Juvenile females	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
Mass (g)	57.23 ± 2.73 (28)	57.24 ± 3.00 (24)	56.72 ± 2.53 (35)	57.02 ± 2.71 (87)
Wing length (mm)	90.11 ± 1.69 (28)	89.58 ± 1.56 (24)	89.34 ± 1.85 (35)	89.66 ± 1.73 (87)
Keel length (mm)	27.35 ± 1.20 (28)	27.52 ± 0.81 (24)	27.39 ± 0.92 (35)	27.42 ± 0.98 (87)
Tarsus length (mm)	27.60 ± 0.83 (28)	27.54 ± 1.00 (24)	27.57 ± 0.79 (35)	27.57 ± 0.86 (87)
Head & bill (mm)	45.61 ± 0.56 (23)	45.52 ± 0.81 (24)	45.68 ± 0.89 (35)	45.61 ± 0.78 (82)
Bill length (mm)	16.03 ± 0.62 (23)	15.46 ± 0.69 (24)	15.39 ± 0.72 (35)	15.59 ± 0.73 (82)
Bill depth (mm)	4.57 ± 0.25 (23)	4.23 ± 0.22 (24)	4.22 ± 0.17 (35)	4.32 ± 0.26 (82)
Size1	0.64 ± 0.03 (28)	0.64 ± 0.03 (24)	0.64 ± 0.03 (35)	0.64 ± 0.03 (87)
Size2	2.09 ± 0.09 (28)	2.08 ± 0.09 (24)	2.07 ± 0.09 (35)	2.08 ± 0.09 (87)
Size3	1.26 ± 0.06 (23)	1.26 ± 0.05 (24)	1.24 ± 0.05 (35)	1.25 ± 0.05 (82)

Note: Mean values ± standard deviation (sample size).

Table 3.8. Body size measures of autumn caught male Dippers.

Adult males	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
Mass (g)	68.66 ± 3.13 (24)	68.78 ± 2.33 (16)	69.40 ± 3.14 (30)	69.01 ± 2.95 (70)
Wing length (mm)	98.54 ± 2.69 (24)	98.60 ± 1.64 (15)	98.07 ± 2.05 (28)	98.36 ± 2.21 (67)
Keel length (mm)	31.43 ± 1.14 (24)	31.65 ± 0.96 (15)	31.79 ± 0.80 (28)	31.63 ± 0.97 (67)
Tarsus length (mm)	29.15 ± 1.23 (24)	29.52 ± 0.76 (15)	29.25 ± 0.82 (28)	29.27 ± 0.93 (67)
Head & bill (mm)	47.34 ± 0.66 (22)	47.69 ± 0.63 (15)	47.76 ± 0.77 (28)	47.60 ± 0.72 (65)
Bill length (mm)	17.12 ± 0.60 (22)	16.52 ± 0.46 (15)	16.73 ± 0.65 (28)	16.82 ± 0.63 (65)
Bill depth (mm)	5.01 ± 0.19 (22)	4.73 ± 0.18 (15)	4.62 ± 0.13 (28)	4.78 ± 0.24 (65)
Size1	0.70 ± 0.04 (24)	0.70 ± 0.02 (15)	0.71 ± 0.04 (28)	0.70 ± 0.03 (67)
Size2	2.19 ± 0.10 (24)	2.18 ± 0.08 (15)	2.19 ± 0.07 (28)	2.19 ± 0.09 (67)
Size3	1.45 ± 0.06 (22)	1.45 ± 0.04 (15)	1.46 ± 0.06 (28)	1.45 ± 0.05 (65)
Juvenile males	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
Mass (g)	68.56 ± 3.35 (35)	67.31 ± 3.65 (21)	67.21 ± 3.94 (27)	67.80 ± 3.64 (83)
Wing length (mm)	98.09 ± 2.02 (35)	96.57 ± 1.63 (21)	96.33 ± 1.47 (27)	97.13 ± 1.92 (83)
Keel length (mm)	31.30 ± 1.01 (35)	31.26 ± 0.88 (21)	31.06 ± 0.95 (27)	31.21 ± 0.96 (83)
Tarsus length (mm)	29.38 ± 0.94 (27)	29.03 ± 0.91 (21)	29.16 ± 0.73 (27)	29.27 ± 0.87 (83)
Head & bill (mm)	47.26 ± 0.57 (27)	47.22 ± 0.97 (21)	47.28 ± 0.70 (27)	47.26 ± 0.74 (75)
Bill length (mm)	17.04 ± 0.73 (27)	16.31 ± 0.76 (21)	16.37 ± 0.78 (27)	16.60 ± 0.82 (75)
Bill depth (mm)	4.84 ± 0.23 (27)	4.52 ± 0.21 (21)	4.56 ± 0.14 (27)	4.65 ± 0.24 (75)
Size1	0.70 ± 0.04 (35)	0.70 ± 0.04 (21)	0.70 ± 0.04 (27)	0.70 ± 0.04 (83)
Size2	2.19 ± 0.12 (35)	2.15 ± 0.10 (21)	2.17 ± 0.14 (27)	2.17 ± 0.12 (83)
Size3	1.45 ± 0.07 (27)	1.43 ± 0.07 (21)	1.42 ± 0.08 (27)	1.43 ± 0.07 (75)

Note: Mean values ± standard deviation (sample size).

Table 3.9. Differences between adult and juvenile Dippers, caught during autumns 1985 to 1987.

Body size measure	Adult v. juvenile females			Adult v. juvenile males		
	t value	d.f.	p value	t value	d.f.	p value
Mass	3.17	167	<0.01	2.22	151	<0.05
Wing length	3.79	163	<0.001	3.74	146	<0.001
Keel length	0.85	161	>0.05	2.59	146	$=0.01$
Tarsus length	1.65	161	>0.05	0.42	145	>0.05
Head & bill	2.55	150	<0.05	2.57	135	<0.05
Bill length	1.49	150	>0.05	1.47	135	>0.05
Bill depth	1.42	150	>0.05	3.05	135	<0.01

Note: Two-tailed tests.

first two years of this study (Table 3.10). Females with a lower body mass in relation to keel length (SIZE2) in autumn 1985 were more likely to survive overwinter, and autumn 1986 males with marginally shorter wing lengths produced more recruits the following spring. In contrast, larger females clearly survived the winter of 1987/88 better. Wing, tarsus, bill length and head and bill measures of recruits were all significantly greater in the recruiting segment of the autumn population (Table 3.10). The tendency for females with longer wings and tarsi to recruit remained when data from all three autumns were pooled. There was no consistent body size difference between recruiting and non-recruiting males for all years combined.

3.3.4.2. Body Size Differences & Autumn Home Range Acquisition

During the autumns of 1985 and 1986 there was a tendency for smaller females to establish settled autumn home ranges, though the only significant relationship was with tarsus length in autumn 1986 (Table 3.11). However, in autumn 1987, females with significantly longer wings and bills were more likely to settle and smaller birds were more likely to be transients. There were no within year differences between males with home ranges and the apparent transients. Pooled data for all three autumns revealed significant relationships in which larger winged females and males in better condition (SIZE2: higher masses relative to keel length) established settled home ranges.

3.3.4.3. Autumn Body Size Differences of Recruits in Relation to Breeding Success

Overwinter mortality has been shown to reduce the juvenile component of the population by over 50% (Section 3.3.1.). Thus, sample sizes in these analyses of recruits are small and significant differences ought to be treated with some caution. Females of lower mass, and apparently in poorer condition (SIZE1-3) in autumn

Table 3.10. Within year and overall differences in autumn body size of juvenile Dippers: recruits versus non-recruits.

Sample	Year	Sex	Variable	One-way ANOVA			Mean surviving cohort(n)	Mean dying cohort(n)	Intro-ductions (Note 2)
				F value	d.f.	p value			
1	1985/86	F	Size2	4.98	1, 36	<0.05	2.07(18)	2.14(10)	
	1985/86	M	No significant differences						
	1986/87	F	No significant differences						
1 + 2	1986/87	M	Wing length	4.36	1, 19	=0.05	95.78(9)	97.17(12)	Included
1 + 2	1987/88	F	Wing length	4.73	1, 25	<0.05	89.75(12)	88.45(15)	Excluded
1 + 2	1987/88	F	Tarsus length	4.30	1, 25	<0.05	27.89(12)	27.24(15)	Excluded
1 + 2	1987/88	F	Head & bill	5.26	1, 25	<0.05	46.10(12)	45.28(15)	Both
1 + 2	1987/88	F	Bill length	5.85	1, 25	<0.05	15.83(12)	15.16(12)	Both
	1987/88	M	No significant differences						
1	1985-88	F	Wing length	3.66	1, 74	<0.06	89.93(40)	89.19(36)	Excluded
2	1985-88	F	Wing length	4.32	1, 74	<0.05	89.97(38)	89.18(38)	Excluded
1 + 2	1985-88	F	Tarsus length	5.20	1, 74	<0.05	27.81(38)	27.37(38)	Both
	1987/88	M	No significant differences						

Notes:

1. M = male; F = female.
2. Analysis includes or excludes introduced birds; or is valid for both.
3. Sample 1 Surviving cohort = all those alive in March
   Dying cohort = all those disappearing between September and the end of February.
4. Sample 2 Surviving cohort = all those alive in April (breeding season).
   Dying cohort = all those disappearing between September and the end of March.

Table 3.11. Within year and overall differences in autumn body size of juvenile Dippers: settled home range birds versus transients.

Year	Sex	Variable	One way ANOVA			Mean settled birds (n)	Mean transient birds (n)	Introductions (Note 2)
			F value	d.f.	p value			
1985/86	F	Head & bill	3.61	1, 19	<0.08	45.49 (16)	46.02 (5)	
1985/86	M	No significant differences						
1986/87	F	Tarsus length	11.98	1, 18	<0.01	27.03 (10)	28.20 (10)	Both
1986/87	F	Head & bill	3.47	1, 18	<0.08	settled < transients		Excluded
1986/87	F	Bill depth	4.30	1, 18	<0.06	4.12 (10)	4.33 (10)	Both
1986/87	F	Size1	3.81	1, 18	<0.07	settled < transients		Excluded
1986/87	M	No significant differences						
1987/88	F	Wing length	8.43	1, 23	<0.01	89.80 (15)	88.10 (10)	Both
1987/88	F	Bill length	6.34	1, 23	<0.05	15.76 (15)	15.01 (10)	Both
1987/88	M	No significant differences						
1985-88	F	Wing length	4.92	1, 69	<0.05	90.07 (45)	89.23 (26)	Both
1985-88	F	Size1	5.92	1, 69	<0.05	0.63 (45)	0.65 (26)	Excluded
1985-88	M	Mass	3.37	1, 75	=0.07	68.36 (45)	66.87 (32)	Included
1985-88	M	Size1	3.33	1, 75	<0.08	0.70 (45)	0.69 (32)	Included
1985-88	M	Size2	4.05	1, 75	<0.05	2.19 (45)	2.14 (32)	Included

Notes:

1. M = male; F = female.
2. Analysis includes/excludes introduced birds; or valid for both.

1985 were more likely to recruit successfully the following spring (Table 3.12). In the following autumn successful recruits were significantly larger in all head measures, but in 1987 smaller keeled birds appeared to perform better. Size differences related to successful recruitment in males paralleled those of females in 1986 and 1987 but not in 1985. In the former two autumns, deeper billed and smaller keeled birds, respectively, were more likely to recruit successfully but in 1985, larger keeled individuals fared better. Overall, females with lower masses in autumn recruited most successfully; no single body size measure was associated with successful male recruits from the pooled data set (Table 3.12).

3.3.5. Body Size Variation Between Autumn & Spring

Juveniles ringed in the nest formed a relatively small proportion of the breeding population in spring. These birds, together with other adults and juveniles from un-monitored areas dispersed over the western Ochil Hills area to breed from March onwards. Some of the latter presumably wintered on parts of the main river not mist-netted in autumn, or remained, at low densities, in upland areas. In this section, the body size measures of the known autumn population of both juveniles and adults are compared with those of the overall spring/breeding season population.

The results of one-way ANOVAs are presented in Table 3.13. These analyses are biased towards females as they were frequently caught on nests during incubation, to facilitate identification and to monitor breeding parameters such as clutch size and hatching success. Males were only caught when there was uncertainty over their identity.

Breeding season females were typically four or more grams heavier than their autumn counterparts as a result of egg development and the build up of nutrient stores for use during incubation. These differences are not considered further. For all years separately, and for the pooled data set, body size differences between autumn and spring adult and juvenile females were similar; i.e., the same measurement varied in the same direction. The wing lengths of autumn 1985 caught females were significantly longer than those of spring 1986 caught birds (possibly due to feather abrasion). In contrast, skull measurements (bill length and depth) of the 1986 and 1987 autumn females were consistently smaller than those of the spring populations the following years. Thus, breeding adult and recruiting juvenile females were significantly shorter winged and had larger and deeper bills than the autumn population of which they formed part. Spring 1987 caught juvenile males had significantly larger tarsi and bills than their autumn counterparts, but adult males from the same spring had shorter head and bill measurements. No differences were apparent in other years or in the pooled data set.

3.3.6. Altitudinal Differences in Body Size

One possible explanation for the findings presented in the previous section is that birds wintering outside the core lowland study area may differ in some body size measures. A considerable proportion of these birds were probably dispersed over upland burns that were primarily used for breeding. The birds in such open terrain proved very hard to catch in autumn and thus sample sizes are small. To facilitate analysis, age cohorts have been combined and the pooled three-year data set was used for these ANOVAs. Females occurring in the upland burns in autumn, had significantly shorter wings than their counterparts on the lowland main river (Table 3.14). They also had shorter tarsi but this difference just lay outside the 5% significance level. Autumn caught upland males also had shorter wings than lowland birds but the relationship was based on a sample size of two upland birds and was not significant.

Table 3.12. Within year and overall differences in autumn body size of juvenile Dippers: successful recruits versus unsuccessful recruits.

Sample	Year	Sex	Variable	One-way ANOVA			Mean successful cohort (n)	Mean unsuccessful cohort (n)	Introductions (Note 2)
				F value	d.f.	p value			
4	1985/86	F	Mass	10.03	1, 14	<0.01	56.54 (14)	61.40 (2)	
4	1985/86	F	Size1	7.31	1, 14	<0.05	0.63 (14)	0.67 (2)	
4	1985/86	F	Size2	5.48	1, 14	<0.05	2.05 (14)	2.19 (2)	
4	1985/86	F	Size3	7.06	1, 14	<0.05	1.25 (14)	1.35 (2)	
3	1985/86	M	Keel length	7.67	1, 13	<0.05	31.80 (7)	30.69 (8)	
3	1986/87	F	Head & bill	5.74	1, 8	<0.05	46.11 (5)	45.29 (5)	Excluded
3	1986/87	F	Bill length	6.50	1, 8	<0.05	15.88 (5)	15.21 (5)	Excluded
3	1986/87	F	Bill depth	6.74	1, 8	<0.05	4.43 (5)	4.14 (5)	Excluded
4	1986/87	F	Bill depth	16.93	1, 8	<0.01	4.40 (7)	4.01 (3)	Excluded
4	1986/87	M	Bill depth	168.23	1, 2	<0.01	4.54 (3)	4.00 (1)	Excluded
3	1987/88	F	Keel length	4.34	1, 12	<0.06	26.81 (7)	27.79 (7)	Included
4	1987/88	F	Keel length	7.41	1, 12	<0.05	27.14 (14)	29.40 (1)	Both
3	1987/88	M	Keel length	5.98	1, 6	=0.05	30.28 (6)	31.65 (2)	Both
4	1985-88	F	Mass	4.73	1, 36	<0.05	56.87 (32)	59.18 (6)	Excluded
4	1985-88	F	Wing length	3.68	-	<0.07	successful < unsuccessful		Both
4	1985-88	F	Size3	4.09	-	<0.06	successful < unsuccessful		Excluded
4	1985-88	M	No significant differences						

Notes:

1. M = male; F = female.
2. Analysis includes/excludes introduced birds; or valid for both.
3. Sample 3: Successful cohort = successful and probably successful breeders.
   Unsuccessful cohort = failed breeders plus birds with unknown nest histories.
4. Sample 4: Successful cohort = successful and probably successful breeders plus those with unknown nest histories.
   Unsuccessful cohort = failed breeders.

Table 3.13. Differences in body size between autumn and spring caught Dippers.

Year	Age	Sex	Variable	One-way ANOVA			Mean autumn (n)	Mean spring (n)
				F value	d.f.	p value		
1985/86	J	F	Mass	20.01	1, 46	<0.001	57.16 (29)	61.71 (19)
	J	F	Wing	9.36	1, 41	<0.01	90.14 (29)	88.50 (14)
1985/86	J	M	No significant differences					
1986/87	J	F	Mass	15.06	1, 34	<0.001	57.24 (24)	62.24 (12)
	J	F	Bill length	8.47	1, 34	<0.01	15.46 (24)	16.20 (12)
	J	F	Bill depth	6.60	1, 34	<0.05	4.23 (24)	4.41 (12)
1986/87	J	M	Tarsus length	4.91	1, 23	<0.05	29.03 (21)	30.15 (4)
	J	M	Bill length	5.78	1, 23	<0.05	16.31 (21)	17.34 (4)
1987/88	J	F	Mass	17.27	1, 48	<0.001	56.72 (35)	60.40 (15)
	J	F	Bill length	31.42	1, 45	<0.001	15.38 (35)	16.61 (12)
1987/88	J	M	No significant differences (Note 2)					
1985-88	J	F	Mass	54.58	1, 132	<0.001	57.00 (88)	61.42 (46)
	J	F	Wing length	8.27	1, 124	<0.01	89.67 (88)	88.74 (38)
	J	F	Bill length	31.99	1, 117	<0.001	15.59 (82)	16.38 (37)
1985-88	J	M	No significant differences					
1985/86	A	F	Mass	18.99	1, 58	<0.001	58.73 (33)	62.27 (27)
	A	F	Wing length	7.85	1, 48	<0.01	90.64 (33)	89.24 (17)
1985/86	A	M	No significant differences					
1986/87	A	F	Mass	10.06	1, 34	<0.01	57.89 (22)	62.54 (14)
	A	F	Bill length	18.59	1, 24	<0.001	15.52 (19)	16.49 (7)
1985/86	A	M	No significant differences					
1987/88	A	F	Mass	11.14	1, 47	<0.01	58.45 (26)	61.51 (23)
	A	F	Bill length	13.45	1, 39	<0.001	15.70 (23)	16.37 (18)
	A	F	Bill depth	15.25	1, 39	<0.001	4.27 (23)	4.44 (18)
1987/88	A	M	Head & bill	7.08	1, 30	<0.05	47.76 (28)	46.68 (4)
1985-88	A	F	Mass	40.01	1, 143	<0.001	58.41 (81)	62.06 (64)
	A	F	Wing length	14.33	1, 117	<0.001	90.66 (77)	89.50 (42)
	A	F	Bill length	14.86	1, 109	<0.001	15.74 (70)	16.24 (41)
	A	F	Bill depth	4.26	1, 109	<0.05	4.37 (70)	4.46 (41)
1985-88	A	M	No significant differences					

Notes:

1. J = juvenile; A = adult; F = female; M = male.
2. Sample sizes too small (autumn: n=27; spring: n=2).

Table 3.14. Altitudinal differences in body size of autumn and spring caught Dippers.

Season	Age	Sex	Variable	One-way ANOVA			Mean lowland (n)	Mean upland (n)
				F value	d.f.	p value		
Autumn	J+A	F	Wing length	20.31	1, 190	<0.001	90.21 (184)	87.63 (8)
Autumn	J+A	F	Tarsus length	3.79	1, 184	<0.06	27.68 (178)	27.12 (8)
Autumn	J+A	M	Wing length	3.23	1, 180	<0.08	97.71 (180)	95.00 (2)
Spring	J	F	Mass	5.53	1, 35	<0.05	62.27 (24)	59.07 (13)
Spring	J	F	Tarsus length	4.92	1, 25	<0.05	28.00 (15)	27.37 (12)
Spring	J	F	Head & bill	7.86	1, 25	<0.01	46.05 (15)	45.48 (12)
Spring	J	F	Size1	4.88	1, 26	<0.05	0.07 (16)	0.66 (12)
Spring	J	F	Size2	3.85	1, 25	=0.06	2.26 (15)	2.15 (12)
Spring	J	M	No significant differences (Note 2)					
Spring	A	F	Keel length	3.95	1, 28	<0.06	26.91 (14)	27.64 (16)
Spring	A	F	Tarsus length	4.53	1, 28	<0.05	27.27 (14)	27.97 (16)
Spring	A	M	Wing length	5.24	1, 9	<0.05	98.00 (8)	95.33 (3)
Spring	A	M	Tarsus length	4.95	1, 8	<0.06	29.33 (8)	30.67 (2)

Notes:

1. J = juvenile; A = adult; F = female; M = male.
2. Sample sizes too small (lowland n=9, upland n=1).

The spring sample of upland birds was dominated by females caught on the nest. The significant difference between body mass of lowland and upland juvenile females may be partly attributable to the later commencement of breeding in upland habitat, but lower SIZE1 and SIZE2 indices indicated that upland birds were possibly in poorer condition (Table 3.14). The tarsus lengths and head and bill measurements of upland juvenile females were also significantly less than those of the lowlands. On the contrary, upland breeding adult females had longer tarsi and larger keels but showed no differences in mass or size-adjusted masses. Adult males caught in the uplands in spring had significantly shorter wings than lowland birds (Table 3.14).

3.4. DISCUSSION

3.4.1. Survival of Juveniles

Elsewhere (Chapter 6) it is shown that the mortality of recently fledged birds is considerable. During the course of this study (four breeding seasons, three winters) approximately 1000 Dippers have been ringed, of which 70% have been nestlings. To date, only four have been recovered through the national ringing scheme: three fledglings and one adult. The former all died within five weeks of fledging, two hit windows in villages near their nest sites and one was taken by a predatory bird, presumably a Sparrowhawk *Accipiter nisus*. The adult recovery was an autumn road casualty. This return rate (0.4%) is much lower than that given by Galbraith & Tyler (1982) for the U.K. as a whole and gives no indication of natural mortality of full grown birds in autumn and winter.

Evidence presented here shows that 43-67% of full grown juveniles and 29-46% of adults disappear from the autumn/early winter population. The majority of these birds are thought to have died, though the precise cause of death was rarely established. On one occasion an adult bird was caught in winter with a broken leg and its mass was well below normal. This bird soon disappeared from the population, presumed dead, as it was probably unable to cope with the severe spates prevalent at the time. None of the three winters under consideration has been particularly severe (see meteorological and river flow/depth data, Chapter 2): upper parts of the main river were partly iced over (<30%) in late winter 1985/86 but only for a short period. All winters were remarkably similar in terms of total precipitation and the number of days with 5mm or more of rain, but the winter of 1987/88 was much milder in terms of temperature than the previous two. The severest weather is usually encountered from January through to March, well after the period of heaviest mortality. Price & Bock (1983) have also differentiated autumn/winter from breeding/summer mortality. Their estimate for the former in the American Dipper, including both adults and juveniles, was 62-65% which exceeded the mean juvenile mortality rates in this study. However, their population undertook a more pronounced altitudinal migration in autumn and presumably some of the apparent loss could be accounted for by juvenile dispersal/emigration.

Mortality in all age/sex cohorts was at its lowest over the winter of 1985/86. Introductions in the following two autumns may have marginally increased mortality of the entire population by some density-dependent process although numbers introduced did not exceed 10% of the study populations. However, "survival" of some birds was not proved until a year or two after their last autumn sighting in the main river. These birds had emigrated to the upland margins of the study area which were only checked once or twice during the breeding season and where birds were hard to approach and identify. Thus, survival of autumn 1985 birds could be expected to be slightly higher. Adult male Dippers survived overwinter slightly better than adult females, a finding in common with other resident passerines such as Nuthatches *Sitta europaea* (Nilsson 1982). Both

Dippers and Nuthatches are sexually dimorphic species with males larger than females; enhanced survival of the former may result from dominance related access to food and secure roosts. In species with reversed sexual size dimorphism such as the Sparrowhawk, the larger females also experience higher survival rates (Newton *et al.* 1983). Alternatively, in the case of the Medium Ground Finch *Geospiza fortis* (Gibbs & Grant 1987) selection against small size (females) has been mediated through their inability to crack the large seeds prevalent during times of drought. Annual survival rates of adult female Great Tits *Parus major* are lower than those of males (Bulmer & Perrins 1973) and in this case the females probably experience an increased risk of predation at nests during laying and incubation.

Many studies have shown poorer overwinter survivorship of first-year birds (Ekman 1984, Jannson *et al.* 1981, Grieg-Smith 1985), although few investigate differences between sexes within this age group. Arcese & Smith (1985) found equal survival rates among juvenile male and female Song Sparrows *Melospiza melodia* in one year though males fared much better in another year. Estimates of survival of first-year female Sparrowhawks were higher than those of the smaller males (Newton *et al.* 1983). The Dippers in this study appeared to be exceptional in that juveniles of the larger sex (male) had overwinter survival rates consistently less than females over the three autumn/winters; however, these differences were not statistically significant.

3.4.2. Autumn Territoriality

Definitions of territoriality often imply the exclusion of conspecifics from defended areas (Kaufmann 1983). On the whole, such a definition does not appear to hold true for autumn/winter Dipper populations on the River Devon. A few well established adults may defend almost exclusive lowland territories year-round and most breeding pairs are strictly territorial when tied to nest sites. Otherwise, the concept of "home range" better describes the Dippers' use of space in the non-breeding season. Home ranges typically overlap and interactions are frequent with birds probably spread over foraging sites of varying quality in relation to dominance status (see Chapter 5). Some dominants move freely over wide areas whereas some subordinates may be pushed around in what amounts to a highly prolonged dispersal phase. Spates often result in the temporary abandonment of settled home ranges and the birds then redistribute themselves over alternative areas where riffles persist. Given normal river conditions most birds could be predictably located on a 1km length of river, though the precise order of census sightings was much less consistent.

The study of home ranges presented here may have been confounded by birds dying or disappearing before their residence status could be determined. Those that survived longest were more likely to be discovered on settled home ranges as long as that was their preferred behavioural habitat. Thus the "transient" class probably includes both birds that held settled home ranges for brief periods before dying as well as those with genuine tendencies to wander. In any one autumn/winter, juvenile males with and without settled home ranges showed no differences in body size though, over all three years, those with higher mass and in good condition maintained settled home ranges. There was no consistent pattern relating body size to home range status in females during individual autumns but, overall, those with larger wing lengths and of relatively light mass were most settled.

Grieg-Smith (1985) has studied home range and winter survival in first-year Bullfinches *Pyrrhula pyrrhula*. He showed that first-year birds were not necessarily excluded from adult feeding areas though their food handling efficiency was much reduced and may have contributed to their poorer survival. In juvenile Great

Tits, only males attempt to establish autumn territories with dominants more likely to succeed (Drent 1983) but the relationships between body size, dominance and territory establishment were not investigated. Townsend (1985) has shown that larger (as measured by wing length) juvenile Grey Plovers *Pluvialis squatarola* were both more likely to establish autumn feeding territories and were more likely to remain at that site throughout the course of the winter. Smaller birds fed non-territorially and tended to disappear later in the autumn (emigrated and/or died). Territorial yearling male Willow Ptarmigan *Lagopus l. alexandrae* removed from potential breeding territories were in better condition (pectoralis mass/keel length) but not necessarily larger than the males which replaced them (Hannon & Roland 1984). No such relationship was detected in the yearling female Ptarmigans.

3.4.3. Body Size & Overwinter Survival

Birds of both sexes caught in autumn 1985 had larger bills (length and depth) and males were also longer winged than in the remaining two years. The late summer of 1985 was one of the wettest ever recorded in Scotland (see meteorological data, Chapter 2) and perhaps spates associated with this rainfall caused differential survival in favour of larger fledglings at a time when benign weather and abundant food supply usually results in little intraspecific competition.

In most autumns, and for both sexes, body size, mass and size-adjusted mass were generally of little value in predicting overwinter survival in juvenile Dippers. Even though individual size measures showed significant differences between survival classes in some years, the positive correlations between most body size measures (Chapter 8) would lead one to expect more characters varying in the same direction in this study. It is possible that selection may have acted on certain characters in particular winters but such relationships could also arise by chance where many variables are examined as in the present data set. The response detected when introduced birds were included or excluded from the survivorship analyses implies that the behaviour of these birds may have been abnormal. However, there seemed to be unequivocal selection for large size in females during the unusually mild winter of 1987/88. When all years were considered together, recruiting females had significantly longer wings and tarsi than birds dying or emigrating during the course of the autumn and winter. Despite considerable body size variation in juvenile males there did not appear to be any survival disadvantage associated with large or small size in the three winters studied.

Searcy (1979a, 1979b) has obtained similar results in his studies of overwinter survival in male Red-winged (*Agelaius phoeniceus*) and Yellow-headed (*Xanthocephalus xanthocephalus*) Blackbirds. All size classes survived equally well, implying no directional selection that could lead to enhancement or reduction of the extent of sexual size dimorphism in these species. Directional selection for large size in males in severe winters has been shown in House Sparrows *Passer domesticus* (Fleischer & Johnston 1984) and Great Tits (Lehikoinen 1986b). In the former, but not the latter study, there was complementary selection for small size in the females. Monaghan & Metcalfe (1986) have shown a similar pattern in the overall mortality rates of Herring Gulls *Larus argentatus*. In this species, stabilising selection seemed to operate in each sex, with the lowest mortality rates recorded for medium sized individuals. Constraints on the size dimorphism between sexes operated through increased mortality of smaller males and larger females.

In some studies of the role of natural selection in overwinter mortality, differences between autumn and spring birds have been described from samples taken (usually killed) out of the respective pool of birds available in each season (Johnston & Fleischer 1981, Weatherhead *et al.* 1987). An implicit assumption is that no immigration or emigration has taken place prior to spring sampling. Immigrant birds may have overwintered under differing selective pressures and the apparent significance of a body size trait could be spurious. The application of this methodology to Dippers in the present study gave contradictory results to those obtained from monitoring survivorship of the known autumn population. Combining all years, spring sampled juvenile females had significantly shorter wing lengths and longer bills than autumn birds. Known survivors from the autumn pool had longer wings and tarsi. Spring caught adult females showed the same differences as juveniles, though bill depths were also significantly greater. The simplest interpretation is that the new birds appearing in the breeding population were from upland areas or adjacent river catchments where selection pressures were subtly different and conditions favoured shorter winged and bigger billed females. Alternatively, bill size (length, depth) may vary seasonally in response to differing food availability or accessibility as has been demonstrated in the Great Tit (Gosler 1987) and Mountain White-crowned Sparrow *Zonotrichia leucophyrs oriantha* (Morton & Morton 1987). Body size did not appear to have much, if any, effect on overwinter survival of juvenile and adult males, irrespective of how the population was sampled or of the conditions during the winter.

3.4.4. Body Size & Breeding Success

Once again, relationships between autumn body size and breeding success were most pronounced in juvenile females. Successfully breeding female recruits were characterised by apparently low mass and poor autumn condition in 1985, large headed/billed birds in 1986 and small keeled individuals in 1987. Overall, there was a tendency for birds of low mass, apparently in poorer condition and with shorter autumn wing lengths to survive best. However, it has already been shown that bigger juvenile females had a better overwinter survival probability and thus the successful recruits were the relatively smaller sized birds in this pool. Schluter & Smith (1986) have also shown an apparent contradiction in the selection of traits for reproduction and overwinter survival. In their Song Sparrow population, adult females producing more young had longer tarsi and shorter bills than other birds but these two characters were associated with reduced survival in juveniles. Perrins (1980) has argued that smaller female Great Tits are able to build up reserves sufficient for breeding sooner than larger individuals and consequently breed earlier and their offspring have higher survival prospects. In a German Dipper population, Schmid & Spitznagel (1985) have shown that larger males mated to smaller females tended to rear more young. Although size differences between pairs were not analysed in this study, it is possible that small females choose, or are sought by, males with high quality territories, usually in lowland areas where an early start to breeding is feasible. Female Herring Gull mortality rates are twice as high in large sized birds than in average or small individuals (Monaghan & Metcalfe 1986). The major part of this increased mortality of large birds occurs during the breeding season whereas few small or medium sized birds die at this time, perhaps because they are able to replenish their reserves more easily.

3.4.5. Body Size & Habitat

The evidence presented here on body size differences and habitat shows that upland residing Dippers tend to be smaller than their lowland counterparts. This tendency was especially noticeable in wing length. Shorter-winged birds are often thought to have increased manoeuvrability in confined spaces (Kokshaysky 1974). Underwater foraging in swift flowing narrow, upland burns may require this but, on the other hand, smaller birds may be ousted from better quality lowland habitat by larger, perhaps more dominant, birds. Ulfstrand *et al.* (1981) and Ebenman & Nilsson (1981) have also shown that smaller Great Tits and Pied Flycatchers *Ficedula hypoleuca* were probably competitively excluded from prime habitat, in this case, deciduous woodland.

CHAPTER FOUR

PLUMAGE VARIATION IN THE DIPPER: MEASUREMENT, CHANGES WITH AGE AND ITS SIGNIFICANCE IN SURVIVAL & BREEDING SUCCESS

4.1. INTRODUCTION

In common with many other passerines, the Eurasian Dipper *Cinclus cinclus* shows considerable geographic variation in plumage colouration (Greenaway & Vaurie 1958, Cramp 1988). The most distinctive component of this variation is the extent and colouration of the lower breast and belly. This may vary from a few millimetres of dull straw-yellow below the white throat and upper breast to the entire belly and under-parts being a rich rufous-brown or chestnut brown. Formerly, many subspecies and races were recognised, yet the discontinuous distribution of colour morphs and lack of obvious clines negates the value of such classifications. For example, typically black-bellied Dippers inhabit much of Fennoscandia (*C.c.cinclus*) and the Pyrenees (*C.c.pyrenaicus*) but are separated on continental Europe by highly variable populations usually referred to as *C.c.aquaticus* with more rufous- and chestnut-brown on the breast and belly (Greenaway & Vaurie 1958, Cramp 1988). Two races are thought to occur in Scotland: *C.c.gularis* on most of the mainland, Skye and Mull, and *C.c.hibernicus* in the Outer Hebrides, Islay, Kintyre, the Clyde Islands and parts of the south-west Mainland (Baxter & Rintoul 1953, Thom 1986). These two races are similar to *C.c.aquaticus* of continental Europe but *C.c.hibernicus* is regarded as separable from *C.c.gularis* by its darker brown-black dorsal/upper parts and both less extensive and duller rufous-brown on the lower breast and belly.

Within Dipper populations, breast and belly colouration can also vary considerably (Cramp 1988) though quantification is generally lacking. Rockenbauch (1985) has measured and described the plumage variation in a

German population of *C.c.aquaticus* but the material presented here is the first thorough quantification of such variability for British races of the Dipper.

Only in the last 15 years has the biological significance of intraspecific plumage variation in passerines been investigated in any detail. Many studies have demonstrated a link between plumage variation and social dominance (see Chapter 5 and references cited therein). Also, juvenile males of many sexually dichromatic species often exhibit delayed plumage maturation (DPM) in which males making their first breeding attempts resemble adult females. Three hypotheses have been proposed to explain the adaptive significance of DPM: female mimicry and deception (Rohwer *et al.* 1980), crypsis (Procter-Gray & Holmes 1981, Hill 1988a) and winter adaptation (Rohwer *et al.* 1983, Rohwer 1986, Brown & Brown 1988). These hypotheses are not necessarily mutually exclusive and summer/breeding season benefits could potentially operate in addition to winter adaptive explanations (Rohwer & Butcher 1988).

Several authors have documented positive correlations between territory quality and plumage brightness (Studd & Robertson 1985a, Hill 1988b) though in the former instance dull males in poorer habitat were able to achieve similar breeding success by increased nestling feeding rates. Male plumage colour in Pied Flycatchers *Ficedula hypoleuca* is very variable and generally darkens with age. However, darker birds do not rear more young (Rõskaft & Järvi 1983) but they were preferred by females (Lifjeld & Slagsvold 1988). Knapton *et al.* (1984) also failed to find any differences between reproductive success of two distinctive colour morphs of White-throated Sparrows *Zonotrichia albicollis*. Thus, it is becoming increasingly apparent that not all components of plumage colour variation are obviously functional or adaptive. Slagsvold & Lifjeld (1985) demonstrated that the yellowness of Great Tits *Parus major* may be attributable to diet and Spellman *et al.* (1987) have shown that bright colouration in the tails of female American Redstarts *Setophaga ruticilla* varies unpredictably between years in the same individuals.

The purpose of this chapter is twofold. In the first part, I describe a method of quantifying the extent of chestnut- or rufous-brown on the breast and belly in a Scottish mainland Dipper population and, by incorporating an assessment of colour tone, I develop a plumage brightness or colour index. Differences between sexes and age groups are investigated together with changes in plumage scores in the same individuals between annual moults. A small number of Hebridean Dippers was caught and scored by the same methods in an attempt to confirm the presence of *C.c.hibernicus* in western Scotland. The second part of the chapter deals with relationships between plumage variation and various aspects of recruitment: overwinter survival, establishment of settled home ranges in autumn and breeding success of first-year birds.

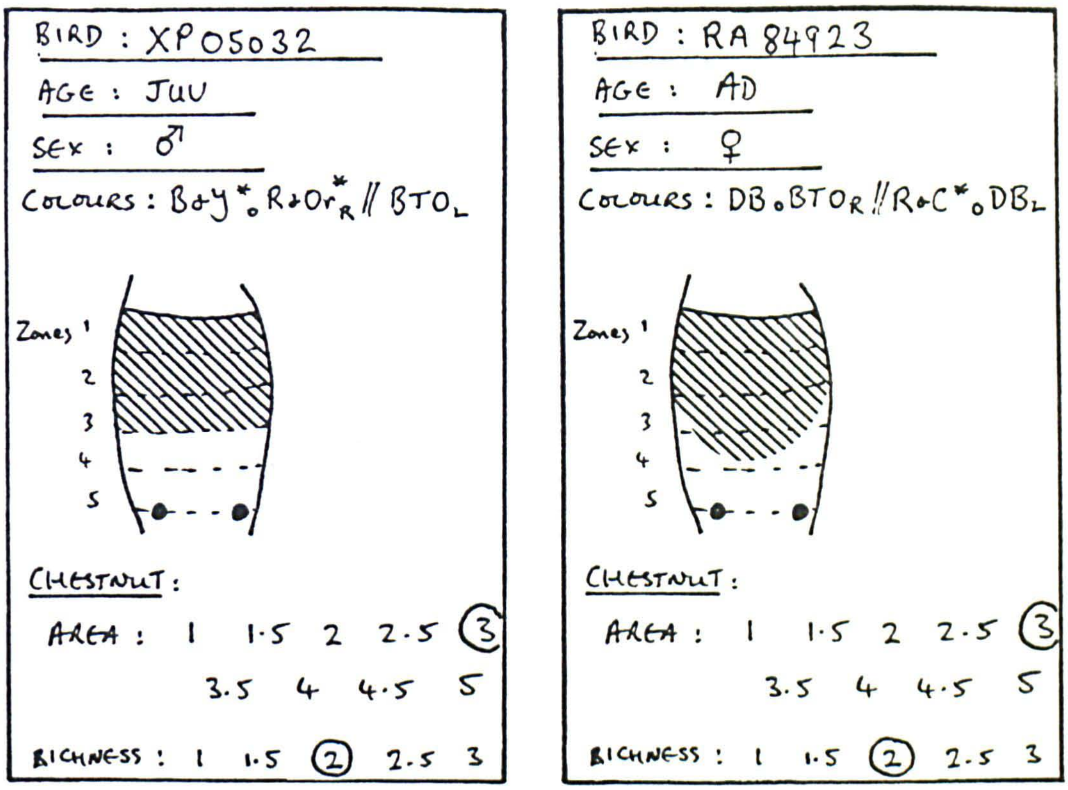
4.2. METHODS

4.2.1. Plumage Scoring in the Field

All post-moult full-grown birds captured during the course of the body size study (see Chapter 3) were plumage scored. The variation in chestnut colouration on lower breast and belly was scored as two components, both in arbitrary units. A decision was made at an early stage against direct physical measurements (i.e. length, width, area, etc.) due to considerable body size variation. Firstly, the proportion of the breast/belly below the white patch that was coloured with any shade of brown or chestnut that contrasted with the general brown-black of the lower belly of the bird was estimated. For this purpose, the bird was placed across the palm of the hand with its head restrained by index and middle fingers. Breast and belly feathers were smoothed with the free hand especially if the bird had just been extracted from a mist-net or hand net. The legs were restrained between thumb and index finger of the free hand at the ankle and the proportion of contrasting brown between the white patch and legs was estimated on a 10 point scale. This was referred to as the "AREA" of chestnut and was recorded as a number between 0 and 5 (with 0.5 increments). In some individuals, there was no sharp boundary between chestnut and black-brown feathering and in such cases AREA was given as the mid-point between the maximum extent down the keel line and the minimum along the flanks (Figure 4.1a). A sketch of the distribution of chestnut was made on a standard recording card with the breast/belly marked off in fifths. The second plumage score was an estimate of the tone or richness of the chestnut colouration. Preliminary observations had shown this to vary from a dull mid-brown or straw yellow-brown to a very rich rufous-brown (contrast Figures 4.2a and 4.2b). This was recorded as "RICH" on a six-point scale (0.5-3.0 with 0.5 increments). Although both plumage measures were subjective, two independent observers would usually record scores of both AREA and RICH to within 0.5 of each other. Plumage scores in the analyses below are the mean of all assessments made for an individual in a particular season. Typical examples of this scoring system for each age and sex group are illustrated in Figure 4.1b. A large collection of reference photographs was built up to check consistency between years. To compensate for the subjectivity in assessing RICH (especially as some birds were scored at night under artificial light), a plumage brightness index ("COLOUR") was derived as follows:

$$\text{Plumage brightness index} = (2 \times \text{AREA}) + \text{RICH}$$

For comparative purposes, a small number of Hebridean Dippers was caught and plumage scored by this system on the Isle of Mull (April 1987) and the Isle of Islay (December 1987). Close-up photographs of all



BIRD : XP05032

AGE : JUV

SEX : ♂

COLOURS : B+Y$^*_o$R+Or$^*_R$ // BTO$_L$

CHESTNUT :

AREA : 1 1.5 2 2.5 [✓ 3] 3.5 4 4.5 5

RICHNESS : 1 1.5 [✓ 2] 2.5 3

BIRD : RA84923

AGE : AD

SEX : ♀

COLOURS : DB$_o$BTO$_R$ // R+C$^*_o$DB$_L$

CHESTNUT :

AREA : 1 1.5 2 2.5 [✓ 3] 3.5 4 4.5 5

RICHNESS : 1 1.5 [✓ 2] 2.5 3

Fig. 4.1a Examples of plumage score cards, each illustrating birds with AREA scores of 3.0.

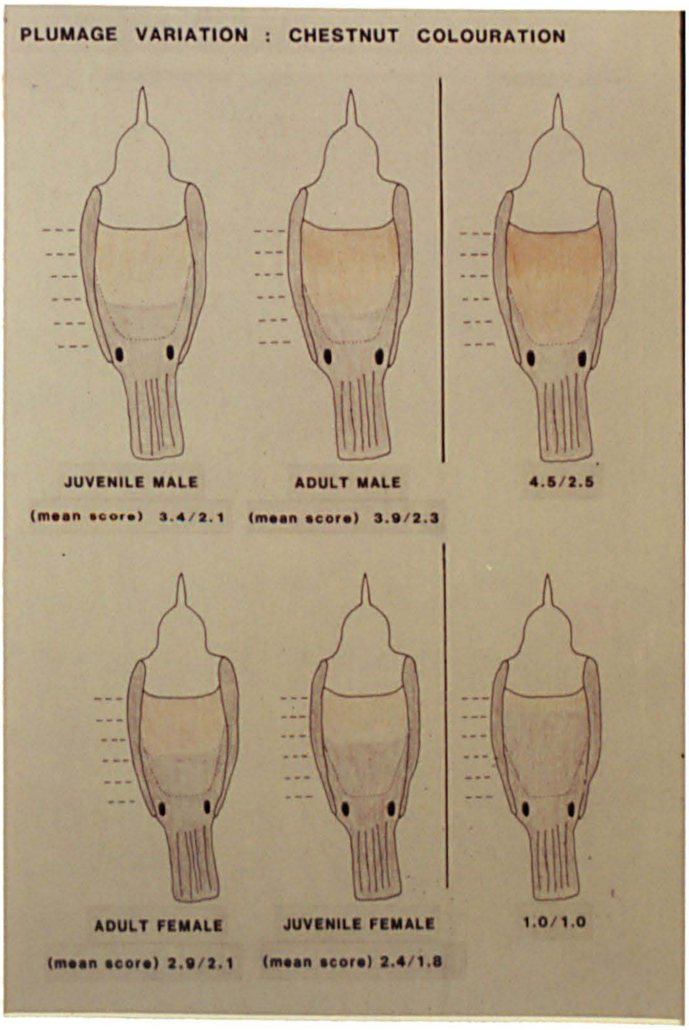


Fig.4.1b Examples of the range of breast/belly plumage variation in a central Scotland Dipper population with typical scores for each age and sex class.

Fig. 4.2a A bright adult male with a plumage score of 4.0/2.5.

Fig. 4.2b A dull adult male with a plumage score of 2.0/1.5.

individuals were taken. Specimens of several races of *Cinclus cinclus*, including *C.c.cinclus* were also inspected at the Sub-Department of Ornithology, British Museum (Natural History), Tring in January 1986.

4.2.2. Analysis

Within age and sex group comparisons between different autumns were made using Student's t tests. Otherwise most analyses of survivorship and breeding success were undertaken using one-way analyses of variance (ANOVAs) in which plumage scores were continuous variables. All procedures were replicates of those made using body size and body mass data presented in Chapter 3. To reiterate: overwinter survivors were those members of the autumn population still alive in March; recruits were those alive in the breeding season (April); successful recruits were those definitely or probably breeding successfully and failed recruits were those known to fail to raise young or which moved out of the study area resulting in an unknown breeding history. Birds with autumn home ranges were those seen at least twice over a period in excess of one month but within a one kilometre stretch of river. "Juvenile" refers to a first-year bird that has completed its post-juvenile moult.

4.3. RESULTS

4.3.1. Age & Sex Differences in Plumage Scores

Mean plumage scores for males and females in three autumn samples are given in Tables 4.1 and 4.2. In all autumns the AREA of the breast/belly covered by chestnut feathering was greater in males than females. Within sexes, AREA of adults was usually higher than in juveniles with the exception of females in autumn 1987 when scores were equal. The pattern was much the same with chestnut richness (RICH) and the overall plumage brightness index (COLOUR). Males were brighter than females and adults brighter than juveniles except in autumn 1987 (Tables 4.1 and 4.2).

Table 4.1. Plumage scores of male Dippers, autumns 1985-87.

Adult males	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
	mean S.D. (n)	mean S.D. (n)	mean S.D. (n)	mean S.D. (n)
AREA	3.64 ± 0.76 (21)	3.71 ± 0.74 (16)	3.83 ± 0.47 (30)	3.74 ± 0.64 (67)
RICH	2.24 ± 0.41 (21)	2.26 ± 0.29 (16)	2.05 ± 0.37 (30)	2.16 ± 0.37 (67)
COLOUR	9.52 ± 1.70 (21)	9.67 ± 1.53 (16)	9.72 ± 1.09 (30)	9.64 ± 1.39 (67)
Juvenile males				
AREA	3.18 ± 0.67 (27)	3.40 ± 0.69 (21)	3.56 ± 0.55 (27)	3.38 ± 0.65 (75)
RICH	2.05 ± 0.38 (27)	2.16 ± 0.38 (21)	2.09 ± 0.45 (27)	2.09 ± 0.40 (75)
COLOUR	8.42 ± 1.58 (27)	8.96 ± 1.72 (21)	9.21 ± 1.44 (27)	8.85 ± 1.59 (75)

Table 4.2. Plumage scores of female Dippers, autumns 1985-87.

Adult females	Autumn 1985	Autumn 1986	Autumn 1987	All years combined
	mean S.D. (n)	mean S.D. (n)	mean S.D. (n)	mean S.D. (n)
AREA	2.87 ± 0.73 (28)	2.79 ± 0.87 (22)	2.66 ± 0.73 (24)	2.78 ± 0.77 (74)
RICH	2.15 ± 0.39 (28)	1.93 ± 0.31 (22)	1.56 ± 0.35 (24)	1.89 ± 0.43 (74)
COLOUR	7.88 ± 1.65 (28)	7.50 ± 1.95 (22)	6.88 ± 1.71 (24)	7.44 ± 1.79 (74)
Juvenile females				
AREA	2.03 ± 0.70 (23)	2.45 ± 0.87 (24)	2.66 ± 0.82 (35)	2.42 ± 0.84 (82)
RICH	1.62 ± 0.43 (23)	1.81 ± 0.47 (24)	1.77 ± 0.34 (35)	1.74 ± 0.41 (82)
COLOUR	5.68 ± 1.63 (23)	6.71 ± 2.14 (74)	7.08 ± 1.86 (35)	6.58 ± 1.95 (82)

Over the course of three years, the AREA of chestnut and the brightness index have been increasing in adult males and in both juvenile males and juvenile females. Adult females have become slightly duller (lower AREA and COLOUR) during the course of this study. The increases in juvenile plumage scores between successive autumns were not significant but were between autumn 1985 and autumn 1987 (males: AREA $t_{52}=2.23$, $p<0.05$; females: AREA $t_{56}=3.01, p<0.01$; COLOUR $t_{56}=2.94$, $p<0.01$). All three plumage scores of adults, for all years combined, were significantly higher than those of the juveniles (Table 4.3). Differences were most pronounced for AREA.

4.3.2. Individual Differences in Plumage Scores Between Years

During the course of the study, some individuals were caught in successive autumns. A total of 13 juvenile males and 22 juvenile females were plumage scored in both their first autumn and one year later as adults. Fifteen adult males and 28 adult females were also caught and plumage scored in successive autumns. The direction of plumage score change for these individuals is summarised in Table 4.4. The AREA of breast and belly covered by chestnut feathering and the plumage brightness index both increased after an individual's first post-nuptual moult (85% of males, 63-73% of females; Table 4.4). Birds first handled as adults showed little predictable change in plumage scores between moults: approximately equal numbers of birds showed increases, decreases or remained the same in terms of AREA of chestnut. Sixty percent of adult males showed decreases in COLOUR index between moults, perhaps indicating some fading of plumage with age. This trend was not so apparent in adult females.

The magnitude of these changes in AREA and COLOUR is given in Table 4.5. The AREA of juvenile females increased by 0.32 (arbitrary units) approximating to an increase of 6% of breast/belly surface covered by

Table 4.3. Differences between plumage scores of autumn caught adult and juvenile Dippers.

Plumage variable	Adult v juvenile females			Adult v juvenile males		
	t value	d.f.	p value	t value	d.f.	p value
AREA	2.76	154	<0.01	3.38	140	=0.001
RICH	2.32	154	<0.05	0.97	140	≥0.05
COLOUR	2.87	154	<0.01	3.16	140	<0.01

Table 4.4. Changes in plumage scores in the same individual between autumns.

	Plumage Scores					
	AREA			COLOUR		
	Increases	Equal	Decreases	Increases	Equal	Decreases
Juvenile - adult female	68.2% (15)	13.6% (3)	18.2% (4)	72.7% (16)	0	27.3% (6)
Adult - adult female	42.9% (12)	32.1% (9)	25.0% (7)	57.1% (16)	0	42.9% (12)
Juvenile - adult male	84.6% (11)	7.7% (1)	7.7% (1)	84.6% (11)	0	15.4% (2)
Adult - adult male	26.7% (4)	33.3% (5)	40.0% (6)	33.3% (5)	6.7% (1)	60.0% (9)

Note: Number of birds is given in parentheses.

Table 4.5. Magnitude of mean plumage score change within individuals and between autumns.

	Plumage score change		
	AREA	COLOUR	
	mean S.D.	mean S.D.	n
Juvenile - adult female	0.320 ± 0.458	0.934 ± 1.002	22
Adult - adult female	0.106 ± 0.444	0.055 ± 1.024	28
Juvenile - adult male	0.896 ± 0.668	2.019 ± 1.525	13
Adult - adult male	0.059 ± 0.466	0.001 ± 1.052	15

chestnut, and that of juvenile males by 0.90 (approximately 18%). Changes in adults were negligible.

There was a significant difference between the median plumage score (AREA) of juvenile Dippers and the same birds recaptured one year later as adults (males: $T = 1$, $n = 12$, $p<0.002$; females: $T = 27$, $n = 19$, $p<0.02$ [Wilcoxon's test for matched pairs, two-tailed]). There was no significant difference in adult plumage scores (AREA) between years (males: $T = 26$, $n = 10$, $p>0.10$; females: $T = 60$, $n = 19$, $p>0.10$ [Wilcoxon's test for matched pairs, two-tailed]).

4.3.3. Relationships Between Plumage Variation & Components of Recruitment

4.3.3.1. Survival

Plumage characteristics associated with overwinter survival (sample 1) and recruitment to the breeding population (sample 2) during the course of the study are given in Table 4.6. Recruiting females from the autumn 1985 population tended to have less chestnut feathering than those dying between September and March although the relationship was not significant ($p<0.06$). There were significant differences in the plumage of the juvenile males disappearing between early autumn and spring and those that recruited in 1986/87. In common with the female recruits the previous year, these males had noticeably less chestnut and had duller plumage brightness indices. Overwinter survivors and recruiting females in 1987/88 had significantly greater AREA of chestnut than non-recruits but the same trend was not apparent in males.

There were no significant plumage differences between overwinter survivors/recruits and all the birds dying or disappearing from the population during the course of the winter when data from all three years were pooled.

Table 4.6. Relationships between plumage scores and overwinter survival in juvenile Dippers.

Sample	Year	Sex	Variable	one-way ANOVA			Mean of surviving cohort (n)	Mean of dying cohort (n)	Introduced birds *
				F value	d.f.	p value			
2	1985/86	F	AREA	3.97	1, 21	<0.06	1.77 (12)	2.32 (11)	None
	1985/86	M	No significant differences						
	1986/87	F	No significant differences						
1 & 2	1986/87	M	AREA	5.39	1, 19	<0.05	3.03 (9)	3.68 (12)	Included
1 & 2	1986/87	M	RICH	9.13	1, 19	<0.01	1.92 (9)	2.34 (12)	Included
1 & 2	1986/87	M	COLOUR	6.41	1, 19	<0.05	7.98 (9)	9.69 (12)	Included
1 & 2	1987/88	F	AREA	4.81	1, 30	<0.05	3.02 (14)	2.39 (18)	Included
	1987/88	M	No significant differences						
	1985-88	F	No significant differences						
	1985-88	M	No significant differences						

Notes:

1. * Analysis includes/excludes introduced birds, or valid for both.
2. Sample 1: Surviving cohort = all those alive in March.
   Dying cohort = all those disappearing between September and the end of February.
3. Sample 2: Surviving cohort = all those alive in April (breeding season).
   Dying cohort = all those disappearing between September and end of March.
4. Abbreviations: F = female, M = male.

4.3.3.2. Autumn Home Range

There were no detectable relationships between plumage characteristics and acquisition of settled autumn home ranges in juvenile male Dippers during any of the autumns under consideration nor in the pooled data set. In autumn 1985, juvenile females acquiring home ranges had less chestnut feathering (AREA: one-way ANOVA, $F_{1,19} = 9.11$, $p<0.01$) and lower colour indices (COLOUR: one-way ANOVA, $F_{1,19} = 7.33$, $p<0.05$) than the transients and birds disappearing very early in the season. The situation was reversed in autumn 1987, when the brighter birds tended to acquire home ranges (AREA: one-way ANOVA, $F_{1,28} = 10.51$, $p<0.01$; COLOUR: one-way ANOVA, $F_{1,28} = 9.11$, $p<0.01$). This relationship held true for both sub-samples including and excluding introduced birds. No significant differences were apparent in the pooled data set (1985-88).

4.3.3.3. Breeding Success

There were no detectable differences (one-way ANOVAs, $p>>0.05$) in autumn plumage scores between successful and unsuccessful juvenile recruits of either sex during any single spring. However, pooling male data for the three years showed that there was a non-significant tendency for brighter individuals (AREA) to be more successful in rearing or probably rearing young when introduced birds were excluded from the analysis (one-way ANOVA, $F_{1,23} = 4.15$, $p<0.06$).

4.3.4. Plumage Comparisons Between Autumn & Spring Populations

In this section, I compare plumage scores for all birds caught in the autumn with those for spring captured birds. The latter principally comprises incubating and brooding females caught on the nest but also includes some mist-netted males; some of the spring birds had also been handled the previous autumn. The results of one-way ANOVAs between autumn and spring samples are presented in Table 4.7. Spring caught juveniles of both sexes were significantly brighter (AREA and COLOUR) in

Table 4.7. Comparisons between autumn and spring plumage scores.

Year	Age	Sex	Variable	One way ANOVA			Mean autumn (n)	Mean spring (n)
				F value	d.f.	p value		
1985/86	J	F	AREA	9.14	1, 39	<0.01	2.03 (23)	2.71 (18)
	J	F	COLOUR	8.88	1, 39	<0.01	5.68 (23)	7.24 (18)
1985/86	J	M	AREA	10.82	1, 32	<0.01	3.18 (27)	4.07 (7)
	J	M	COLOUR	10.35	1, 32	<0.01	8.42 (27)	10.40(7)
1986/87	J	F	No significant differences					
1986/87	J	M	No significant differences					
1987/88	J	F	No significant differences					
1987/88	J	M	No significant differences					
1985-88 (all years)	J	F	AREA	6.09	1, 125	<0.05	2.42 (82)	2.78 (45)
	J	F	COLOUR	6.36	1, 125	<0.05	6.58 (82)	7.43 (45)
1985-88 (all years)	J	M	AREA	8.07	1, 86	<0.01	3.38 (75)	3.91 (13)
	J	M	COLOUR	7.20	1, 86	<0.01	8.85 (75)	10.06 (13)
1985/86	A	F	No significant differences					
1985/86	A	M	No significant differences					
1986/87	A	F	No significant differences					
1986/87	A	M	No significant differences					
1987/88	A	F	AREA	6.45	1, 45	<0.05	2.66 (24)	3.14 (23)
	A	F	RICH	32.15	1, 45	<0.001	1.56 (24)	2.11 (23)
	A	F	COLOUR	11.52	1, 45	<0.01	6.88 (24)	8.38 (23)
1987/88	A	M	No significant differences					
1985-88 (all years)	A	F	AREA	4.80	1, 135	<0.05	2.78 (74)	3.04 (63)
	A	F	RICH	4.84	1, 135	<0.05	1.89 (74)	2.04 (63)
	A	F	COLOUR	5.78	1, 135	<0.05	7.11 (74)	8.11 (63)
1985-88 (all years)	A	M	AREA	4.85	1, 83	<0.05	3.74 (67)	4.09 (18)
	A	M	COLOUR	4.61	1, 83	<0.05	9.64 (67)	10.39 (18)

Note. Abbreviations: J = juvenile, A = adult, F = female, M = male.

1985/86, but no differences were apparent in 1986/87 and 1987/88. The pooled juvenile data sets for 1985-88 also demonstrated the higher incidence of bright birds in the breeding population, especially in males. Within years there were few plumage differences between autumn and spring caught samples of adults. The only exception was in 1987/88 when spring females were significantly brighter (AREA, RICH and COLOUR) than their autumn counterparts. Pooling data for all three years gave similar results to those of the juveniles: brighter birds predominated in the spring population (Table 4.7).

4.3.5. Plumage Differences Between Upland and Lowland Birds in Spring

No differences in plumage scores were detected between upland and lowland caught adult females in spring (data for all years pooled). Samples of both upland adult and juvenile males were too few to permit valid comparisons. However, upland caught juvenile females were significantly brighter than their lowland counterparts (one-way ANOVAs: AREA, $F_{1,34} = 4.46$, $p<0.05$; COLOUR, $F_{1,34} = 5.11$, $p<0.05$). In this case, the sample comprised 23 lowland birds and 13 from upland areas (pooled 1985-88 data set).

4.3.6. Plumage Scores of Hebridean Dippers

A total of eight Hebridean Dippers was caught and plumage scored: four from the Isle of Mull and four from the Isle of Islay (Table 4.8). None of the characteristics expected of the race *Cinclus cinclus hibernicus* were detected in these Hebridean birds. The extent and tone of chestnut feathering on the breast and belly was very similar to that of the mainland population of *C.c.gularis* from Central Scotland. All Hebridean birds tended to be at the "bright" end of the plumage scoring scale for their respective age and sex (see Tables 4.1 and 4.2).

Table 4.8. Plumage scores of Hebridean Dippers.

Site	Age	Sex	AREA	RICH	COLOUR
Islay 1	Juvenile	Male	4.2	2.3	10.7
Islay 2	Juvenile	Male	3.5	1.5	8.5
Islay 3	Adult	Male	3.8	1.8	9.4
Islay 4	Adult	Male	3.6	2.3	9.5
Mull 5	Adult	Male	4.0	2.2	10.2
Mull 6	Juvenile	Male	3.8	2.0	9.6
Mull 7	Adult	Female	3.5	1.8	8.8
Mull 8	Juvenile	Female	3.5	1.8	8.8
Mean	Adult	Male	3.80	2.10	9.70
Mean	Juvenile	Male	3.83	1.93	9.59

Subtle differences in the overall dark brown-black body colouration of Hebridean and mainland Dippers were not apparent in close-up photographs, though perhaps this was due to a combination of non-standardised backgrounds, variable natural light conditions and the different colour saturation levels in the developed transparencies of film from different manufacturers.

4.4. DISCUSSION

Dippers in the mainland study population showed considerable variation in the extent and tone of the chestnut feathering on the lower breast and belly. Using the scoring system presented here (AREA/RICH) birds commonly ranged from 1.0/1.0 to 4.5/2.5: the former were almost invariably juvenile females and the latter males. Twenty skins of the nominate (black-bellied) race *C.c.cinclus* from Fennoscandia have been scored using this system: seven were 0/0, five 0.5/≥0.5 and six of the remaining eight were ≥1.0/≥1.0, demonstrating some overlap in these characters with the Scottish race *C.c.gularis*.

There were consistent differences in plumage brightness scores between age and sex cohorts; juvenile females were dullest and adult males brightest. Since all birds were handled in a short time period (September to November) immediately following post-juvenile or post-nuptual moults, these differences cannot be attributed to feather wear and fading. Juveniles became significantly brighter following their first full moult during their second summer.

To my knowledge, the only other quantitative study of plumage variation in a resident Dipper population is that of Rockenbauch (1985). He presented his data as measured lengths ("widths") of the chestnut/rufous feathered band for his German population of *C.c.aquaticus*. The mean lengths were 2.27cm (n = 85) for males and 2.19cm (n = 79) for females with age groups combined. These plumage differences between sexes would have been greater if the smaller body size of females had been taken into account. However, Rockenbauch (1985) also demonstrated the tendency for the size of the chestnut band to increase with age in both sexes and to darken. The latter presumably equates with the increase in tone or richness of the chestnut colour documented here.

In the following chapter, the significance of plumage variation in dominance relations is discussed in more detail. To summarise briefly, males dominate females and, within sexes, adults dominate juveniles. This hierarchy is exactly paralleled by the plumage brightness differences. Although the overall appearance of juvenile and adult Dippers is rather similar, subtle differences in the chestnut feathering appear to have significance in status signalling and thus in access to key resources. Subtle plumage brightness variability between age and sex groups also exists in several North American *Zonotrichia* sparrows, but relationships with dominance are unclear (Fugle & Rothstein 1985).

Why should juvenile Dippers delay acquisition of plumage maturity until their second autumn? The delayed plumage maturation hypothesis developed by Rohwer *et al.* (1980) perhaps sheds some light on this problem. Juvenile Dippers could benefit by signalling subordinate status during their first winter and breeding attempt since their relatively dull plumage may prevent costly involvement in prolonged agonistic encounters. Dominant adult males possibly react more aggressively toward other intruding adult males or brighter juvenile males whereas duller females or "female mimics" (juvenile males) may be tolerated and allowed access to food or other resources. Such submissiveness has been recorded in bright House Finch males *Carpodacus mexicanus* (with red feathering) as they yield access to food in favour of dull (grey) females and sub-adult males (Brown & Brown 1988).

Relationships between overwinter survival, recruitment and plumage types in Dippers varied between years. In the two winters where temperatures were average, there was a tendency for duller plumaged juveniles to recruit (females in 1985/86 and males in 1986/87), whereas the untypically mild conditions of 1987/88 favoured brighter juvenile females. However, comparisons between autumn caught birds on the main River Devon and spring caught birds on the Devon and surrounding upland burns consistently showed the latter to comprise more bright plumaged individuals than would be expected had they all overwintered on the main river. Perhaps brighter plumaged individuals (apparently signalling high social status), but behaviourally subdominant are competitively excluded from prime wintering habitat on the main river. These birds tended to have shorter wing lengths and larger bills (Chapter 3) and may have been more efficient at utilising the more meagre or dispersed resources of marginal habitats (upland burns and the lower, deeper reaches of the main river). Balat (1961) considered that the plumage morphs in his Czechoslovakian population were adapted to differing habitats. The birds of enclosed, well vegetated ravines had darker underparts than those of more open and warmer valleys which were occupied by rufous-breasted birds. Cramp (1988) broadened this hypothesis to cover the whole of the Western Palearctic: dark-breasted birds occupy cooler, wetter areas (Scandinavia, Pyrenees) and rufous- or chestnut-breasted birds are prevalent in warmer, drier areas (Britain and Germany). The present study area in the western Ochil Hills and River Devon catchment comprises a very heterogeneous mix of steep wooded gorges and areas of more open aspect flanked by moorland, grassland and arable land. This diversity of habitat and the mobility of the birds during post-fledging dispersal and seasonal altitudinal migrations renders the hypothesis redundant in this relatively small area.

Several recent authors have upheld the notion that the Irish race of Dipper *C.c.hibernicus* inhabits western Scotland and most of the Hebrides (Thom 1986, Cramp 1988). However, I have been unable to trace any descriptions of birds caught or collected from these areas in recent times to support this view. From the evidence presented here, it seems equally likely that Dippers on the Inner Hebridean islands of Islay and Mull belong to the more rufous-breasted mainland race of *C.c.gularis.* A comparison of distribution maps in the British and Irish breeding and winter atlases (Sharrock 1976, Lack 1986) shows that although the Dipper may breed regularly on Islay, it may more or less desert the island in the winter. Birds recolonising the island in the spring could come from either Northern Ireland or the Scottish mainland, perhaps leading to a mixing of races in this area. Any recolonisation of outlying breeding haunts further north than Islay (Eigg, Rhum, South Uist) would be more likely to come from adjacent parts of the Scottish mainland or Skye, not Ireland, and thus only *C.c.gularis* would be likely to persist.

CHAPTER FIVE

DOMINANCE RELATIONS AMONG DIPPERS IN A TEST ARENA

5.1. INTRODUCTION

Dominance is defined as a relationship between birds in agonistic encounters that has a predictable outcome: a dominant individual regularly defeats or displaces its rival, a subordinate. Dominant status often confers priority of access to key resources such as food (Hogstad 1988), safe roosting sites (Weatherhead & Hoysak 1984) and territories (Smith 1976, Arcese & Smith 1985). Some studies have also shown that dominants are more likely to survive overwinter (Kikkawa 1980, Arcese & Smith 1985).

A prevailing view is that body size measures are poor predictors of dominance but that age and sex are more reliable (Arcese & Smith 1985, Eden 1987a, Weatherhead & Teather 1987). Frequently, dominants are more conspicuously coloured (plumage "badge") and thus signal their status to conspecifics (Järvi & Bakken 1984, Möller 1987a, Rohwer 1975, see Chapter 4 for further background). Although many workers imply that dominance is an inflexible, fixed trait, some degree of plasticity may be expressed through site-relatedness (De Laet 1984, Krebs 1982) or if it is dependent upon the value each individual places on the resource under dispute (Popp 1987, Theimer 1987).

Some Dippers appear to be territorial throughout the year and thus frequent interaction with neighbours is likely. This in turn indicates that some form of dominance hierarchy may exist on a local, or possibly wider, scale. In this chapter, I describe a novel technique for assessing dominance relations among Dippers which were held temporarily in captivity. The tests were conducted under laboratory conditions specifically to remove the likelihood of site-related familiarity influencing the outcome of contests.

5.2. MATERIALS & METHODS

5.2.1. Field Methods & Laboratory Protocol

Samples of five Dippers, exceptionally four or six, were caught at their roost sites, mostly within four hours of dusk during late summer and autumn. Birds were weighed and processed in the field or soon after return to the laboratory and were then roosted overnight in numbered cloth bags in a cool, dark room. Dominance tests were commenced in the laboratory around dawn the following morning and most birds then returned to their roosts or daytime territories within two or three hours of day-break.

A typical test, with five birds, comprised 10 contests in which each bird was tested in turn against the remaining four. Behavioural observations on each dyad were made in a grey coloured fibre-glass tank measuring 95cm x 95cm x 37cm (Figure 5.1) that was covered with a green nylon mesh which permitted entry of light but prevented a clear view of the laboratory environs. A standard red brick (21cm x 10cm x 7cm) was placed on end in the centre of the tank. The tank was filled with freshwater to within 3cm of the top of the brick. Water was continuously circulated via two inflow portals and a single outflow thus maintaining a constant level. The sound of running water was deliberately enhanced by setting water inflow portals above the water level and this countered any extraneous noise from the laboratory (doors opening, human speech). The brick top thus comprised the only dry perch site in the tank; birds were thus on the perch or in the water except briefly during flight.

Prior to the contests, each bird was placed singly in the tank for five minutes to acclimatise and discover the perch site. All birds flew immediately to the perch and the vast majority remained there for the duration of the acclimatisation period, even if food was available (trout eggs scattered liberally around the

Fig. 5.1 Exterior view of test arena used for assessing dominance relations in Dippers.

bottom of the tank). A few birds made brief forays around the tank, presumably with the intention of escaping, but the perch was clearly the most favoured location in the tank. Birds were recaptured in the tank using a small hand net (Figure 5.1) and returned to cloth bags. Usually, two observers worked together assisted by a third person acting as a recorder and time keeper. The two observers each sat at a corner of the tank and watched the contests from behind screens. Each contest lasted three minutes, though if there was no clear dominant, the proceedings were allowed to continue for up to five minutes. The experimental set-up was designed to induce the two birds into challenging for tenancy of the single perch. The two birds were released simultaneously into the tank from opposite corners and the following parameters were recorded: total number of interactions, number of songs sung by each contestant, number of displacements scored by each bird and whether these were made by active or passive means. An active interaction occurred when a challenger approached the perched bird (by swimming or flight) and either landed on the brick and attempted to push the latter off or topple it into the water after landing on its back. Such interactions occasionally continued in the water with both individuals floating on their backs, grappling with claws and intermittently pecking at each other. The winner would return to the perch as soon as possible. A failed passive interaction was one in which the challenger veered away from the perch and occupant after initiating an approach, whereas a successful one occurred when the challenger occupied the brick perch after it had been vacated by a bird upon the approach of the challenger. The cumulative time each bird spent on the brick perch and in the water was also recorded. At the end of the contest the two observers agreed on a qualitative outcome whereby one bird was allocated dominant status and the other was subordinate. Occasionally a contest was judged a tie (no consensus between the two observers) and each bird was allocated a half win. At the outset the five birds were randomly assigned to numbered bags and contests usually ran according to the following sequence: 1 v 2, 3 v 4, 5 v 1, 2 v 3, 4 v 5, 1 v 3, 2 v 5, 4 v 1, 3 v 5 and 2 v 4. Thus, no bird had to face two consecutive contests and they usually received five minutes' rest. The duration of test sessions, from the first bird's acclimatisation to the end of the last contest was between 90 and 120 minutes.

5.2.2. Data Manipulation

The following estimates of dominance were computed for each bird: proportion of total time (all contests) in which bird had tenancy of the perch (PNTOR); proportion of interactions won (PNFWON); the proportion of qualitative wins (PNQUALW) and the number of songs (SONGS). PNACTWIN is the proportion of wins for a bird in which physical contact was observed (1 - PNACTWIN = proportion of wins by passive means), and PNACTLOS is the proportion of defeats after physical contact occurred. Finally, two indices of "aggressiveness" were calculated as the number of interactions a bird was involved in per minute in the tank (DISPERMI) and the number of interactions per contest (DISPERCO) in a particular test.

These dominance scores were then treated as dependent variables in stepwise multiple regression analyses with body mass, body size measurements and plumage scores entered as independent variables. A plumage brightness index (COLOUR) was computed from the two routinely collected plumage scores: (2 x AREA) + RICH. The reliability of the chestnut "badge" in predicting the outcome of individual interactions over perch occupancy and whole contests was tested using the chi-squared test. Expected values were calculated with the null hypothesis that wins were distributed equally, i.e. 50% of interactions should be won by brighter and 50% won by duller plumaged birds. Values of p are for one degree of freedom.

Some of the juveniles used in summer (July and August) tests were still in speckled fledgling plumage and in such cases their plumage scores were excluded from the analyses. The first test (February 1986) was by way of a trial run and no quantitative measures (time on perch, etc.) were recorded. This was also excluded from all numerical analyses.

5.3. RESULTS

5.3.1. Qualitative Estimates of Dominance

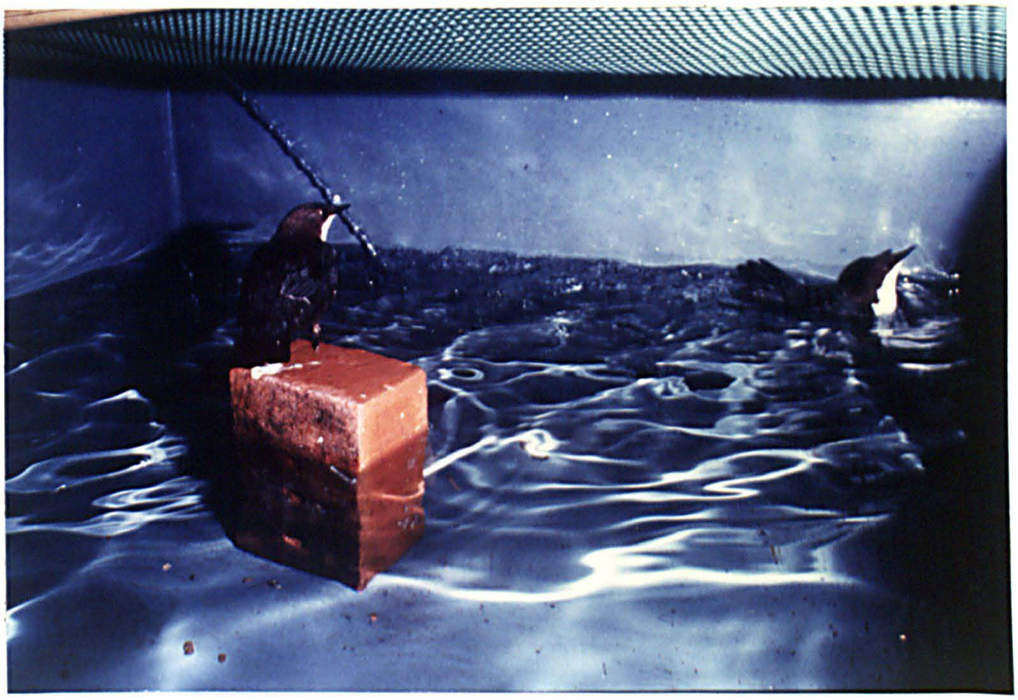
Dippers seemed to be remarkably unconcerned by their temporary confinement to a small tank. The range of threat- and advertising- displays performed in combination with a varied song repertoire and normal maintenance activities (preening, swimming and diving), was representative of those performed routinely and during interactions and chases in the wild (Cramp 1988, Glutz Von Blotzheim & Bauer 1985, personal observations). Typical scenes during the course of a contest between two individuals are given Figures 5.2a and 5.2b.

A total of 15 tests was undertaken between February 1986 and November 1987. They involved 70 different individuals, comprising 15 adult males, 23 juvenile males, 10 adult females and 22 juvenile females. Four individuals were used on two occasions, one adult male, one juvenile female and two juvenile males. The age and sex composition of the 15 tests are given in Table 5.1. together with quantitative dominance rankings. In six of the tests, the aim was to use juveniles only, but on the last two of these occasions, single adult females were included to keep the numbers at five and prevent too much use of the same individuals. Otherwise, most samples represented random collections of birds from areas of differing river quality and altitude in the Stirling area. On some occasions, two or three of the birds came from the same or adjacent roosts and there was a reasonable chance that they would have prior

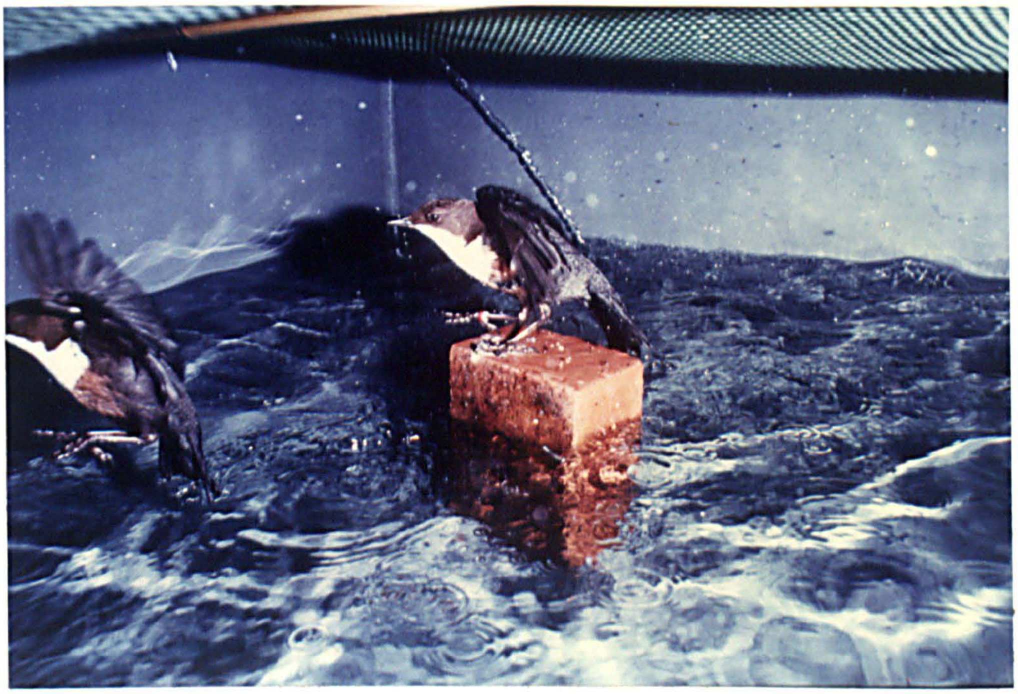
Table 5.1. Age and sex composition and qualitative dominance rankings in 15 tests with Dippers.

Expt. no.	Date	Total no.birds	Adult males	Juv. males	Adult females	Juv. females	Subjective dominance rankings (wins) Dominant (------------) Subordinate						Linear hierarchy
1	Feb 1986	5	1	1	1	2	JM (4)	AF (3)	JF (2)	AM (1)	JF (0)		Yes
2	Mar 1986	5	3	0	1	1	AM (3)	AM (2)	JF (2)	AM (2)	AF (1)		No
3	Sept 1986	5	0	5	0	0	JM (3.5)	JM (3)	JM (2)	JM (1.5)	JM (1)		No
4	Oct 1986	5	0	3	0	2	JM (4)	JM (2)	JF (2)	JM (2)	JF (0)		No
5	Dec 1986	6	3	1	1	1	AF (4.5)	AM (4)	AM (3.5)	JF (1)	JM (1)	AM (1)	No
6	July 1987	5	0	3	0	2	JM (4)	JM (2.5)	JF (1.5)	JM (1.5)	JF (0.5)		No
7	Aug 1987	5	0	3	0	2	JM (4)	JM (3)	JF (2)	JF (1)	JM (0)		Yes
8	Sept 1987	5	0	1	1	3	JM (3)	JF (3)	JF (1.5)	JF (1.5)	AF (1)		No
9	Oct 1987	5	0	3	1	1	JM* (4)	JM (3)	AF (2)	JF (1)	JM$^{@}$ (0)		Yes
10	Oct 1987	4	3	1	0	0	AM (3)	JM (1.5)	AM (1.5)	AM (0)			No
11	Oct 1987	5	1	0	0	4	AM (4)	JF (3)	JF^{+} (2)	JF (1)	JF (0)		Yes
12	Oct 1987	5	0	0	2	3	AF (4)	AF (3)	JF^{+} (2)	JF (1)	JF (0)		Yes
13	Nov 1987	5	2	2	1	0	AM (4)	AM$^{\circ}$ (3)	JM* (2)	JM (1)	AF (0)		Yes
14	Nov 1987	4	2	0	1	1	AM (2)	AF (1.5)	AM (1.5)	JF (1)			No
15	Nov 1987	5	1	2	1	1	AM$^{\circ}$ (4)	AF (2.5)	JM (1.5)	JF (1.5)	JM$^{@}$ (0.5)		No
Totals		74	16	25	10	23							6/15

Note: A = adult, J = juvenile, M = male, F = female; *, +, ° & @ indicate same individuals).



A



B

Fig. 5.2a,b Interior view of dominance test arena with two Dippers disputing tenancy of single perch.

experience of some of their opponents in the wild. However, there was no noticeably qualitative difference in their performance in the dominance tank. On only one occasion was a bird suspected of pairing rather than agonistic behaviour: an adult male in test 2 was completely submissive towards two females. This test was the closest of all 15 to the breeding season and the male in question was possibly seeking a mate. In view of this, all other tests were carried out between July and December.

On the basis of qualitative wins, in all juvenile tests (Table 5.1) a male always achieved dominant status. In mixed-age tests, six out of eight of those including adult males had a dominant adult male. The two exceptions were test 1 in which a juvenile male achieved top rank (note date) and test 5 in which an adult female came out on top with respect to qualitative wins. In the latter case, the second ranking adult male spent a comparable proportion of time occupying the perch and had a far superior record in terms of the proportion of interactions won (75.6% versus 50.0% for the female). In the remaining mixed-age tests, both of those with adult females present were headed by juvenile males whilst the single female only test was dominated by two adult females.

The four birds used twice are indicated in Table 5.1. These birds achieved consistent and predictable rankings when the overall age and sex of the remaining four birds was considered. In summary, a qualitative assessment of status indicates males are virtually always dominant over females, and within sexes adults usually dominate juveniles. In only six out of 15 tests were the hierarchies linear, with higher ranking birds always dominant over those below. However, in the remaining cases there were usually obvious dominant and subordinate individuals with a varying number of rather evenly matched mid-ranking birds.

5.3.2. Age and Sex Variation in Quantitative Estimates of Dominance

Mean body size measures, plumage brightness and dominance scores for all age and sex cohorts are given in Table 5.2. The biometrics of birds involved in the tests follow patterns established in the study as a whole with adult males slightly larger than juvenile males and adult and juvenile females more closely matched (see Chapter 3). All birds were captured at roost, usually between 22.00 and 02.00 hours and consequently masses were slightly lower than would be recorded for the same birds during the daytime. Plumage scores were also similar to those described in Chapter 4, with adults brighter (i.e. greater AREA of chestnut and high COLOUR indices) than juveniles and males brighter than females.

Quantitative measures of dominance (PNTOR and PNFWON) paralleled the quantitative outcomes described in the previous section (Table 5.2). Adult males occupied the perch (PNTOR) for a considerably greater proportion of time than juvenile females; juvenile males and adult females fell between and were approximately evenly matched. Males won a higher proportion of their interactions (PNFWON) than females and, within sexes adults were more successful than juveniles. Singing was most frequent in adults and was predominantly performed on the perch after a successful interaction. Songs were not recorded in juvenile males in the July or August tests, were infrequent in September and October but became common in November. Juvenile females did not sing in any test.

PNACTWIN is the proportion of successful interactions won which entailed physical contact. Juvenile males and adult females achieved two thirds of their supplants after physical contact whereas adult males and juvenile females used passive means to win a slightly higher proportion of their supplants. The actual number of supplants achieved by juvenile females was small and

Table 5.2. Mean body size and plumage brightness measures and estimates of dominance in age/sex cohorts of Dippers.

	Adult male	Juvenile male	Adult female	Juvenile female
Mass (g)	69.66 ± 3.90	67.23 ± 3.72	57.70 ± 3.39	56.58 ± 4.05
Wing length (mm)	98.87 ± 1.92	96.63 ± 1.47	89.56 ± 2.70	90.33 ± 1.24
Keel length (mm)	31.43 ± 0.73	31.52 ± 0.81	27.04 ± 0.86	27.18 ± 0.90
Tarsus length (mm)	29.71 ± 1.08	29.08 ± 0.71	27.41 ± 1.04	27.57 ± 0.81
Head & bill (mm)	47.66 ± 0.57	47.49 ± 0.77	45.51 ± 1.18	45.56 ± 0.68
Bill length (mm)	16.99 ± 0.55	16.35 ± 0.87	15.59 ± 0.50	15.49 ± 0.83
Bill depth (mm)	4.68 ± 0.21	4.60 ± 0.17	4.30 ± 0.17	4.24 ± 0.18
AREA	3.71 ± 0.61	3.31 ± 0.76*	2.81 ± 0.90	2.62 ± 0.84*
RICH	2.03 ± 0.28	2.01 ± 0.43*	1.71 ± 0.29	1.75 ± 0.35*
COLOUR	9.44 ± 1.21	8.62 ± 1.83*	7.33 ± 1.88	6.98 ± 1.89*
Proportion of time on perch (PNTOR)	0.581 ± 0.246	0.515 ± 0.274	0.537 ± 0.275	0.374 ± 0.171
Proportion of I/As won (PNIWON)	0.657 ± 0.248	0.528 ± 0.244	0.472 ± 0.288	0.332 ± 0.164
Proportion of qual. wins (PNQUALW)	0.658 ± 0.299	0.529 ± 0.328	0.531 ± 0.327	0.341 ± 0.214
No. of songs (SONGS)	5.53 ± 6.01	1.00 ± 1.89	4.33 ± 4.39	0.00
Proportion of physical wins (PNACTWIN)	0.606 ± 0.220	0.675 ± 0.201	0.655 ± 0.253	0.543 ± 0.266
Proportion of physical defeats (PNACTLOS)	0.707 ± 0.286	0.781 ± 0.210	0.574 ± 0.222	0.597 ± 0.168
No. of I/As per min. in tank (DISPERMN)	2.28 ± 0.94	2.61 ± 1.08	2.59 ± 0.60	2.80 ± 1.09
No. of I/As per contest (DISPERCO)	6.92 ± 2.97	8.22 ± 3.37	8.32 ± 2.12	8.64 ± 3.41
Sample size (excludes Speckled birds)	15 --	24 20	9 --	21 17

Notes: (1) Mean values ± standard deviation are given; (2) Derivations of PNTOR - DISPERCO are given in the text, (3) I/A = interaction.

these were mostly scored over other juvenile females. Males lost between 71% and 78% of their unsuccessful interactions after physical contact (PNACTLOS) whereas females appeared less willing to enter into physical clashes that they were unlikely to win (PNACTLOS < 60%). The aggressiveness indices (DISPERMI and DISPERCO) were remarkably similar in juvenile males and all females with approximately 2.7 interactions per minute and 8.4 interactions per contest. Adult males appeared to be involved in fewer interactions, both per minute in the tank and per contest.

The potential seasonality of aggressiveness in overall tests was investigated using two variables: DISPERMI and the proportion of active wins. The median number of interactions per minute was significantly higher in 10 autumn tests (September to November inclusive) than in the four tests in the remaining seasons ($U<0.1$; $p<0.01$, Mann-Whitney U-test). No significant difference was found in the equivalent test on the proportion of active wins ($U = 14.5$; $p = 0.45$, Mann-Whitney U-test).

5.3.3. Correlations Between Dominance, Body Size and Plumage Brightness

Correlations between dominance measures, body size and plumage brightness indices are given in Tables 5.3 to 5.6. In adult males, bright plumage (AREA and COLOUR) was positively correlated with the three primary dominance estimates (PNTOR, PNFWON, PNQUALW). No body size measures appeared important, with no significant correlations (Table 5.3). The significant negative relationship between PNACTWIN and head and bill length implies a possible intimidatory role for the bill, perhaps avoiding escalation into interactions involving physical contact.

Dominance in juvenile males was matched by various body size measures, especially keel and wing lengths, with mass and tarsus length also important (Table 5.4). Thus big birds occupy the perch for longer periods and have

Table 5.3. Correlations between body size and plumage brightness measures and estimates of dominance in adult male Dippers.

Adult males	Mass	Wing length	Keel length	Tarsus length	Head & bill	Bill length	Bill depth	AREA	RICH	COLOUR
Proportion of time on perch (PNTOP)	0.295 n.s.	-0.154 n.s.	-0.042 n.s.	0.274 n.s.	-0.158 n.s.	-0.203 n.s.	0.008 n.s.	0.544 *	-0.050 n.s.	0.536 *
Proportion of I/As won (PNYWON)	0.367 n.s.	-0.191 n.s.	-0.135 n.s.	0.063 n.s.	-0.129 n.s.	-0.255 n.s.	0.383 n.s.	0.655 **	0.022 n.s.	0.664 **
Proportion of qual. wins (PNQUALW)	0.310 n.s.	-0.375 n.s.	-0.108 n.s.	0.135 n.s.	-0.203 n.s.	-0.254 n.s.	0.033 n.s.	0.696 **	0.018 n.s.	0.695 **
Proportion of physical wins (PNACTWIN)	-0.116 n.s.	-0.289 n.s.	-0.409 n.s.	-0.222 n.s.	-0.642 **	-0.359 n.s.	0.053 n.s.	0.238 n.s.	0.542 *	0.343 n.s.
Proportion of physical^{+} defeats (PNACTLOS)	0.335 n.s.	0.105 n.s.	-0.037 n.s.	0.466 *	0.073 n.s.	0.173 n.s.	0.319 n.s.	-0.159 n.s.	0.548 *	-0.033 n.s.
I/As per minute in tank (DISPERMI)	0.016 n.s.	0.320 n.s.	-0.077 n.s.	0.183 n.s.	-0.099 n.s.	-0.196 n.s.	-0.353 n.s.	0.438 n.s.	-0.039 n.s.	0.420 n.s.
Sample size	15	15	15	15	15	15	15	15	15	15

Note: Values are Pearson correlation coefficients; n.s. = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$; $^{+}$ = sample size = 14 (excludes single bird that won all disputes); I/A = interaction.

Table 5.4. Correlations between body size and plumage brightness measures and estimates of dominance in juvenile male Dippers.

Juvenile males	Mass	Wing length	Keel length	Tarsus length	Head & bill	Bill length	Bill depth	AREA	SIZE	COLOUR
Proportion of time on perch (PNTOR)	0.435 *	0.559 **	0.653 ***	0.374 *	0.329 n.s.	0.057 n.s.	-0.082 n.s.	0.512 *	0.369 n.s.	0.511 *
Proportion of I/As won (PNFWON)	0.432 *	0.439 *	0.622 **	0.298 n.s.	0.283 n.s.	0.065 n.s.	-0.086 n.s.	0.441 *	0.516 *	0.487 *
Proportion of qual. wins (PNQUALW)	0.403 *	0.491 **	0.654 ***	0.300 n.s.	0.271 n.s.	0.058 n.s.	-0.094 n.s.	0.448 *	0.430 *	0.473 *
Proportion of physical wins (PNACTWIN)	-0.294 n.s.	-0.176 n.s.	0.031 n.s.	0.024 n.s.	-0.178 n.s.	-0.128 n.s.	0.237 n.s.	-0.157 n.s.	0.194 n.s.	-0.097 n.s.
Proportion of physical defeats (PNACTLOS)	-0.180 n.s.	-0.178 n.s.	0.142 n.s.	-0.120 n.s.	0.022 n.s.	0.008 n.s.	0.258 n.s.	0.083 n.s.	0.174 n.s.	0.157 n.s.
I/As per minute in tank (DISPERMI)	0.180 n.s.	-0.107 n.s.	-0.123 n.s.	-0.032 n.s.	-0.226 n.s.	0.223 n.s.	0.319 n.s.	0.037 n.s.	0.134 n.s.	0.062 n.s.
Sample size	24	24	24	24	24	24	24	20	20	20

Note: Values are Pearson correlation coefficients; n.s. = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$; I/A = interaction.

Table 5.5. Correlations between body size and plumage brightness measures and estimates of dominance in adult female Dippers.

Adult females	Mass	Wing length	Keel length	Tarsus length	Head & bill	Bill length	Bill depth	AREA	RICH	COLOUR
Proportion of time on perch (PNTOP)	0.186 n.s.	0.037 n.s.	-0.145 n.s.	-0.471 n.s.	0.020 n.s.	0.073 n.s.	-0.103 n.s.	0.445 n.s.	0.315 n.s.	0.475 n.s.
Proportion of I/As won (PNFWON)	0.274 n.s.	0.211 n.s.	0.024 n.s.	-0.101 n.s.	0.177 n.s.	-0.036 n.s.	-0.324 n.s.	0.486 n.s.	-0.059 n.s.	0.456 n.s.
Proportion of qual. wins (PNQUALW)	0.141 n.s.	0.074 n.s.	-0.211 n.s.	-0.515 n.s.	-0.050 n.s.	0.021 n.s.	-0.139 n.s.	0.394 n.s.	0.330 n.s.	0.429 n.s.
Proportion of physical wins (PNACTWIN)	-0.512 n.s.	-0.468 n.s.	-0.537 n.s.	-0.337 n.s.	-0.673 *	-0.567 n.s.	0.075 n.s.	-0.455 n.s.	0.253 n.s.	-0.397 n.s.
Proportion of physical defeats (PNACTLOS)	0.055 n.s.	0.146 n.s.	0.149 n.s.	-0.344 n.s.	0.285 n.s.	0.179 n.s.	-0.064 n.s.	0.408 n.s.	0.040 n.s.	0.397 n.s.
I/As per minute in tank (DISPERMI)	-0.054 n.s.	0.567 n.s.	-0.116 n.s.	-0.035 n.s.	0.198 n.s.	0.358 n.s.	-0.623 *	0.679 *	0.166 n.s.	0.676 *
Sample size	9	9	9	9	9	9	9	9	9	9

Note: Values are Pearson correlation coefficients; n.s = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$; I/A = interaction.

Table 5.6. Correlations between body size and plumage brightness measures and estimates of dominance in juvenile female Dippers.

Juvenile females	Mass	Wing length	Keel length	Tarsus length	Head & bill	Bill length	Bill depth	AREA	RICH	COLOUR
Proportion time on perch (PNTOR)	0.480 *	0.083 n.s.	0.496 *	0.393 *	0.072 n.s.	0.109 n.s.	0.333 n.s.	0.408 n.s.	0.300 n.s.	0.417 n.s.
Proportion I/As won (PNFWON)	0.556 **	0.284 n.s.	0.529 **	0.287 n.s.	0.189 n.s.	0.250 n.s.	0.229 n.s.	0.188 n.s.	0.141 n.s.	0.193 n.s.
Proportion qual. wins (PNQUALW)	0.513 **	0.151 n.s.	0.492 *	0.453 *	0.158 n.s.	0.195 n.s.	0.257 n.s.	0.336 n.s.	0.139 n.s.	0.324 n.s.
Proportion of physical wins (PNACTWIN)	0.127 n.s.	-0.098 n.s.	0.303 n.s.	-0.195 n.s.	0.016 n.s.	0.195 n.s.	-0.154 n.s.	-0.196 n.s.	-0.501 *	-0.267 n.s.
Proportion of physical defeats (PNACTLOS)	0.331 n.s.	0.433 *	0.440 *	0.076 n.s.	0.302 n.s.	0.441 *	0.317 n.s.	0.181 n.s.	0.243 n.s.	0.226 n.s.
I/As per minute in tank (DISPERMI)	-0.139 n.s.	0.050 n.s.	-0.039 n.s.	-0.011 n.s.	-0.015 n.s.	0.122 n.s.	-0.097 n.s.	0.169 n.s.	0.288 n.s.	0.203 n.s.
Sample size	21	21	21	21	21	21	21	17	17	17

Note: Values are Pearson correlation coefficients; n.s. = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$; I/A = interaction.

a higher success rate in their challenges for, or defence of, the perch. Plumage brightness is of less importance than for adult males.

There were no significant correlations between the three dominance measures and body size or the plumage variables listed in Table 5.5. for adult females. However the positive correlations between AREA and COLOUR only just failed to reach the 5% significance level. In common with adult males, a negative relationship between PNACTWIN and head and bill length indicated that large headed adult females won more of their interactions by passive means. Correlations between DISPERMI and chestnut AREA and COLOUR imply brighter birds are involved in more interactions than duller birds.

Mass and keel length yielded the most significant positive correlations with dominance scores in juvenile females (Table 5.6). Plumage brightness was positively correlated with PNTOR but this relationship failed to reach the 5% significance level. The positive correlations between PNACTLOS and keel and wing length may indicate that the bigger birds were more willing to dispute tenancy of the perch even though they were likely to lose such interactions.

5.3.4. Multiple Regression Analysis of Factors Influencing Dominance

The results of this analysis amplify the findings of the Pearson Correlation analyses in the previous section. However, in this case, coefficients of determination (r^2 x 100) allow the relative contribution of each significant independent variable to be determined (Table 5.7).

In adult males the plumage brightness index COLOUR gave consistently greater coefficients of determination with dominance scores than the AREA of chestnut on the breast alone. This indicates that the colour tone may

Table 5.7. Multiple regression analysis of factors affecting dominance in Dippers.

Dependent variable	All birds	All males	Adult males	Juvenile males	All females	Adult females	Juvenile females
Proportion of time on perch (PNTOP)	COLOUR *** r^2= 26.5% 20.93 1,58	AREA ** r^2= 28.4% 12.70 1,32	COLOUR * r^2= 31.2% 5.43 1,12	Keel *** r^2= 47.5% 16.29 1,18	MASS ** r^2= 19.7% COLOUR r^2= 40.1% Tarsus r^2 = 50.2% 7.38 3,22	No significant correlations	Mass * r^2= 35.5% COLOUR r^2 = 51.6% 7.48 2,14
Proportion of interactions won (PNTWON)	COLOUR *** r^2= 28.9% Mass r^2= 37.0% Sex r^2 = 41.9% 13.47 3,56	COLOUR *** r^2= 32.8% Mass r^2= 40.9% 10.73 2,31	COLOUR ** r^2= 47.2% 10.74 1,12	Keel ** r^2= 42.2% 13.16 1,18	Mass * r^2= 19.0% 5.64 1,12	No significant correlations	Mass * r^2= 30.9% Bill$_d$ r^2 = 51.8% 7.51 2,14
Proportion of qual. wins (PNQUALW)	COLOUR *** r^2= 26.6% 21.05 1,58	COLOUR *** r^2= 31.9% 14.99 1,32	COLOUR ** r^2= 50.0% 12.02 1,12	Keel ** r^2= 43.9% 14.10 1,18	Mass * r^2 = 16.7% COLOUR r^2 = 31.8% 5.36 2,23	No significant correlations	Mass * r^2= 29.3% 6.20 1,15
Number of songs (SONGS)	Age *** r^2= 25.40% AREA r^2= 34.4% 14.93 2,57	Age ** r^2= 20.8% AREA r^2= 30.6% 6.85 2,31	No significant correlation	No significant correlations	Age *** r^2= 41.8% 17.22 1,24	No significant correlations	No singing recorded in this age class
Proportion of physical wins (PNACTWIN)	No significant correlation	Head * r^2= 13.7% 5.07 1,32	Head ** r^2= 34.5% 6.32 1,12	No significant correlations	Wing * r^2= 18.4% 5.41 1,24	Head * r^2= 45.3% 5.80 1,7	RICH * r^2= 25.1% 5.02 1,15
Proportion of physical defeats (PNACTLOS)	RICH *** r^2= 16.6% Head r^2= 24.1% 9.05 2,57	RICH * r^2= 16.1% 6.15 1,32	RICH * r^2= 30.0% 5.15 1,12	Mo * r^2= 25.3% 6.11 1,18	Bill$_n$ * r^2= 15.3% 4.34 1,24	No significant correlations	Bill$_n$ * r^2= 24.3% 4.81 1,15
Number of interactions per minute in tank (DISPERMT)	Mo ** r^2= 13.8% Wing r^2= 19.5% 6.91 2,57	Mo * r^2= 15.0% 5.65 1,32	No significant correlation	Mo * r^2= 27.6% 6.86 1,18	No significant correlations	COLOUR ** r^2= 45.8% Wing r^2= 76.2% Keel r^2= 91.2% 17.37 3,5	No significant correlations
Number of interactions per contest (DISPERCO)	Mo ** r^2= 14.5% 9.81 1,58	Mo * r^2= 15.4% 5.81 1,32	No significant correlation	Mo * r^2= 26.4% 6.45 1,18	No significant correlations	COLOUR * r^2= 47.6% Wing r^2= 75.1% 9.06 2,6	No significant correlations

Table 5.7. Multiple regression analysis of factors affecting dominance in Dippers. (continued):

Note: Each cell comprises the cumulative coefficients of determination ($r^2 \times 100$) for combinations of independent variables with significant standardised partial regression coefficients; the results of an analysis of variance with F, degrees of freedom (explained, residual) and the significance of F for the overall relationship are also given (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

also have some effect in signalling the status of a bird. In both PNFWON and PNQUALW approximately 50% of the variation was explained by COLOUR. Keel length proved the single most reliable predictor of dominant status in juvenile males and alone explained 42-47% of the variation in PNTOR, PNFWON and PNQUALW. Thus, in their first autumn, body size appears to be the most important factor governing dominance and, by implication, access to resources in juvenile males.

Dominance in adult females was not influenced by any measurable independent variable, whereas higher mass was critical in enabling a juvenile female to hold tenancy of the perch or win interactions. In the latter case, coefficients of determination were 28-36%, perhaps indicating that body mass was of less importance than plumage brightness and body size (keel length) were to adult and juvenile males respectively. In no instance was more than 50% of the variation in dominance score explained by the listed independent variables. Consequently the residual variation in dominance may be partly explained by a heritable component not expressed in the phenotype, except in the outcome of agonistic encounters.

Singing during dominance contests was mostly influenced by the age of the birds involved and was often delivered during interactions and chases within the tank, and as a sign of continued perch occupancy. Adults with greater head and bill lengths achieved a higher proportion of their successful interactions without physical contact, but no single variable consistently explained differences between age cohorts with respect to how interactions were lost (PNACTLOS). Correlations between DISPERMI and month were presumably the result of the increase in aggressiveness between summer and late autumn.

5.3.5. The Role of Plumage Brightness in Determining the Outcome of Contests and Interactions Over Perch Occupancy

Although plumage brightness only appeared as a highly significant predictor of dominance status in adult males in both correlation and multiple regression analyses, the relationships between plumage and dominance were further investigated for each age and sex cohort with respect to the outcome of both three minute contests and individual interactions. Table 5.8 gives the overall percentage of contests won by the brighter plumaged birds, broken down by both AREA of chestnut and COLOUR index. Sample sizes in each class of contest are small and few results differed significantly from the null hypothesis of 50:50 but in each case more contests were won quantitatively by the brighter bird of each dyad. Plumage difference was of least importance in all-juvenile female contests (54% won by brighter birds) and mixed-age female contests (ca. 60%) whereas in all-male groupings over 70% were won by brighter birds. On the whole, AREA of chestnut was a slightly better predictor of dominance status than COLOUR index and in three-quarters of 104 contests, the brighter bird won.

During the 14 tests, a total of 1103 interactions was observed, of which 62.2% involved physical contact. In the analysis presented in Table 5.9a, b, 985 of these interactions with definite outcomes have been used to examine the predictive role of plumage asymmetry. The results given in Table 5.9a are derived from instances in which the two birds could be clearly separated into brighter and duller plumage classes, whilst the results in Table 5.9b include equally coloured birds in the percentage of interactions won by the brighter plumaged birds. This gives an upper limit to the likelihood of plumage based status signalling occurring within a given cohort.

Table 5.8. Percentage of dominance contests won by brighter plumaged birds, broken down by age and sex classes.

No.	Type of contest	Percentage of contests won by brighter plumaged birds	
		AREA	COLOUR
1	Adult male v. adult female	60.0% (10) n.s.	54.5% (11) n.s.
2	Adult male v. adult male	80.0% (10) n.s.	80.0% (10) n.s.
3	Adult female v. adult female	[100.0% (1)] ---	[100.0% (1)] ---
4	Juvenile male v. juvenile female	85.7% (14) n.s.	88.2% (17) *
5	Juvenile male v. juvenile male	71.4% (14) n.s.	70.6% (17) n.s.
6	Juvenile female v. juvenile female	53.8% (13) n.s.	53.8% (13) n.s.
7	Adult male v. juvenile male	77.8% (9) (sample too small)	70.0% (10) n.s.
8	Adult female v. juvenile female	63.6% (11) n.s.	57.1% (14) n.s.
9	All adult contests (1+2+3)	71.4% (21) n.s.	68.2% (22) n.s.
10	All juvenile contests (4+5+6)	70.7% (41) n.s.	72.3% (47) *
11	All male contests (2+5+7)	75.8% (33) *	73.0% (37) *
12	All female contests (3+6+8)	60.0% (25) n.s.	57.1% (28) n.s.
13	Total: all contests	75.0% (104) ***	73.5% (117) ***

Note: Sample sizes are given in parentheses; X^2 tests: n.s. = not significant; * = $p<0.05$; *** = $p<0.001$.

Table 5.9. Percentage of individual disputes won by brighter plumaged birds, broken down by age and sex classes.

Part (a).

		Percentage I/As won by "brighter" plumaged bird					
Row	Type of I/A	Active I/As		Passive I/As		All I/As	
		AREA	COLOUR	AREA	COLOUR	AREA	COLOUR
1	Adult male v. adult female	67.3% (49) n.s.	63.5% (52) n.s.	80.8% (26) *	61.8% (34) n.s.	72.0% (75) **	62.8% (86) n.s.
2	Adult male v. adult male	75.0% (32) *	75.0% (32) *	69.2% (13) n.s.	69.2% (13) n.s.	73.3% (45) *	73.3% (45) *
3	Adult female v.adult female	80.0% (5) ------ Sample size was too small for X^2 test ---------------	80.0% (5)	100.0% (4)	100.0% (4)	88.9% (9)	88.9% (9)
4	Juvenile male v. juvenile female	76.3% (76) **	75.9% (87) ***	81.8% (44) **	83.7% (49) ***	78.3%(120) ***	78.7%(136) ***
5	Juvenile male v. juvenile male	57.7%(104) n.s.	58.2%(134) n.s.	54.5% (22) n.s.	61.3% (31) n.s.	57.1%(126) n.s.	58.8%(165) n.s.
6	Juvenile female v. juvenile female	52.5% (59) n.s.	52.5% (59) n.s.	46.4% (56) n.s.	46.4% (56) n.s.	49.6%(115) n.s.	49.6%(115) n.s.
7	Adult male v. juvenile male	70.5% (44) n.s.	60.5% (38) n.s.	88.2% (34) **	89.3% (28) **	78.2% (78) ***	72.7% (66) **
8	Adult female v. juvenile female	59.3% (54) n.s.	52.3% (65) n.s.	73.9% (46) *	66.7% (51) n.s.	66.0%(100) *	58.6%(116) n.s.
9	All adult I/As (Rows 1+2+3)	70.9% (86) **	68.5% (89) *	79.1% (43) **	58.5% (41) n.s.	73.6%(129) ***	65.4%(130) *
10	All juvenile I/As (Rows 4+5+6)	62.3%(239) **	62.5%(280) **	60.7%(122) n.s.	63.2%(136) *	61.8%(361) **	62.7%(416) ***
11	All male I/As (Rows 2+5+7)	63.9%(180) **	61.3%(204) *	73.9% (69) **	73.6% (72) **	66.7%(249) ***	64.5%(276) ***
12	All female I/As (Rows 3+6+8)	56.8%(118) n.s.	53.5%(129) n.s.	60.4%(106) n.s.	57.7%(111) n.s.	58.5%(224) n.s.	55.4%(240) n.s.
13	Total: all I/As	68.5%(527) ***	68.6%(563) ***	75.8%(326) ***	73.6%(349) ***	71.3%(853) ***	70.5%(912) ***

Note: Sample sizes are given in parentheses; X^2 tests: n.s. = not significant; * $p<0.05$; ** $p<0.01$; *** $p<0.001$; I/A = interaction.

Part (b).

Row	Type of I/A	Percentage I/As won by equally coloured and "brighter" plumaged birds combined (where different to Table 5.9a)					
		Active I/As		Passive I/As		All I/As	
		AREA	COLOUR	AREA	COLOUR	AREA	COLOUR
1	Adult male v. adult female	69.2% (52) *	--------	85.3% (34) **	--------	75.6% (86) ***	--------
2	Adult male v. adult male	--------	--------	--------	--------	--------	--------
3	Adult female v.adult female	--------	--------	--------	--------	--------	--------
4	Juvenile male v. juvenile female	79.3% (87) ***	--------	83.7% (49) ***	--------	80.1%(136) ***	--------
5	Juvenile male v. juvenile male	67.2%(134) **	--------	67.7% (31) n.s.	--------	67.3%(165) **	--------
6	Juvenile female v. juvenile female	56.3% (64) n.s.	56.3% (64) n.s.	50.8% (61) n.s.	50.8% (61) n.s.	53.6%(125) n.s.	53.6%(125) n.s.
7	Adult male v. juvenile male	78.7% (61) **	75.4% (61) **	90.9% (44) ***	90.9% (44) ***	83.8%(105) ***	81.9%(105) ***
8	Adult female v. juvenile female	66.2% (65) n.s.	--------	76.5% (51) **	--------	70.7%(116) **	--------
9	All adult I/As (Rows 1+2+3)	71.9% (89) **	--------	82.4% (51) **	--------	75.7%(140) ***	--------
10	All juvenile I/As (Rows 4+5+6)	68.1%(285) ***	63.2%(285) **	66.0%(141) **	64.5% (141) *	67.4%(426) ***	63.6%(426) ***
11	All male I/As (Rows 2+5+7)	71.4%(227) ***	65.2%(227) **	76.9% (78) ***	77.3 % (88) ***	72.8%(305) ***	68.6%(315) ***
12	All female I/As (Rows 3+6+8)	61.9%(134) n.s.	55.2%(134) n.s.	63.8%(116) *	59.5 %(116) n.s.	62.8%(250) **	57.2%(250) n.s.
13	Total: all I/As	72.7%(612) ***	70.2%(593) ***	78.8%(373) ***	75.2% (371) ***	75.0%(985) ***	72.1%(964) ***

Note: Sample sizes are given in parentheses; X^2 tests: n.s. = not significant; * $p<0.05$; ** $p<0.01$; *** $p<0.001$; I/A = interaction.

The results broadly follow the pattern already established. Plumage asymmetry is a more reliable predictor of the outcome of interactions in adults over juveniles (Tables 5.9a, b, rows 9, 10) than in males over females (rows 11, 12). However, some interesting differences occur between active and passive interactions within particular types of dyads. A higher proportion of all-adult and adult-juvenile passive disputes were won by brighter birds in comparison to active interactions (rows 1, 3, 7-9, 11, 13). Within all-juvenile same-sex dyads (rows 5, 6) plumage asymmetry seems of little predictive value in settlement of both active and passive interactions in contrast to mixed-sex dyads where deviations from the null hypothesis were highly significant. Overall, two-thirds of active interactions and three-quarters of passive interactions were won by brighter birds. Both brightness variables AREA and COLOUR seemed to perform equally well, though the former was a marginally better status signal in adults and the latter in juveniles (rows 9, 10).

5.4. DISCUSSION

5.4.1. Methodology

The methodology used in this study with a non-flocking resident, aquatic bird was rather different to that in many other studies on terrestrial winter flocking passerines. Here, birds were matched in exclusive dyads for short time periods with estimates of dominance based on interactions over a single, easily defensible perching site. Other workers have concentrated on assessing dominance in flocks, mostly housed in aviaries, by tallying supplants between dyads at feeders (Institute of Ecological Research 1986, Watt 1986a) and/or over more dispersed food and other resources (Jackson *et al.* 1988, Theimer 1987). The test arena used here allowed more or less complete logging of all interactions between the two birds and prevented any observer selectivity and bias that may confound studies on flocks where only single interactions from a concurrent series of events can be monitored. Even if two or more observers are present, many events that may contribute to the development of a dominance hierarchy may occur outwith the observation period. Some workers have deliberately starved their birds to increase the number of interactions during any observation period (Richison 1985) or to enhance the value of the resource itself (Popp 1987). This may change the pattern of response in such experimental birds. Although my tests were conducted at dawn, a time when birds would have empty guts, hunger did not appear to affect their willingness to interact. In this study the predominant activity of subordinate birds between interactions was swimming and diving: something which would not entail discomfort for Dippers, but presumably prevented them from undertaking other non-interactive maintenance activities (preening) that were observed in the perched dominant.

In a study of status signalling in captive flocks of House Sparrows *Passer domesticus*, Möller (1987a) deliberately ignored non-contact, passive interactions on the grounds that the outcomes could be ambiguous. I would argue that evidence for status signalling would be better supported by observations of passive interactions rather than of direct physical attacks. In this study, passive attacks were often much less ambiguous than physical ones. The current subordinate bird would approach the perch (swimming or, rarely, flying) but would veer off before reaching the perch or opponent, who by then would be facing the attacker, often displaying his or her chestnut patch in an upright posture. Physical interactions could precipitate into prolonged events which sometimes required subjective decisions in order to allocate wins and losses to each bird.

De Laet (1984) has described differences in the social position of Great Tits *Parus major* in relation to the site of a feeder. Yet in studies of dominance in the wild, it is hard to locate a feeder in a spatially neutral location. Even when placed at territory or habitat boundaries, access for all local residents and unestablished birds will be unequal. The laboratory set-up described for Dippers avoided bias due to factors such as site-relatedness as the observation tank provided a truly neutral site. None of the birds was kept in captivity for more than 12 hours (22.00 - 10.00 hours) and most of this fell within their roosting period. Thus the dominance test procedure should not have interfered unduly with the Dipper's routine in the wild.

Virtually all birds in these tests experienced approximately similar lengths of time in the dominance tank, and thus no one bird should have had better knowledge of the scant resources present. Four birds were used in two tests each: in each case prior experience in the tank did not boost their dominance status when allowance was made for the age and sex of the other contestants (Table 5.1).

5.4.2. Dominance Relations Amongst Age and Sex Cohorts

In size dimorphic species it is often difficult to distinguish the relative importance of age, sex and body size in determining dominance. Many other studies have shown broadly similar results to those presented here, with adults and males usually dominant over juveniles and females respectively (Eden 1987a, Rohwer *et al.* 1981, Smith *et al.* 1980, Watt 1986b). In both the Harris' Sparrows *Zonotrichia querula* studied by Rohwer *et al.* (1981) and the Song Sparrows *Melospiza melodia* observed by Smith *et al.* (1980), adults of both sexes were ranked higher than juveniles in contrast to Dippers where sex was of more importance than age. In the latter case dominance status closely paralleled the continuum shown by most body size and plumage brightness measures (Table 5.2).

Factors affecting relative dominance within age or sex cohorts need not necessarily be the same. This study has demonstrated that different body size or plumage brightness measures correlate with both qualitative and quantitative estimates of dominance status in each age and sex cohort. In each case, causal relationships cannot be identified, but some measures such as high body mass and head and bill, or bill length alone may help in the retention of a favoured perch site or in winning physical interactions respectively. In adult Dippers there were no significant correlations between body size and dominance (tables 5.3. and 5.5), whereas mass, wing, keel and tarsus were all significantly correlated with one or more quantitative measures of dominance in juveniles (Tables 5.4. and 5.6).

Arcese & Smith (1985) studied juvenile Song Sparrows and concluded that no body size measures had any effect on dominance. A similar finding was reported within each sex for immature Magpies *Pica pica* by Eden (1987a) and, within mixed adult-juvenile groups of male House Sparrows, Möller (1987a) failed to detect any significant relationships between body size or size-adjusted mass and dominance. Some authors have described size effects but they have usually failed to differentiate between ages and sexes. Shaw (1986) found that dominant Greater Sheathbills *Chionis alba* had longer and deeper bills but were not necessarily heavier. Also Searcy (1979c) demonstrated strong positive correlations in adult and adult-juvenile cohorts of male Red-winged Blackbirds *Agelaius phoeniceus* between dominance and wing length. Similarly, Watt (1986b) reported a wing length - dominance relationship in Harris' Sparrows. In these results there is a suggestion that body size may be more important in determining dominance in bird species that are individually territorial (e.g. Dippers, Red-wing Blackbirds) than in flocking species (e.g. immature Magpies and House Sparrows) during the part of the annual cycle investigated.

The relative age of juveniles has been cited as the key predictor of dominance status in two studies of species lacking body size effects. Early hatched juvenile Song Sparrows (Arcese & Smith 1985) and Capricorn Silvereyes *Zosterops lateralis* (Kikkawa *et al.* 1986) were both more likely to be dominant than later hatched or second brood juveniles. Unfortunately, most of the juveniles in the Dipper experiments were of unknown age and origin and the importance of this factor could not be tested.

The heritable component of dominance has received relatively little attention to date, though Kikkawa *et al.* (1986) surmised that the performance of juvenile Silvereyes was little affected by parental ability. A similar finding may apply to other species especially if the conclusion of Arcese & Smith (1985), that dominance status predominantly depends on the cumulative experience gained in interactive encounters, is upheld.

5.4.3. Plumage Variability and Dominance

Within virtually all age and sex subdivisions that included adults in the test Dippers, plumage brightness (AREA and COLOUR) emerged as the single most important measured factor in explaining variability in dominance scores (Table 5.7). This implies that bright plumage, in this case a really extensive and richly coloured chestnut breast band, is a good indicator of social status or fighting ability.

The status signalling hypothesis (SSH) was first postulated by Rohwer (1975) to give a functional explanation for the observed plumage variation in winter flocking birds. This, and subsequent papers on Harris' Sparrows (Rohwer 1978, 1985, Rohwer & Ewald 1981, Rohwer *et al.* 1981, Rohwer & Rohwer 1978) sparked widespread interest in the topic and many authors have since described similar findings (Fugle *et al.* 1984, Fugle & Rothstein 1987, Järvi & Bakken 1984, Möller 1987a, 1987b, Studd & Robertson 1985b). Others were more sceptical or felt the hypothesis was only valid in some circumstances such as in age or sex recognition (Shields 1977, Balph *et al.* 1979, Richison 1985, Searcy 1979c, Watt 1986a). Alternatively, plumage variability could enable individuals to recognise one another (the individual recognition hypothesis, IRH) and this has been demonstrated in the Harris' and White-throated Sparrows *Zonotrichia albicollis* (Watt 1986a) and Turnstones *Arenaria interpnes* (Whitfield 1986, 1988).

Whitfield (1987) has reviewed the roles of SSH and IRH and suggested that a wider range of species with differing social organisations should be studied before the selective advantages of either hypothesis can be fully evaluated. Recently, Rohwer himself has conceded that the SSH may be restricted to mixed age and sex flocks and that predictions were not upheld within single age and sex cohorts of Harris' Sparrows (Jackson *et al.* 1988).

In contrast, the evidence presented here suggests that the SSH is upheld in many classes of Dippers, particularly adults; and overall, plumage asymmetry can be used as a predictor of likely victors in over 70% of individual interactions (Table 5.9a) and 75% of more prolonged contests (Table 5.8).

Even so, the IRH cannot be ruled out in Dippers and, also, the two hypotheses are not necessarily mutually exclusive. In each of the last five Dipper tests, most birds were caught at roosts in close proximity so their daytime territories/home ranges may have abutted or overlapped. Some of these birds would presumably have had prior agonistic experience with other contestants and would thereby be expected to be aware of each others relative status. However, no diminution in the number of interactions per minute was observed (mean, 3.32 for tests 10 to 14 and 2.21 for tests 1 to 9), though the proportion of active interactions was lower for the supposed neighbours (of tests 10 to 14) (mean, 57% versus 68%). Seasonality may have accounted for the former relationship but was unlikely to influence the active/passive ratio. In the wild, the establishment of dominance hierarchies in territorial species such as the Dipper is likely to be a prolonged affair and may take many days, weeks or even months.

5.4.4. Overview: the Acquisition of Dominance in the Dipper

The plumage "badge" is critical to the working of the SSH. However badges cannot directly help a bird in a physical encounter and although a juvenile may have inherited a good badge, he or she can only learn the social significance of their badge by engaging in intraspecific agonistic encounters. This study has shown that the subordinate cohorts (juvenile males, adult and juvenile females) engage in more interactions than the dominant adult males. Dominant status is acquired as the cumulative result of scoring wins; these are likely to be more easily achieved by bigger birds. Throughout a juvenile's first autumn, the ability to read plumage badges as indicators of fighting ability or social status presumably develops and this in turn should discourage engagement in interactions that a particular individual is unlikely to win. The field behaviour of Dippers of differing social status is explored in Chapter 7.

CHAPTER SIX

POST-FLEDGING SURVIVAL & DISPERSAL OF JUVENILE DIPPERS

6.1. INTRODUCTION

Many resident, temperate passerines have average annual adult mortality rates of about 40-60% (Kluyver 1951, Galbraith & Tyler 1982, Dobson 1987). Consequently, the probability of any single fledgling recruiting to its vacant natal territory is slight. Thus, some form of post-fledging dispersal phase away from natal sites is both inevitable and common to most avian species. Dispersal may range from a few metres, perhaps to an adjacent vacant territory, to many kilometres, though in the latter case some confusion with partial migration is likely.

The proximate causes of a young bird's tendency to disperse includes the search for food (Drent 1984), avoidance of predation by larger siblings (Newton 1979) or increasing hostility from parents (Alonso *et al.* 1987) or other conspecific juveniles (Dhondt 1979, De Laet 1985). Costs of philopatry include the increased risk of inbreeding which may lead to reduced breeding success (Greenwood *et al.* 1978) but on the other hand, dispersing individuals may experience greater mortality (Eden 1987b, Greenwood & Harvey 1976).

Dispersal of juveniles may involve a two stage process: a post-fledging movement away from the natal site to a non-breeding/overwintering home range, hereafter referred to as autumn dispersal and secondly a move into suitable breeding habitat in the spring (spring dispersal). The overall move between birth site and first breeding site is usually referred to as the natal dispersal of an individual. Such dispersal distances have been described in many species (for review, see Greenwood & Harvey 1982) and are commonly measured as linear distances, though the number of home ranges or territories crossed may be an alternative measure (Waser 1985, Buechner 1987).

The post-fledging period is usually a time of high mortality (Dhondt 1979) and attempts to follow individuals through the course of dispersal are few and have mainly been limited to radio telemetric studies of raptors (Wyllie 1985, Alonso *et al.* 1987).

In this chapter, I describe autumn, spring and natal dispersal of Dippers over three years, specifically looking at sex- and between-year differences and the influence of body size, relative age and natal habitat on these. A small number of fledglings was successfully radio-tracked through the course of their autumn dispersal phase and the overall first year mortality of Dippers from known nest sites is documented.

6.2. MATERIALS & METHODS

6.2.1. General Field Procedure

Large scale ringing of nestlings was fundamental to this study. In 1985, nest searches were limited to the River Devon between the lower Glendevon Reservoir and Dollar and to three upland burn systems: the South Queich, the Burn of Sorrow with the Burn of Care above Dollar, and the Mill, Gannel and Whum Burns near Tillicoultry. In 1986 and 1987, the whole of the River Devon catchment and parts of the adjacent Allan Water and its Ochil Hill tributaries were covered. All nestlings were ringed with standard British Trust for Ornithology (BTO) rings and were fitted with unique combinations of celluloid colour rings (Supplier: A.C.Hughes, Hampton Hill, Middlesex). A limited suite of biometric measurements was taken, usually comprising mass (g), wing length (mm), tarsus length (mm) and head & bill length (mm). Most nestlings were processed in the period 7-15 days post-hatching to prevent premature fledging.

Intensive searches for colour-ringed birds of the year were made in the autumn, primarily during September and October, and their progress through to recruitment the following spring was monitored by less frequent censusing. Where possible, "known origin" birds (i.e. ringed as nestlings) were caught by mist-netting or at roosts to permit sexing (from biometrics) or to confirm colour ring identifications by means of BTO ring numbers. Autumn and winter censusing was mainly restricted to the main river and the three upland burn systems mentioned previously, with infrequent checks at other upland sites. From 1986 onwards, identification and catching of breeding birds formed an integral part of nest searching as some known origin recruits had not been located and sexed during the autumn and winter.

6.2.2. Radio Tracking of Fledglings

Five birds were tracked by radio for varying lengths of time in June/July 1987 with the aim of determining the timing of departure and rate of movement away from natal territories. One-stage transmitters ("radio tags") were mounted onto small (5 x 15mm) perspex tail clips (as per Bray & Corner 1972, Kenwood 1987) and these were fitted across the central four to six retrices as close as possible to their base. Total package weight varied between two and three grams, depending on battery size. The radio tags did not interfere with the bird's access to its preen gland and, although the weight caused the tail to droop slightly (periodically immersing the aerial into water), normal flight and swimming activities were not impeded. Radio signal frequencies were in the range 173.20 to 174.00 MHz and were detected using a three-element hand-held Yagi antenna and a RX-81 receiver. All radio-tracking equipment was supplied by Biotrack, Stoborough Croft, Wareham, Dorset.

Radio detection range varied from about 10m when a bird was crouched under a deeply overhanging section of riverbank to one kilometre if a bird was perched centrally on a wide stretch of river with open aspect. Where possible, both daytime and roosting fixes were made on each bird on a daily or alternate day basis until contact was lost, either following a prolonged move away from the usual daily range (approximate radius of search was 5-10km from last field location) or until radio loss or battery failure. The usual battery life was two to four weeks but in some cases birds were followed for longer periods, after the radios had failed, by means of colour rings.

6.2.3. Computation of Dispersal Distances

Habitats were classified as upland or lowland using the criteria presented in Chapter 2. In the analyses, the relative age of juveniles is expressed in terms of their date of hatch. Fledging usually occurred 20-22 days post-hatch. Relative age was either recorded by direct observation or was computed from the regression of wing length on age given in Feltham (1987):

$$\text{Nestling age in days} = (0.275 \times \text{wing length}) + 0.149$$

Autumn dispersal distances were calculated in two ways: firstly, the straight line ("as the crow flies") distance between natal site and mean autumn (September to November inclusive) daytime location; and secondly, the minimal distance between these two points following a water course all the way. In some cases, the latter may have involved an apparent movement down one tributary burn, then some distance along a length of main river before a further movement up a second tributary burn. If a bird apparently crossed a watershed into an adjacent catchment, then this dispersal distance could not be computed and the case was excluded from the analysis, though the bird's history was used in the survivorship analyses.

Spring and natal dispersal distances were only calculated using the river-distance method. Spring dispersal constituted the distance between the last autumn or winter sighting (usually within the already defined autumn home range) and the nest site location of the bird's first breeding attempt. Natal dispersal distance was the overall minimal river distance between natal site and site of first breeding the following spring. Each dispersal distance was allocated to one of four habitat-movement classes: intra-lowland, intra-upland, lowland-upland or upland-lowland.

The frequency distributions of all dispersal distances proved to be skewed and thus only non-parametric statistics were calculated (Mann-Whitney U tests for differences between medians; Spearman rank correlations). However, hatchdays (= fledglings' ages) were normally distributed within a year and Student's t-tests were used in analyses of these data. All statistical treatment of dispersal was done using river distances rather than direct distances.

6.3. RESULTS

6.3.1. Post-fledging Survival & Recruitment of Dippers Ringed as Nestlings

A total of 585 Dipper nestlings was ringed and aged in the course of this study (Table 6.1). About 40% of these birds originated from upland nest sites and 60% from lowland sites. There was no significant difference in the proportion of upland birds between years ($X^2_2 = 1.93$, $p>0.05$). The proportion of nestlings known to have fledged that survived through to the autumn (i.e. at least to three months) varied between 13.2 and 26.8%, with a mean of 17.9% (Figure 6.1). The lowest survivorship was recorded in the year with the wettest spring (1986). The very wet late summer of 1985 did not appear to influence fledgling survival, implying that the first month or so post-fledging was the most critical period. The mortality rate decreased dramatically from autumn through to the following spring, so between 55-60% of autumn survivors eventually recruited in all years.

Table 6.1. Post-fledging survivorship and recruitment of Dippers ringed as nestlings in relation to location of natal site.

Year		Natal site						All birds		
		Lowland			Upland					
		M	F	M+F	M	F	M+F	M	F	M+F
1985	No. ringed			77			40			117
	No. fledging			72			40			112
	No.surviving to autumn (%)			--			--			30(26.8%)
	No.recruiting (%)	5	6	11	2	4	6	7	11	17(15.2%)
	No.recruits remaining in natal habitat	4	6	10	1	3	4	5	9	14
	No.recruits changing habitat	1	0	1	1	1	2	2	1	3
1986	No. ringed			144			93			237
	No. fledging			131			88			219
	No.surviving to autumn (%)			--			--			29(13.2%)
	No.recruiting (%)	6	6	12	1	4	5	7	10	17 (7.8%)
	No.recruits remaining in natal habitat	5	5	10	1	2	3	6	7	13
	No.recruits changing habitat	1	1	2	0	2	2	1	3	4
1987	No. ringed			134			97			231
	No. fledging			123			95			218
	No.surviving to autumn (%)			--			--			39(17.9%)
	No.recruiting (%)	3	8	11	4	7	11	11	11	22(10.1%)
	No.recruits remaining in natal habitat	3	6	9	0	5	5	3	11	14
	No.recruits changing habitat	0	2	2	4	2	6	4	4	8
All years	No. ringed			335			230			585
	No. fledging			326			223			549
	No.surviving to autumn (%)			--			--			98(17.1%)
	No.recruiting (%)	14	20	34	7	15	22	21	35	56(10.2%)
	No.recruits remaining in natal habitat	12	17	29	2	10	12	14	27	41
	No.recruits changing habitat	2	3	5	5	5	10	7	8	15

Notes:

1. Abbreviations: M = male; F = female.
2. Percentages (in the last column) refer to the proportion of nestlings known to have fledged that survived to autumn or recruited.

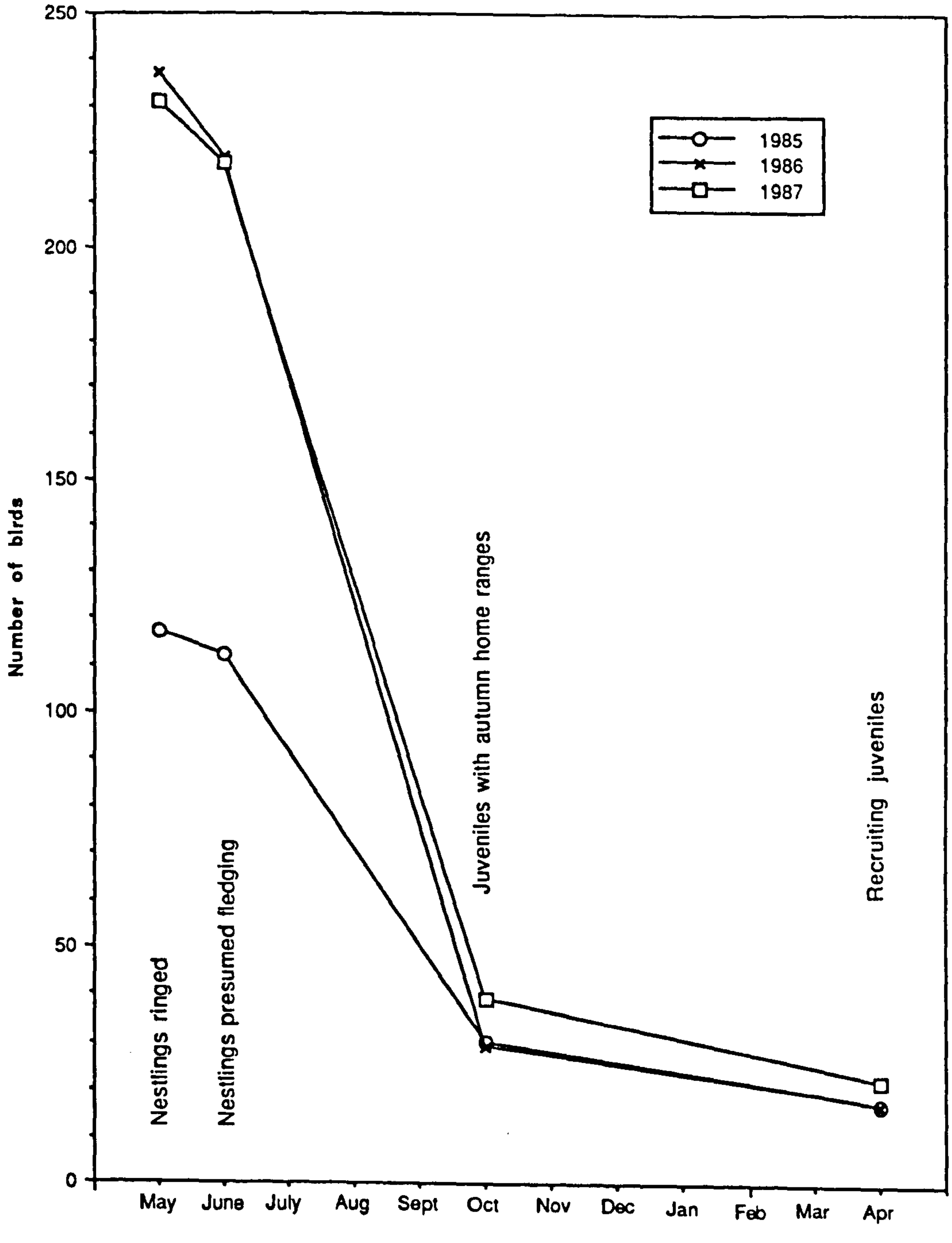


Fig. 6.1 Post-fledging survivorship of Dippers ringed as nestlings.

The probability of recruitment was independent of natal origin in each year and overall (1985-87 nestlings), commonly with an apparently equal proportion of recruits coming from upland and lowland habitats relative to numbers fledging (all years combined: X^2_1 = 0.05, $p>>0.10$; data from Table 6.1). The vast majority of survivors from lowland sites recruited to breed in lowland sites themselves with no difference between sexes (all years combined: $X^2_1<0.01$, $p>>0.10$). Two thirds of upland origin females recruited to upland sites with the remainder switching to lowland sites. However, a greater proportion of upland males (5 out of 7) recruited to breed at lowland sites. This difference between sexes approached significance at the 5% level (X^2_1= 2.79, $p<0.10$). Combining sexes, significantly more upland birds switched habitats, whereas virtually all lowland birds remained faithful to their natal habitat (X^2_1= 6.44, $p<0.05$).

6.3.2. Dispersal Distances

6.3.2.1. Autumn

Median autumn dispersal (river) distances for different years, sex and habitat groupings are given in Table 6.2. Both mean and median straight line distances for the whole population by year and sex are presented in Table 6.3. Autumn dispersal could usually be categorised into two broad classes: firstly a move of varying distance upstream or downstream on the main river (for birds from lowland natal sites) or secondly a move from an upland natal site downstream to an adjacent stretch of main river. Moves entirely within or between upland burns were relatively rare and were undertaken by females only. In such cases an individual may have crossed an upland watershed or moved between upland burns *via* the main river. Maps illustrating potential direct autumn dispersal flight lines are given in Appendix Figures 1, 2 and 3; frequency histograms for each sex by year are given in Figure 6.2.(a-f). Females usually moved further than males (mean and median distances, Table 6.3) with four or

Table 6.2. Median autumn, spring and natal distances (metres) of juvenile Dippers in the River Devon catchment.

MALES:				
Type of movement	Year	Natal site		All birds (n)
		Lowland (n)	Upland (n)	
Autumn dispersal	1985	1090 (11)	2665 (3)	1125 (14)
	1986	4415 (9)	26070 (5)	5063 (14)
	1987	1545 (6)	7005 (6)	4870 (12)
	Overall	1245 (26)	6190 (14)	3020 (40)
Spring dispersal	1985	447 (4)	---- (0)	447 (4)
	1986	215 (1)	9200 (1)	4708 (2)
	1987	865 (2)	1110 (3)	910 (5)
	Overall	499 (7)	1190 (4)	700 (11)
Natal dispersal	1985	2528 (6)	680 (1)	1400 (7)
	1986	9615 (3)	44490 (1)	25500 (4)
	1987	1385 (3)	23830 (3)	4710 (6)
	Overall	2893 (12)	23830 (5)	4000 (17)
FEMALES:				
Autumn dispersal	1985	4760 (5)	11520 (4)	6020 (9)
	1986	5092 (6)	14383 (2)	6739 (8)
	1987	5180 (9)	15345 (7)	7041 (16)
	Overall	4955 (20)	12630 (13)	6923 (33)
Spring dispersal	1985	190 (3)	2085 (2)	1770 (5)
	1986	705 (5)	32030 (1)	973 (6)
	1987	1280 (5)	1498 (2)	1280 (7)
	Overall	705 (13)	2180 (5)	1260 (18)
Natal dispersal	1985	5583 (4)	18593 (2)	7385 (6)
	1986	6218 (5)	17320 (1)	7689 (6)
	1987	5593 (8)	25018 (6)	7624 (14)
	Overall	6210 (17)	17320 (9)	7624 (26)

Note:

Dispersal distances were measured following the course of the River Devon and its tributaries, even if shorter, more direct routes crossing watersheds were feasible routes.

Table 6.3. Mean and median autumn dispersal distances (kilometres, straight line) for juvenile male and female Dippers 1985-87.

Year	Male			Female		
	Mean	Median	n	Mean	Median	n
1985	1.56	1.10	15	4.95	4.50	10
1986	3.99	2.65	12	4.01	3.80	10
1987	3.23	3.80	12	5.20	3.50	15

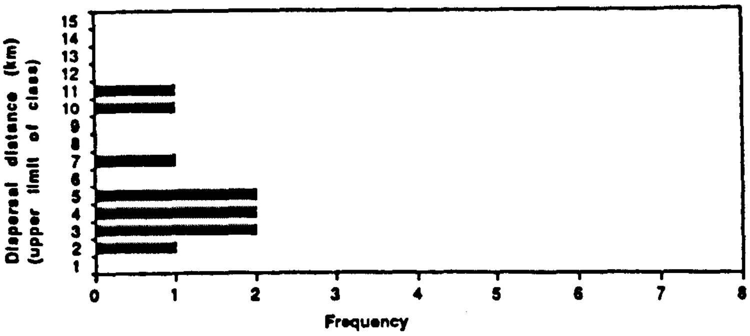


Fig. 6.2a Autumn dispersal distances (straight line) of juvenile female Dippers, 1985.

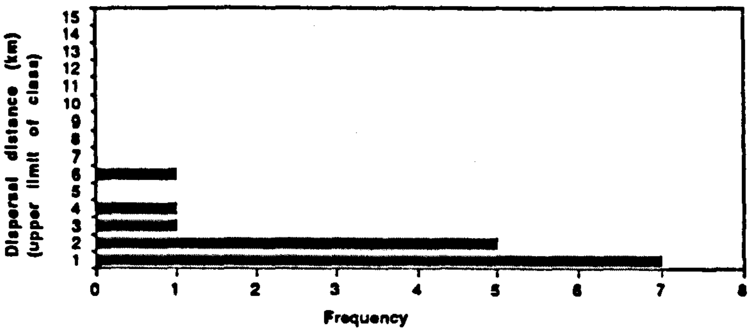


Fig. 6.2b Autumn dispersal distances (straight line) of juvenile male Dippers, 1985.

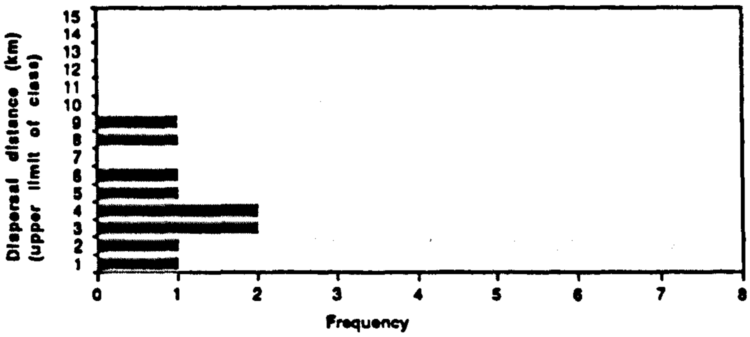


Fig. 6.2c Autumn dispersal distances (straight line) of juvenile female Dippers, 1986.

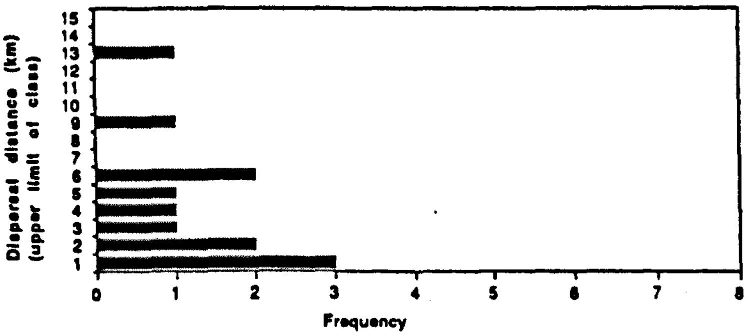


Fig. 6.2d Autumn dispersal distances (straight line) of juvenile male Dippers, 1986.

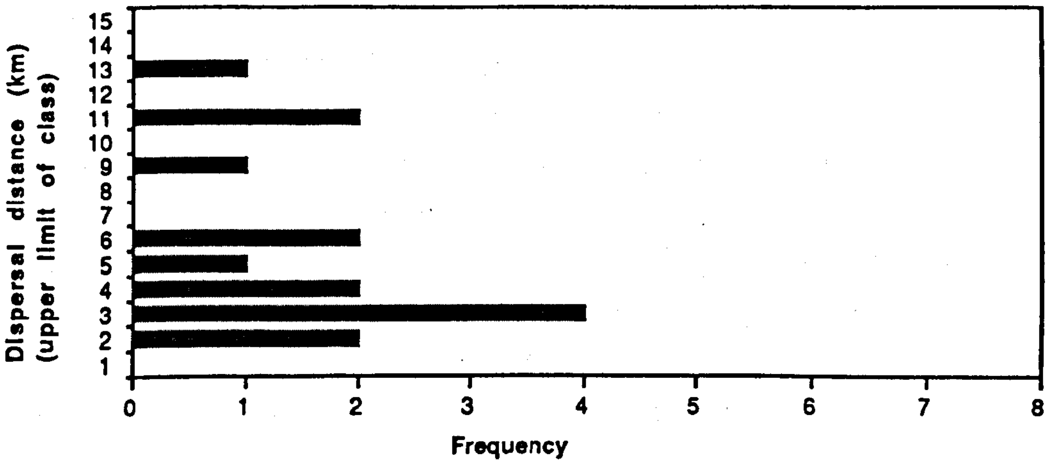


Fig. 6.2e Autumn dispersal distances (straight line) of juvenile female Dippers, 1987.

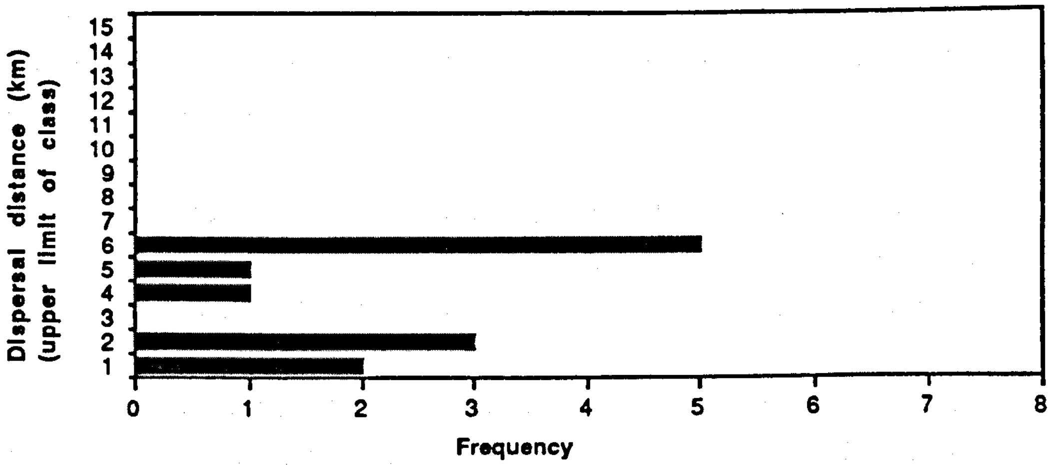


Fig. 6.2f Autumn dispersal distances (straight line) of juvenile male Dippers, 1987.

five kilometres typical for the former and one to three for the latter. Males showed more variability between years: dispersal distances were very low in the first year of study (1985). Frequency distributions (Figure 6.2) were mostly similar within sexes: males very much skewed towards the shorter distances and females more evenly spread over the recorded range. The pattern for males in 1987 was distorted by the presumed chance behaviour of siblings from two nests (Appendix Figure 3.a). Brothers from two nests on the upper Burn of Sorrow moved six kilometres apiece to overlapping or abutting autumn home ranges on the main river.

True autumn dispersal distances (birds following watercourses) are presented as histograms in Figures 6.3a, 6.5a, 6.5b for females and 6.4a, 6.6a and 6.6b for males. A skew towards the shorter distances mostly applied to both males and females from lowland natal sites; upland birds tended to move longer distances and their distribution was more unpredictable though medians remained more or less constant (Table 6.2) especially in females.

Significant differences (Mann-Whitney) between median autumn dispersal distance of males and females are given in Table 6.4. Differences were most pronounced in 1985, with males dispersing shorter distances than females. This trend persisted in the three year combined data set for birds from lowland natal sites and both habitats combined.

Within each sex, birds from upland natal sites dispersed significantly further than lowland raised birds when data from all three years were combined (Table 6.5) The trend was the same in each autumn and differences between medians were significant in 1985 females and both males and females in 1987.

There were no between year differences in median autumn dispersal distances in females (Mann-Whitney U tests,

Table 6.4. Differences in the autumn and natal dispersal distances between juvenile male and female Dippers.

Type of movement	Year	Natal site		All birds
		Lowland	Upland	
Autumn dispersal	1985 1986 1987 Overall	U=7, p<0.05 U=21, n.s. U=11, n.s. U=130,p<0.01	U=0, p<0.06 U=4, n.s. U=16,n.s. U=64,n.s.	U=13, p<0.001 U=51, n.s. U=70, n.s. U=395,p<0.01
Natal dispersal	1985 1986 1987 Overall	U=5, n.s. U=2, n.s. U=1, p<0.05 U=69, n.s.	U=0, n.s. U=0, n.s. U=7, n.s. U=20,n.s.	U=5, p<0.05 U=4, n.s. U=29, n.s. U=168,n.s.

Note: Mann-Whitney tests between medians.

Table 6.5. Differences in the autumn, spring and natal dispersal distances between juvenile Dippers from lowland and upland natal sites.

Sex	Year	Autumn dispersal	Spring dispersal	Natal dispersal
Males	1985 1986 1987 Overall	U=14,n.s. U=11,n.s. U=4, p<0.05 U=78,p<0.01	No data U=0, n.s. U=2, n.s. U=3, p<0.05	U=1, n.s. U=0, n.s. U=0, n.s. U=15,n.s.
Females	1985 1986 1987 Overall	U=0, p<0.05 U=3, n.s. U=7, p<0.01 U=26,p<0.001	U=2, n.s. U=0, n.s. U=4, n.s. U=15,n.s.	U=1, n.s. U=0, n.s. U=10,n.s. U=28,p<0.01

Note: Mann-Whitney tests between medians.

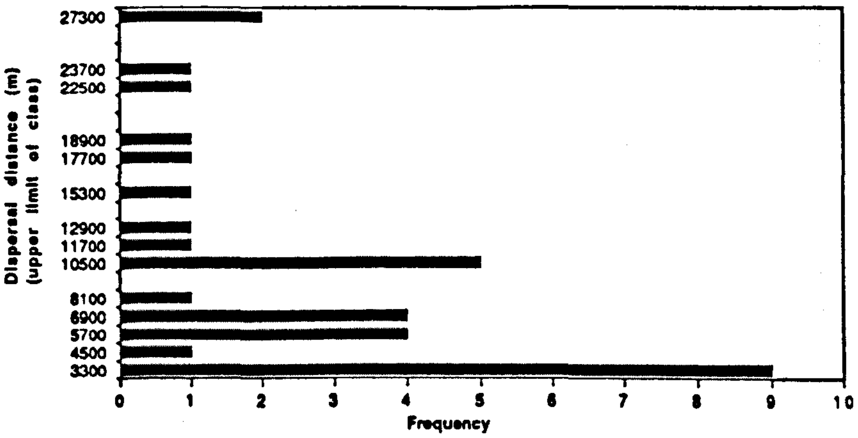


Fig. 6.3a Autumn dispersal distances of juvenile female Dippers, 1985 - 1987.

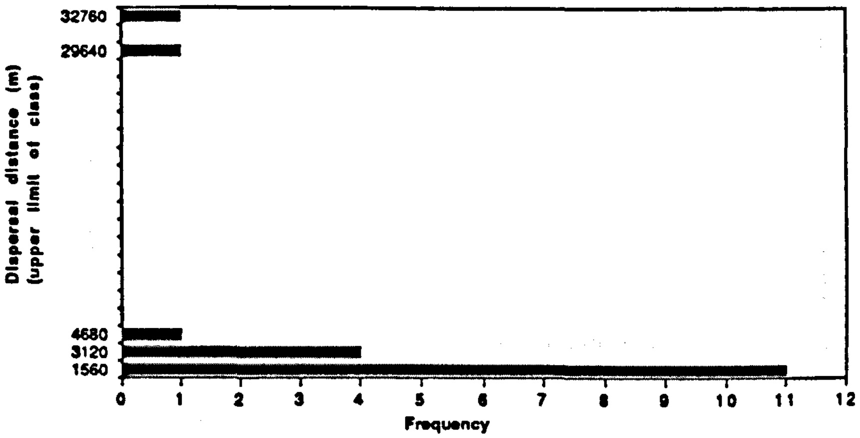


Fig. 6.3b Spring dispersal distances of juvenile female Dippers, 1985 - 1987.

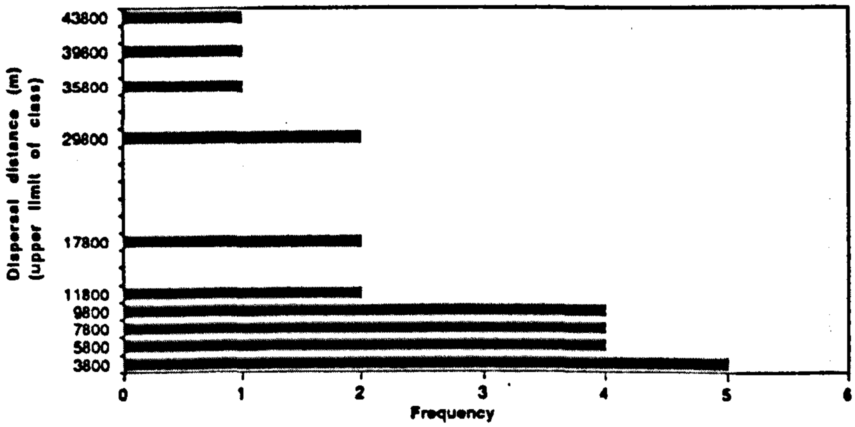


Fig. 6.3c Natal dispersal distances of juvenile female Dippers, 1985 - 1987.

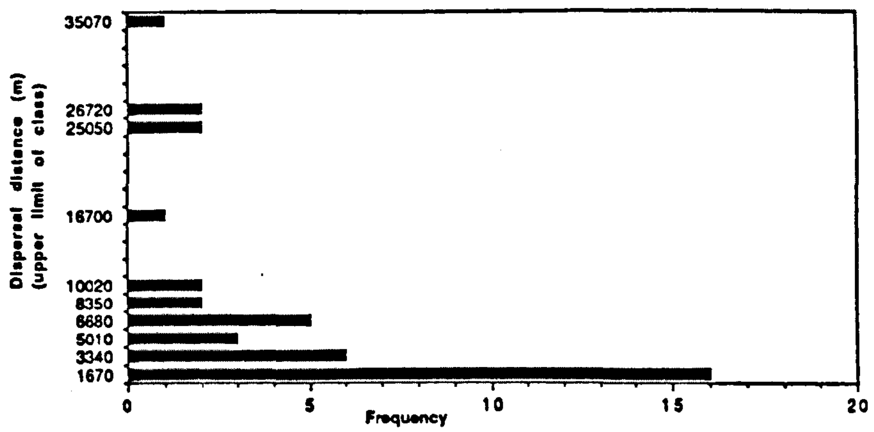


Fig. 6.4a Autumn dispersal distances of juvenile male Dippers, 1985 - 87.

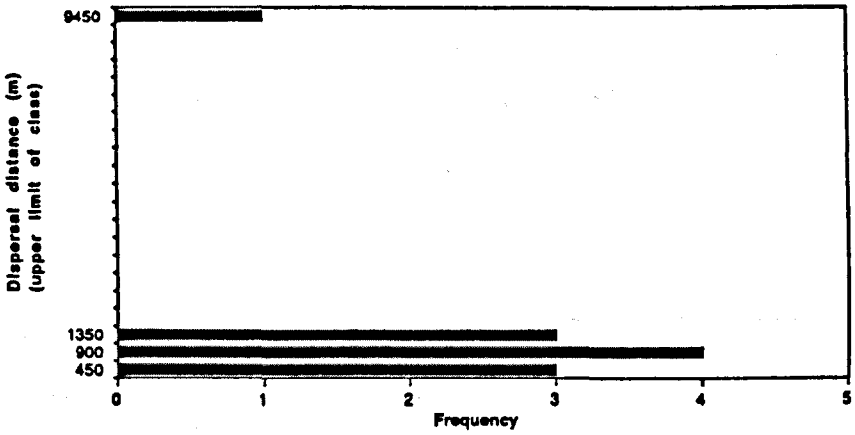


Fig. 6.4b Spring dispersal distances of juvenile male Dippers, 1985 - 1987.

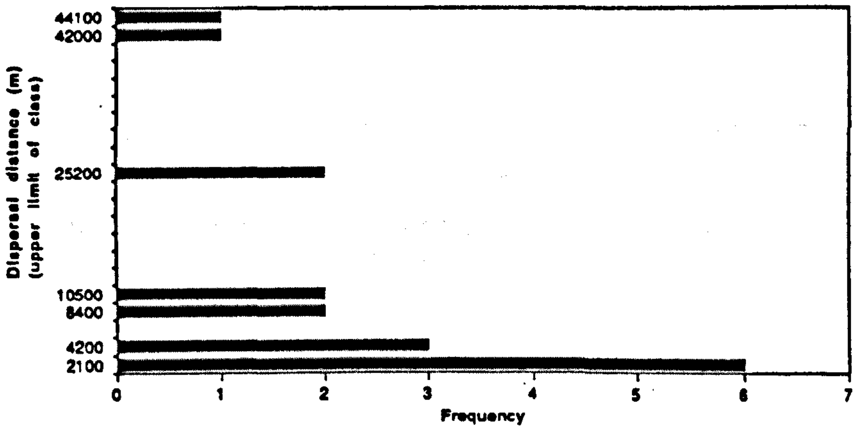


Fig. 6.4c Natal dispersal distances of juvenile male Dippers, 1985 - 1987.

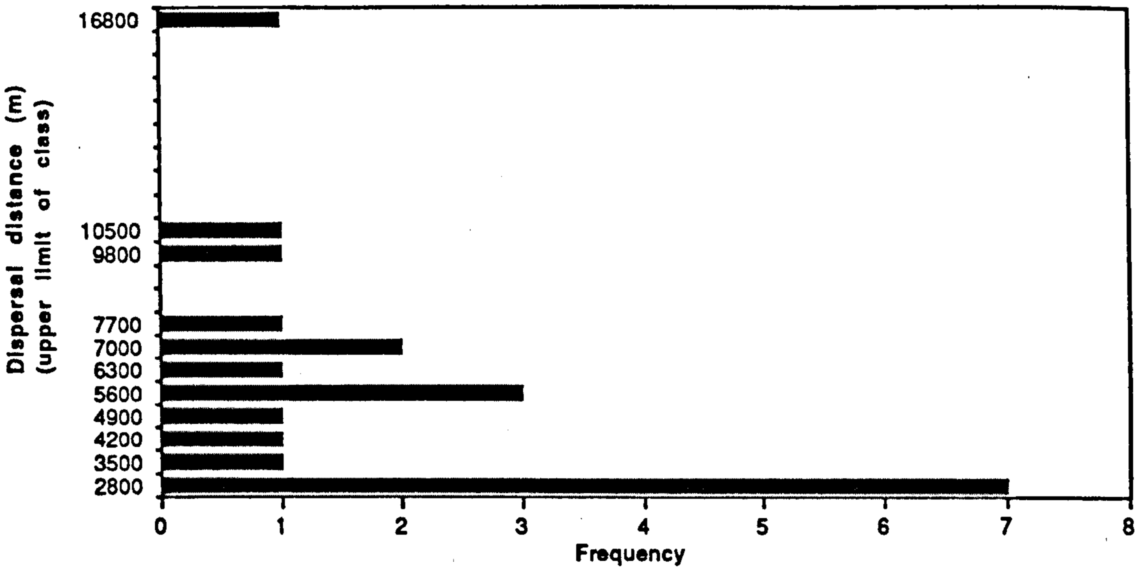


Fig. 6.5a Autumn dispersal distances of juvenile female Dippers ringed as nestlings at lowland sites, 1985 - 1987.

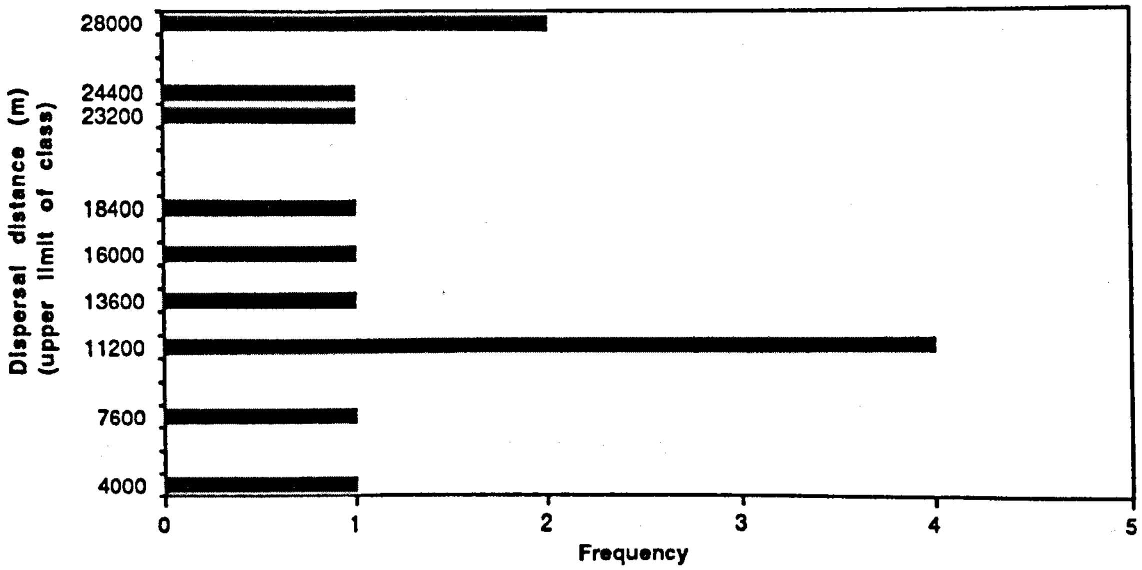


Fig. 6.5b Autumn dispersal distances of juvenile female Dippers ringed as nestlings at upland sites, 1985 - 1987.

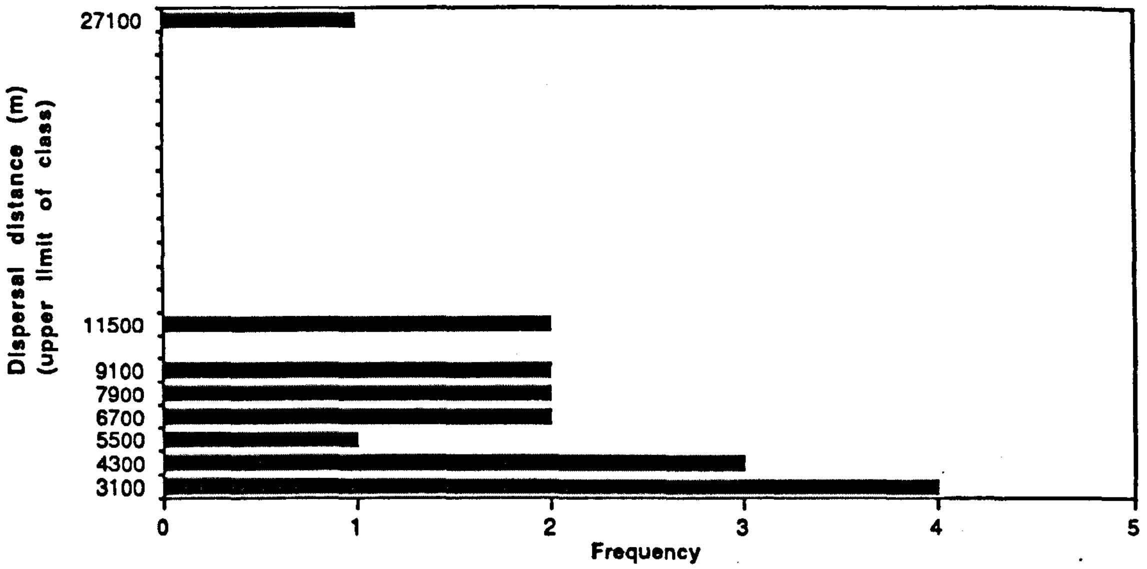


Fig. 6.5c Natal dispersal distances of juvenile female Dippers ringed as nestlings at lowland sites, 1985 - 1988.

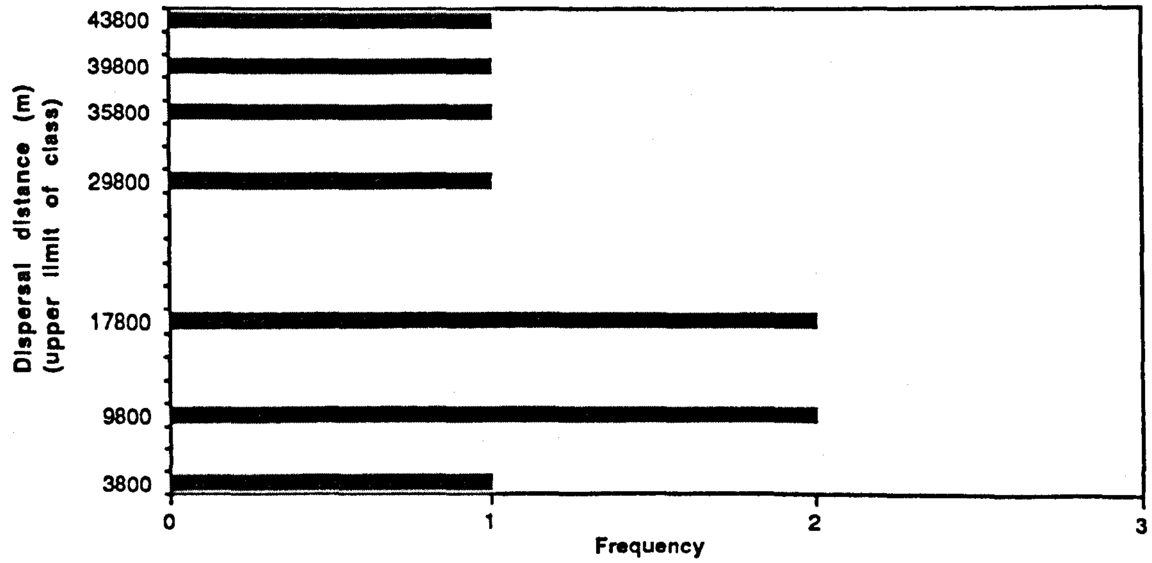


Fig. 6.5d Natal dispersal distances of juvenile female Dippers ringed as nestlings at upland sites, 1985 - 1988.

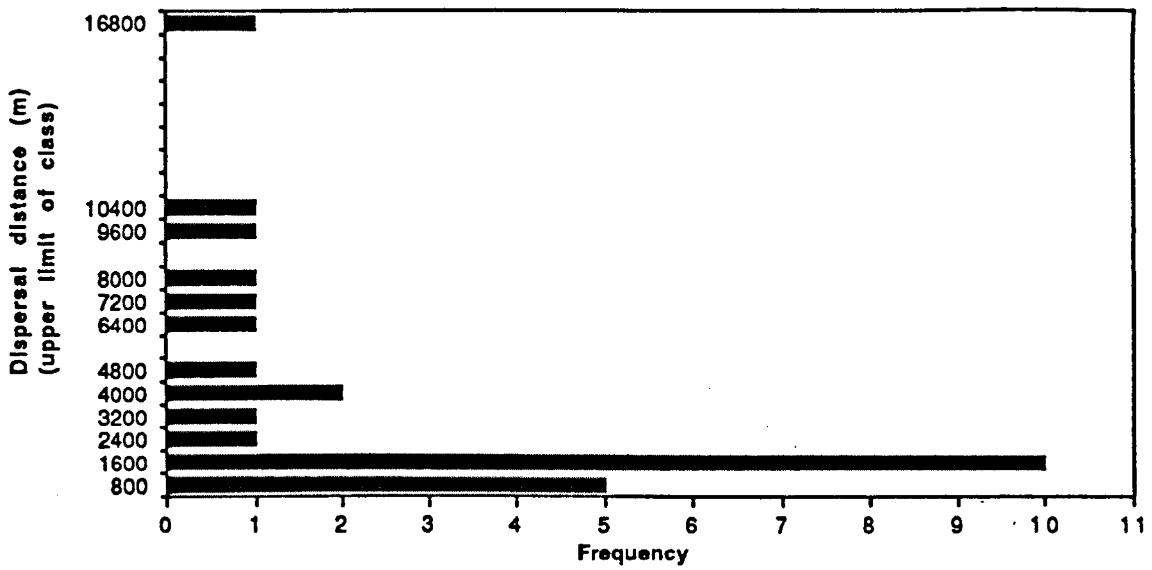


Fig. 6.6a Autumn dispersal distances of juvenile male Dippers ringed as nestlings at lowland sites, 1985 - 1987.

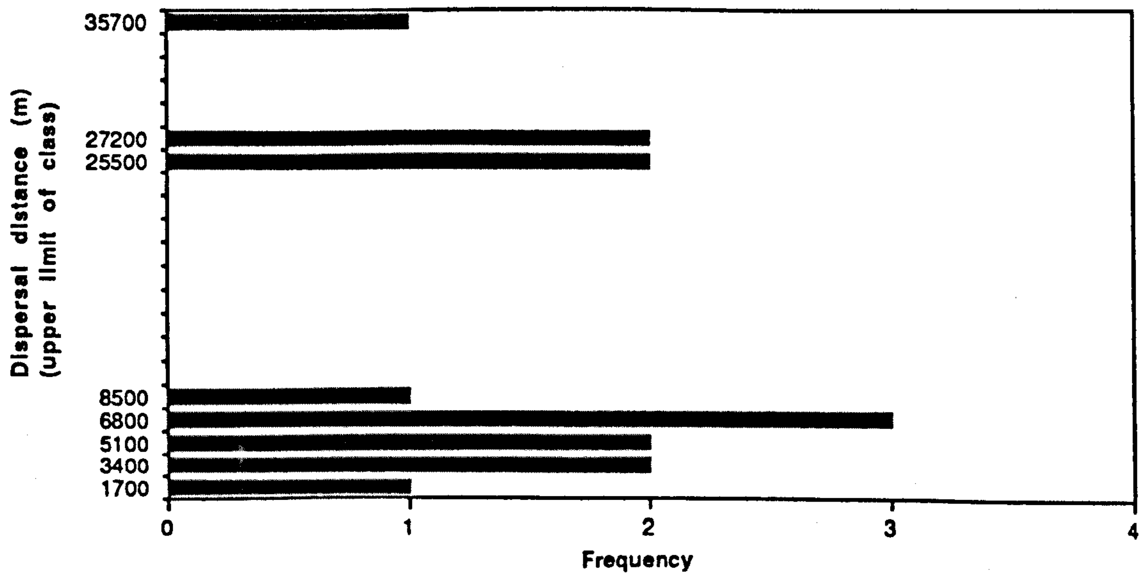


Fig. 6.6b Autumn dispersal distances of juvenile male Dippers ringed as nestlings at upland sites, 1985 - 1987.

p>0.10) but in males, distances in 1985 were significantly shorter than both 1986 and 1987 (Table 6.6).

6.3.3.2. Spring

The spring dispersal distances measured in this study represented the move an individual made between the centre of its autumn daytime home range and the nest site location at which it made its first breeding attempt. All median spring dispersal distances are given in Table 6.2. Generally, distances of less than one kilometre represented hypothetical intra-autumn/winter home range movements to the sites at which nests were built. Movements greater than one kilometre implied the bird had to move outwith its autumn/winter home range to look for a mate or nest site. In many instances the latter was an altitudinal migration to establish an upland breeding territory. The frequency distribution of spring dispersal distances for all years combined are given in Figures 6.3b (females) and 6.4b (males). These probably show a bias towards birds censused intensively on lowland sections of the main river. Spring dispersal of some known-origin birds located during the autumn and winter probably took them outwith the study area.

The majority of juveniles that established themselves on lowland parts of the main river in autumn recruited to sites nearby irrespective of their natal origin. Consequently there were few significant differences in median spring dispersal distances between birds originating from lowland or upland natal sites (Table 6.5). Overall, sample sizes were too small to compare spring dispersal distances between years (Table 6.6).

6.3.2.3. Natal

Most juveniles from lowland natal sites tended to recruit to breed at lowland sites (Section 6.3.1). Median natal dispersal distances for lowland males

Table 6.6. Between year differences in autumn, spring and natal dispersal distances of juvenile male Dippers.

		Natal site		All birds
		Lowland	Upland	
1985v.1986	Autumn	U=33,n.s.	U=3,n.s.	U=48, p<0.05
	Spring	U=1, n.s.	Sample too small	U=3, n.s.
	Natal	U=0, p<0.05	U=0,n.s.	U=0, p<0.01
1986v.1987	Autumn	U=19,n.s.	U=11n.s.	U=74, n.s.
	Spring	U=0, n.s.	U=0,n.s.	U=5, n.s.
	Natal	U=0, n.s.	U=0,n.s.	U=4, n.s.
1985v.1987	Autumn	U=28,n.s.	U=1,p<0.05	U=41, p<0.05
	Spring	U=0, n.s.	Sample too small	U=1, p<0.05
	Natal	U=5, n.s.	U=0,n.s.	U=14, n.s.

Notes:

1. Mann-Whitney tests between medians.
2. No significant differences between years in female data set.

ranged between 1.4 and 9.6km in different years but the overall median (2.9km) was less than that of lowland origin females (6.2km). The latter showed more consistency between years (Table 6.2). The only significant difference between sexes was observed in juveniles from lowland natal sites in 1987. Very few of the known origin recruits were from upland natal sites but most median natal dispersal distances indicated moves in excess of 17km (Table 6.2). A considerable proportion of these probably involved flights across watersheds and actual distances travelled would have been less than the minimum river distance. Individual natal dispersal distances are illustrated in Figures 6.3c (females) and 6.4c (males) for all years combined (not differentiating between natal site habitats). The frequency distribution and actual dispersal distances were very similar for both sexes. Median natal dispersal distances of males and females were only significantly different in 1985 (habitats combined), primarily because the single upland male recruit had moved a few hundred metres to the territory neighbouring his natal site.

Differences between females from both natal habitat types are illustrated in Figures 6.5c (lowland) and 6.5d (upland). The majority (14/17) of lowland females moved less than 10km whereas only 3/9 upland females recruited within 10km of their natal site; in this case combined medians were significantly different (Table 6.5). There were no significant differences in natal dispersal distances between upland and lowland origin males (Table 6.5). Natal dispersal distances of 1985 fledged young were significantly less than those recorded in 1986 and 1987 (Table 6.6).

6.3.3. Influence of Relative Age on Survival & Recruitment

Mean hatchdays for all nestlings processed are given in Table 6.7. The earliest season was 1985 and the latest 1986 with the differences between lowland and upland nests ranging between 10 and 15 days. The mean hatchdays of cohorts surviving to autumn and recruiting are given in Table 6.8, alongside those of the dying or disappearing cohorts. There was no consistent difference in age between autumn survivors and non-survivors nor between recruits and non-recruits in 1985 and 1987. In 1986 autumn survivors and recruits from both lowland and upland natal sites came from marginally earlier nests, though these age differences were not significant (Student's t-test, Table 6.8). Thus, relative age appeared to have little effect on an individual's probability of survival.

6.3.4. Body Size, Fledging Date and Dispersal Distance

Correlations between autumn and natal dispersal distances, fledging date and body size measures are given in Table 6.9. These were significant negative correlations between wing length and autumn dispersal distances in females (1985 and all years combined) and natal dispersal distances in males (1987 and all years combined). Thus, shorter winged juveniles moved further from natal sites in their first year. Fledging date (as indicated by hatch day) was significantly correlated with autumn dispersal distance in females in two out of three years. Late fledged birds moved further than earlier birds during the course of their autumn dispersal. No such relationship was found in 1986 nor in any year for males. Other body size measures (mass, keel, head and bill length) showed fewer relationships with dispersal distance though tarsus length was positively correlated with natal dispersal distance in both sexes for 1987 fledged young.

6.3.5. Radio Telemetry During Dispersal

The purpose of radio-tracking juveniles during the post-fledging period was to investigate the timing and extent of movements away from natal territories as the birds became independent of their parents. Preliminary radio telemetry trials were undertaken in 1986 and these showed that for the first two weeks post-

Table 6.7. Mean date of hatch of lowland and upland nest sites, 1985-87.

Year	Lowland nests	Upland nests	All nests	Difference (upland - lowland)
1985	23 April	3 May	26 April	10 days
1986	6 May	21 May	12 May	15 days
1987	27 April	10 May	3 May	13 days

Note: (1) All second broods excluded.
(2) Fledging usually occurs 20-22 days post-hatch.

Table 6.8. Differences in mean hatch day of nestlings surviving to autumn and recruiting and those disappearing post-fledging and before spring.

Year	Fate	Natal Site		All birds
		Lowland	Upland	
1985	Disappear as fledglings Autumn survivors	23 April 20 April	3 May 4 May	26 April 24 April
1985	Non-recruits Recruits	23 April 23 April	2 May 5 May	26 April 27 April
1986	Disappear as fledglings Autumn survivors	7 May 5 May	21 May 20 May	13 May 11 May
1986	Non-recruits Recruits	7 May 5 May	21 May 19 May	13 May 9 May
1987	Disappear as fledglings Autumn survivors	26 April 30 April	10 May 10 May	2 May 5 May
1987	Non-recruits Recruits	26 April 26 April	9 May 11 May	2 May 4 May

Notes:

1. Sexes combined in these analyses.
2. No significant differences between any pair of dates in each cell (Student's t-tests).
3. All second broods excluded.
4. Fledging usually occurs 20-22 days post-hatch.

Table 6.9. Correlations (Spearman rank) between body size measures, fledging date and dispersal distances.

Year	Sex	Character	Autumn dispersal distance	Character	Natal dispersal distance
1985	F	Fledge date Wing	0.767,n=9,p<0.01 -0.700,n=9,p<0.05	Head + bill	1.000,n=5,p<0.001
	M	None		None	
1986	F	None		None	
	M	None		None	
1987	F	Fledge date	0.473,n=16,p<0.05	Body mass	0.754,n=6,p<0.05
	M	Tarsus	0.564,n=12,p<0.05	Wing Keel Tarsus	-0.837,n=6,p<0.05 -1.000,n=6,p<0.001 0.771,n=6,p<0.05
All years combined	F	Wing	-0.402,n=32,p<0.05	None	(n=23)
	M	None	(n=38)	Wing	-0.625,n=16,p<0.01

fledging, juveniles were still dependent on parents for food and remained well within their natal territory. Consequently, in this study, radio tags were attached to juveniles that had fledged two to three weeks previously.

6.3.5.1. Fledglings from "Nest A"

This nest was located on a stone bridge in river section 02 (see Figure 7.5) where the A91 road crosses the River Devon 1.75km downstream from the Castlehill Reservoir Dam. Much of this breeding territory is flanked by flat-lying permanent pasture (sheep grazed) and the river banks are generally of open aspect with some cover provided by occasional clumps of willow bushes *Salix* spp. A brood of five had been colour-ringed as eight day old nestlings on May 5th and they fledged on May 18th. Radio transmitters were fitted to two female fledglings mist-netted below their natal nest on June 3rd.

The centre of daytime activity (mean of one to five radio fixes over a one to two hour period) and roost location of radio-tracked individuals is given relative to the nest site location in Figure 6.7. At the time of tagging, both females were still very close to the natal nest, though food provisioning by the adults had virtually ceased. Daytime behaviour comprised skulking in willow thickets or foraging in river edge shallows and riffles in a part of the territory with some shade or cover provided by an avenue of mature trees on the river bank just upstream from the nest. Both birds roosted in willow bushes, overhanging water, close to the nest bridge. Nineteen days after fledging (day 19), bird 84876 moved outwith its natal territory and was located approximately 1km upstream of its previous range. This move coincided with, or was accompanied by, a switch of roosting location to a site offering a wider choice of trees and bushes with better cover. Her daytime range usually lay between roost and natal territory. On day 26 the radio was recovered detached from the bird in the middle of its usual daytime range and the individual was not seen again in this area or elsewhere despite an intensive search effort for colour ringed birds combined with regular mist-netting and roost catching later in the summer and autumn. Two possibilities may account for the disappearance of 84876: predation by a Sparrowhawk *Accipiter nisus* or mustelid, or a prolonged dispersal flight out of the study area.

The second female from "Nest A" (84878) remained in the natal nest environs for a much longer period (Figure 6.7). She did not explore outwith the natal territory until post-fledging day 25 when she began to use a small side burn during daytime, but returned to roost in or adjacent to her natal nest. On the eve of day 31, she roosted in a tree or bush a short distance up a second side burn and had disappeared the following morning. Assuming no radio malfunction, then this bird made a rapid long distance movement. The following May (1988) she was relocated, at a remote upland breeding territory in the central Ochil Hills, 12km to the west. Routine autumn censusing and mist-netting on the main river and some intervening upland burns had failed to locate her and presumably she had overwintered in an upland area close to the eventual nesting site.

The recovered radio from female 84876 was fitted to one of the male siblings (84874) from "Nest A" on June 14th (post-fledging day 27). This bird had previously been visually located outwith the natal territory on three occasions (Figure 6.7) often associating with 84876. Presumably it had left the natal territory at about the same time as 84876, two to three weeks post-fledging. This male roosted on the Castlehill Reservoir Dam and during the daytime was increasingly recorded on both adjacent parts of the main river and on a side burn close by. Regular observations ceased on day 37 (June 24th), but intensive work recommenced in the area in early September with this bird still present within its

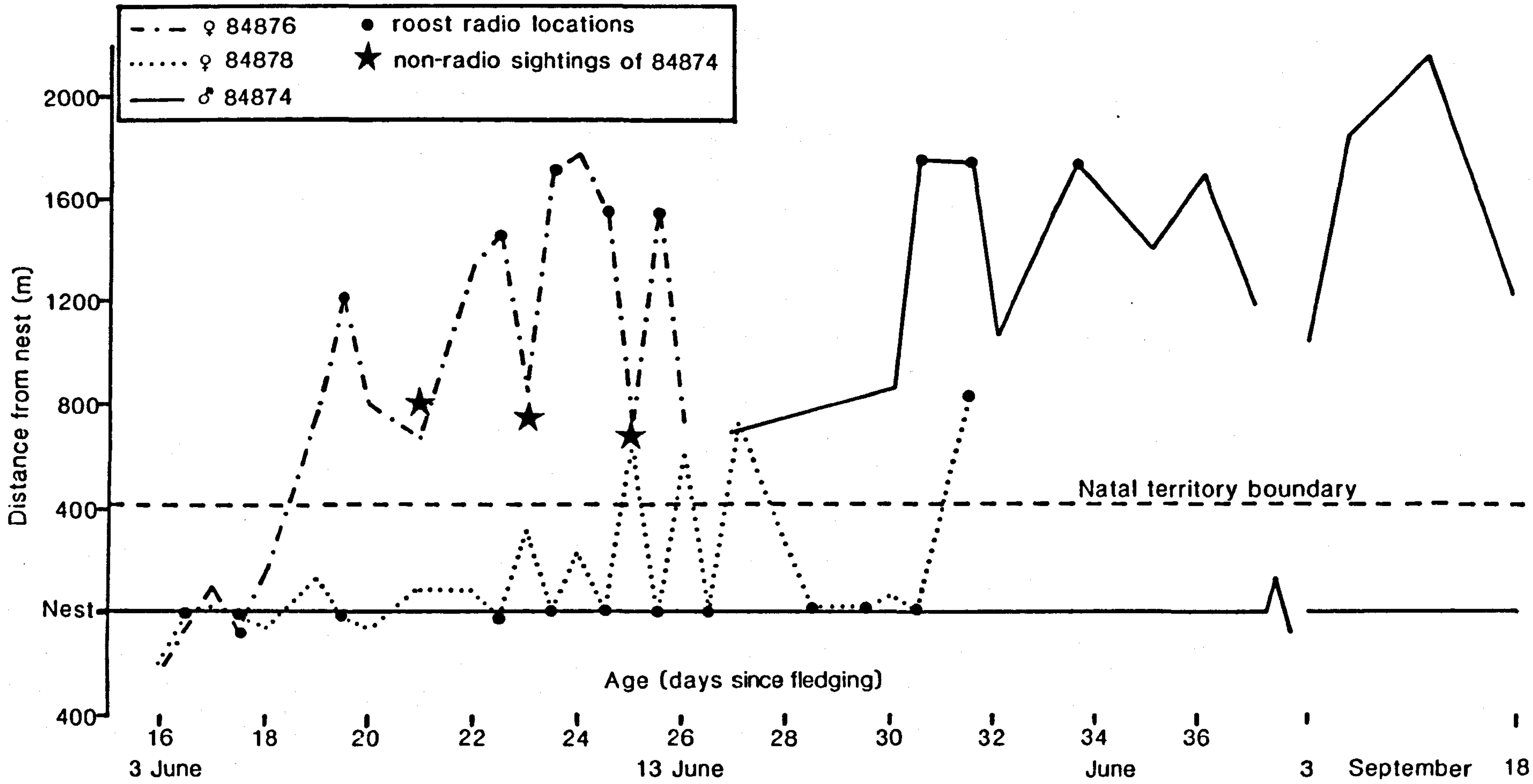


Fig. 6.7 Post-fledging movements of 3 siblings from "Nest A" as determined by radio telemetry.

earlier range (colour ring observations). This individual recruited to breed on his side burn territory the following May (1988), though he had also been recorded in the vicinity of his natal nest site consorting with his mother.

6.3.5.2. <u>Fledglings from "Nest B"</u>

Five nestlings were ringed at this nest on May 16th (1987) and they fledged on May 26th. The nest was situated on the River Devon bank approximately 1km upstream of the village of Crook of Devon (river section 02). Open arable and permanent grassland flanked the banks of the river upstream from the nest providing little cover for the four fledglings but downstream the banks were over-shadowed by many trees, bushes and rank vegetation. In the latter area, the river had been partially dammed by a weir feeding a variety of lades, sluices and other watercourses associated with an old watermill and a fish farm. The fish farm, campsite and close proximity of the village could lead to much human disturbance, especially at weekends, but the mosaic of watercourses and presence of dense willow thickets below the weir provided Dippers with some quiet refuges.

Two female fledglings from the brood were caught on day 21 (June 16th) about 200m downstream of the nest and were fitted with tail-mounted radio transmitters. Their movements over the summer, relative to nest and natal boundary, are given in Figure 6.8. One of the two females (84895) spent most of the first week within 200m of the natal nest and on one evening roosted in or very close to it. On the evening of day 28 or the early morning of day 29, this bird suddenly moved 1750m downstream and also roosted in that vicinity. Over the next ten days, she moved as far as 3km from her natal nest to roost in a favoured rocky gorge (Rumbling Bridge) but appeared to become more settled on a home range 2.0km to 2.5km from her natal site. Further observations (of colour rings) over the last ten days of July and towards the end of August confirmed that the bird had become established in this area (Figure 6.8).

During the first ten days of radio observations on the second bird (84893), most time was spent towards the downstream end of the natal territory. She roosted in small riverside Sycamore trees *Acer pseudoplatanus* with branches overhanging flowing water. On day 31, links with the natal territory were broken and she moved a short distance downstream to a new daytime range and a roost site on a weir in Crook of Devon village. At some time during the evening of day 32, the radio signals were lost and a prolonged dispersive movement out of the study area, or predation, was suspected. However, in late July the bird was visually recorded approximately 1km downstream in the vicinity of 84895.

Both birds were caught in this area at the end of August and dead radios were removed. Water had seeped into the radio of 84893 and the battery had shorted. The birds were in an apparently healthy condition albeit with above normal tail feather wear. Female 84893 was still resident in this area on November 20th 1987, but neither was recorded as a successful recruit in the overall western Ochil Hills/River Devon study area.

6.4. DISCUSSION

6.4.1. Post-fledging Survival

This study has demonstrated a considerable fledgling mortality over the course of the first summer, resulting in approximately 18% surviving to September. This figure must represent a minimum as some long distance dispersers will move outwith the study area. Galbraith & Tyler (1982) have also shown high mortality of fledgling Dippers in the first two months of life. Forty five percent of first year Dipper BTO ringing recoveries were from May and June. During the course of this study, only three of the 549 nestlings known to

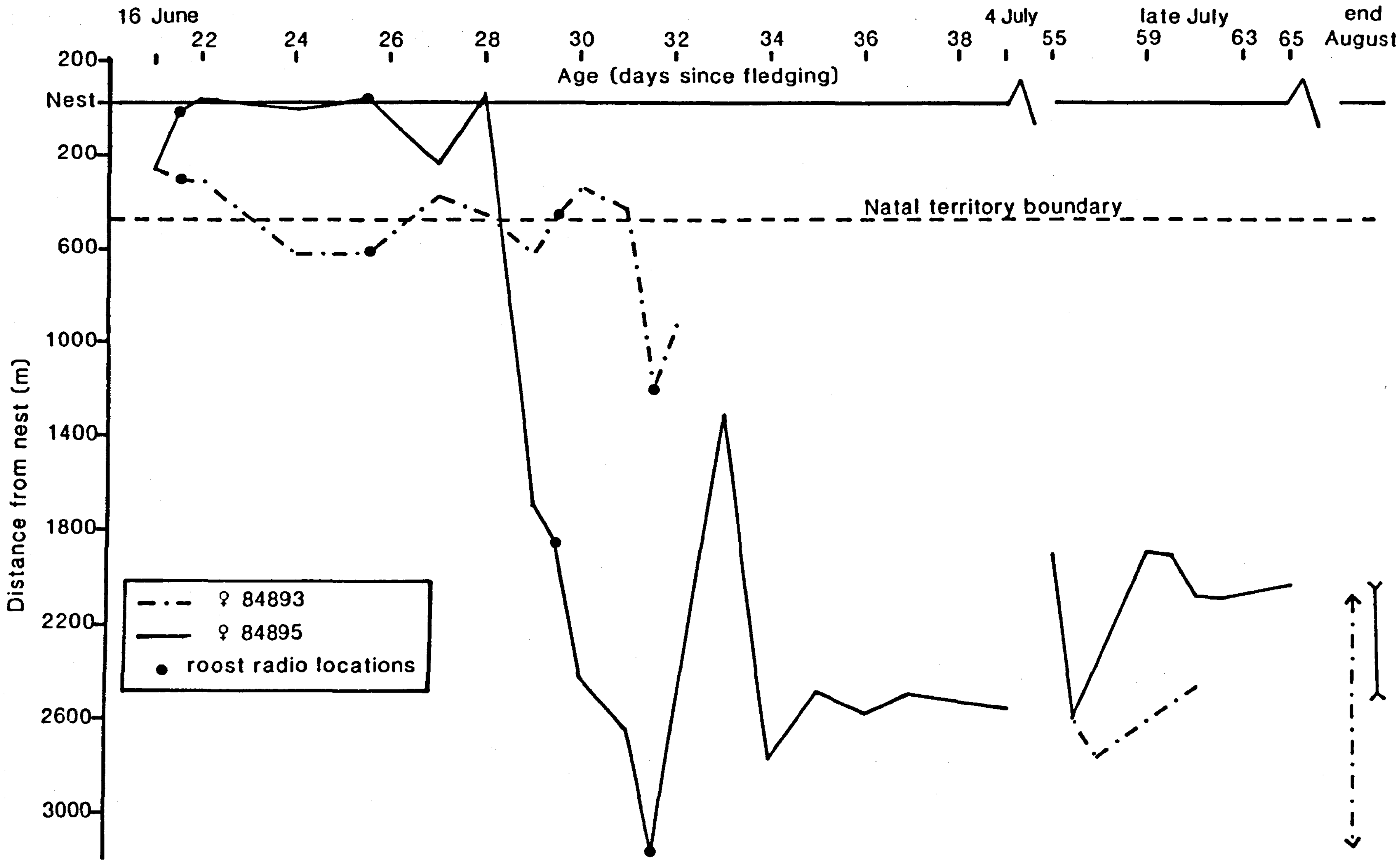


Fig. 6.8 Post-fledging movements of 2 siblings from 'Nest B' as determined by radio telemetry.

have fledged were recovered by members of the public. Two had flown into windows in Hillfoot villages close to their natal sites and the third had been taken by a Sparrowhawk. Predation by the latter and river-based mustelids, notably Mink *Mustela vision*, is thought to account for a considerable part of the summer losses. Perrins & Geer (1980) have shown that Sparrowhawks may take up to 34% of young tits (*Parus caeruleus* and *P.major*) during the immediate post-fledging period in a closely monitored population in southern England. Carrion Crows *Corvus corone* have also been seen attempting to catch recently fledged Dippers. Ormerod & Tyler (1988) re-trapped 11.5% of Dippers ringed as nestlings during the following autumn and winter in their Welsh study area. Fledgling period mortality rates have not been described for many resident passerine species, though Dhondt (1979) has shown that 22% of first brood Great Tits *Parus major* survived to September in Sweden, and Drent (1984) 32-43% in two Dutch populations.

The overall recruitment rate of "known origin" (young ringed in the nest) Dippers in this study was 10% indicating a rather high overwinter survival of birds known to be alive in autumn. However, these birds formed less than one third of all juvenile recruits, implying significant immigration into the River Devon catchment from adjacent areas. In migratory passerines, local recruitment rates are very much lower, House Wrens *Troglodytes aedon* 2.8% (Drilling & Thompson 1988), Barn Swallows *Hirundo rustica* 2.0% (Shields 1984).

6.4.2. Dispersal Distances & Natal Philopatry

In all measures of post-fledging dispersal investigated here (autumn, spring, natal), males tended to move less than females. Male biased philopatry has been widely documented in the avian literature (see review by Greenwood 1980, Dhondt 1979, Greenwood *et al.* 1979, Newton & Marquiss 1983, Dunn & Braun 1985, Schroeder

1986, Ormerod & Tyler 1988). Although dispersal reduces the likelihood of inbreeding with close relatives, the wider biological significance of differences in dispersal distances are not clear in many studies. In homogeneous habitat, distances moved may correlate well with the number of conspecifics encountered or territories crossed, but not if the dispersal phase includes a migratory component as is the case with upland reared Dippers in the Ochil Hills. Adult Dipper territoriality is at a low ebb during the annual moult (Galbraith *et al.* 1981), the time when most juveniles are dispersing, so adult-juvenile aggression should not unduly influence distance travelled during the summer months (June-August). Overall, Dippers from upland sites, in common with Sparrowhawks (Newton & Marquiss 1983), dispersed further than lowland birds. However, distances measured here (following watercourses) may have over-estimated the actual distance moved since some birds were strongly suspected of crossing watersheds between adjacent upland burn systems.

In this study, most classes of juveniles were faithful to their natal habitat: lowland reared males and females generally overwintered and recruited to lowland sites and upland females were more likely to recruit to upland sites. Upland raised males were to be an exception, mainly recruiting to lowland stretches of the main river.

Several studies have shown reduced survival rates in cohorts that dispersed as opposed to recruiting to their natal territory (Magpies *Pica pica*: Eden 1987b) and in those dispersing greater distances (Blackbirds *Turdus merula*: Greenwood & Harvey 1976, House Sparrow *Passer domesticus*: Fleischer *et al.* 1984), whereas Newton & Marquiss (1983) demonstrated that some components of future breeding performance were poorer in Sparrowhawks that had dispersed longer distances. In common with the Ochil Dippers, Hines (1986) also failed to detect increased mortality in longer distance dispersers in his Blue Grouse *Dendragapus obscurus* population.

Some of the maps presented in Appendix Figures 1-3 (particularly 3a) show that sibling Dippers may apparently associate during autumn dispersal and eventually occupy similar autumn-winter home ranges. The tendency for brood mates to disperse similar distances, but not necessarily in the same direction, has been recorded previously (Dhondt 1979, Keppie 1980, Newton & Marquiss 1983) and thus dispersal distance may in part be a heritable trait. However, the benefits of autumn proximity of siblings are obscure and may have arisen from chance with dispersing birds following an "obvious" route defined by the terrain.

6.4.3. Relative Age, Dispersal & Recruitment

This study failed to detect any significant relationship between either hatching or fledging date and survival to autumn or recruitment into the breeding population. Nevertheless, in 1986 autumn survivors and recruits were on average up to four days older than non-surviving birds. This was the coldest and wettest spring recorded during the study period. Many early nesting attempts failed and thus the surviving juveniles were the earlier fledged members of a relatively late cohort. Enhanced local recruitment or overall survival of earlier fledged juveniles, especially from first broods, has been reported in many population studies (Dhondt & Hublè 1968, Dhondt & Olaerts 1981, Arcese & Smith 1985, Nilsson & Smith 1988). In at least two of these studies (Arcese & Smith 1985, Nilsson & Smith 1988) high dominance status was the key factor common to early fledglings. On the other hand, there was a tendency for later fledged juvenile female Dippers to move further during the course of their autumn dispersal. However, this may only reflect altitudinal or habitat differences discussed elsewhere.

6.4.4. Proximate Mechanisms of Dispersal

Factors driving dispersal in resident species are poorly understood. Birds may have some innate tendency to move away from natal sites but the answer may also lie in competition with conspecifics (parents, other adults, or peer group members) and partial migration (altitudinal) due to the unsuitability of breeding terrain for overwintering. The radio-tracking results presented in this study throw some light on when and how dispersal takes place in recently independent Dippers. Although radio-monitored birds were only followed for one or two hours per day, none was seen to be fed by adult birds, or was involved with them in any competitive interactions. Thus, parental dependency was limited to the first two weeks post-fledging. In common with Willow Tits *Parus montanus* (Nilsson & Smith 1985), fledglings were not noticeably driven off by their parents, unlike Imperial Eagles *Aquila heliaca* (Alonso *et al.* 1987). The movements of Dippers from about three weeks post-fledging were more likely to be governed by the need to locate suitable food resources and safer roosts. Most of the radio-tracked fledglings made a rapid, single movement out of the natal territory sometime in the third or fourth week, that was apparently associated with the discovery and use of a new roost. Subsequently these dispersed birds showed no tendency to return to their natal territories. The areas into which Dippers moved were already occupied by fledgling and adult conspecifics and thus they were not moving into vacant habitat. Presumably food was relatively abundant and the resident, moulting adults were tolerant of their presence. Intraspecific competition in the Dipper increases noticeably in the autumn, following the completion of post-juvenile (fledgling) and annual (adult) moults (personal observations). It coincides with the resurgence of song (Bryant & Tatner 1988). Dominance in juvenile Dippers is largely influenced by body size (see Chapter 5). Thus, the negative correlations between dispersal distances and wing lengths strongly suggest that intraspecific competition may drive the later stages of dispersal, resulting in the greater distance moved by the smaller juveniles shown to be subordinate in laboratory tests (Chapter 5). Clearly, there is still a lot to be learned about the proximate causes of dispersal. Although radio-tracking of dispersing individuals is labour intensive, it probably remains one of the best avenues to pursue, especially as the adverse effects of radio packages on the behaviour of other small birds (Massey *et al.* 1988) were not apparent in this study.

CHAPTER SEVEN

EXPERIMENTAL INTRODUCTIONS: MANIPULATIONS OF POPULATION DENSITY IN NON-BREEDING DIPPERS

7.1.INTRODUCTION

Manipulation of population density in wild birds has been an important component of studies on territoriality and density dependent recruitment. In most cases, however, manipulation has involved the removal of individuals or pairs by trapping or shooting. Replacement of these has often been very rapid (Beletsky & Orians 1987, Stutchbury & Robertson 1987) and such studies, together with other non-manipulative observations, have demonstrated the presence of non-territorial or non-breeding birds, called "floaters", ready to take advantage of vacancies (Arcese 1987, Eckert & Weatherhead 1987, Pedersen 1988, Smith 1978, 1987). Reduction of fledgling production, by egg removal, in an isolated population of Great Tits *Parus major* significantly increased the overwinter survival of adults and a similar trend was apparent in the remaining juveniles (Kluyver 1971). Culling of the breeding birds in a long-lived colonial species such as the Herring Gull *Larus argentatus* reduced the emigration rate of younger birds and decreased the age of recruitment (Coulson *et al.* 1982). Removal experiments have also been used to determine the relative contributions of males and females towards the success of nesting attempts (Lyon *et al.* 1987) and in studies of mate replacement behaviour (Bowman & Bird 1987).

Introduction experiments have usually been the domain of game biologists and conservationists. Taxa often introduced by the former include phasianids, tetraonids and wildfowl, with the introduced birds mainly hatched in captivity from wild-laid eggs. The principal philosophy behind such introductions has been to enhance local breeding populations and to create larger shootable surpluses for hunters, though some studies have monitored the pre- and post-introduction population demography of the study species concerned in a scientifically rigorous manner (Sellers 1973). Rare and endangered species, often rendered locally extinct by human interference, have been the focus of several reintroduction programmes by conservation organisations. The most notable recent British example has been the release of White-tailed Sea Eagles *Haliaeetus albicilla* on Rhum in western Scotland in the hope that birds will recolonise some of their former haunts (Love & Ball 1979, Love 1980).

The use of introductions has rarely been explored by behavioural ecologists though the technique may give insight into how birds become established in new areas. Normally this occurs during the dispersal of fledged birds in a resident species, though juveniles of migratory species may prospect potential breeding territories before their autumn departure to wintering quarters (Adams & Brewer 1981). Slagsvold *et al.* (1988) used introduction experiments in their study of mating patterns and costs of mate-searching in Pied Flycatchers *Ficedula hypoleuca*. Females were released into new nesting areas in which only unmated males were present, and to a second area where mated and unmated males were present. Such experiments may be confounded by the homing abilities of introduced birds (Hudson *et al.* 1988, Slagsvold *et al.* 1988). Thus, it is necessary to transport birds well beyond their home range, or area of familiarity, which may extend from the environs of their natal territory, through a zone along which they dispersed, to the area in which they eventually settled.

In this chapter, I report a series of introductions involving the release of juvenile Dippers into unfamiliar stretches of river between late July and December. The underlying rationale was that none of the introduced birds could gain advantage from prior residency in the area. The settlement, survivorship and recruitment of these birds was monitored and compared with the performance of the already established, resident population. In particular, the behaviour of introduced birds was investigated in relation to dominance status, body size, date of release and relative age of juveniles; and to overall density-related recruitment.

7.2. METHODS

7.2.1. Study Area

Between September 1986 and October 1987, seven releases of five (once, six) Dippers were made at three sites. Experiments 1, 2, 4 and 5 were conducted on river section 05, 3 on section 02 (mid) and 6, 7 on 02 (upper). All three sections were approximately 2km long and were contained within a 7.7km stretch of the middle reaches of the river Devon. The upstream end of 02 (upper) was defined by the imposing Castlehill Reservoir Dam and the downstream limit of 05 by the very narrow and deep Rumbling Bridge Gorge. Both features are used for roosting and nesting by resident birds and it was thought that they may have represented partial barriers to movement.

Section 02 (upper) was considered to be high quality Dipper habitat: it was occupied year round; it had several safe roosts, a fair number of secure nest sites (5-7) that reliably produced fledged young and had three inflowing side burns that provided valuable cover and foraging refuges during spates. Section 02 (mid) lay immediately downstream of the former and was the most open of all three sections, being flanked by predominantly flat agricultural land. It holds considerable numbers in winter on its wide, shallow riffle areas, but had few good nest sites. Two of the three regularly used nest sites were in trees and did not produce fledged young during the course of this study. Similarly section 05 generally lacked secure nest sites (apart from Rumbling Bridge gorge) but was still a well used autumn habitat with a fair degree of cover. Despite these slight differences, all sections were relatively good habitat and were much used by Dippers.

7.2.2. Introduction Protocol

The introduction experiments ran in conjunction with seven of the laboratory dominance tests described in Chapter 5. Where possible, birds were collected from roosts to the west and north of Stirling at least 20-30km from the study area. Elsewhere it is shown that the majority of juvenile Dippers disperse less than 20km from their natal sites in the first four months post-fledging. Thus it was safe to assume that all or most introduced birds had no prior knowledge of the study area. Unmarked juveniles were captured preferentially to minimise interference with the population demography of ringed birds from the western Ochil Hills and River Devon to the east of Stirling. However, a temporary scarcity of unmarked birds at remote sites in September 1987, led to the use of three juveniles from a major roost only 5km upstream (above the Castlehill Reservoir Dam) from the release point in the penultimate experiment. During the two months following the last release, many of the residents (present in the study area pre-July 1987 release) were caught in batches of four or five at their roosts or by mist-netting just before dusk. These birds were also tested for dominance status in the laboratory and were returned to their capture site in the early morning.

Two measures of dominance were presented in the results: DOMINANCE A is a ranking based on the number of tests an individual qualitatively won; whereas DOMINANCE B is a three-point classification of birds into dominant, intermediate and subordinate based on the proportion of interactions over perch occupancy that each bird won (see Chapter 5 and foot-notes to Table 7.4). The relative age of juveniles was based on a six-point scale of the development and extent of the chestnut breast plumage as it replaced the speckled, creamy-yellow fledgling plumage during the post-juvenile moult. A score of 0 indicates the moult has not started whereas 5 refers to a bird with completed moult, more or less resembling an adult. Juveniles with low moult scores at the time of the experiment probably originated from second broods or late upland first broods.

Introductions involved the release of five or six birds, over about one minute in rapid succession, at the mid-point of each study section. They were allowed a free choice of flight direction.

7.2.3. Post-release Monitoring

Prior to an introduction, two censuses were undertaken of the study section concerned; one of these was usually the day before the release. The locations of all birds were registered on 1:10,000 scale field maps. Unringed birds were caught and colour marked the same day or soon after.

Short-term movements of released birds were monitored by daily censuses for the first three to five days and subsequently on alternate days for a further seven to ten days. A census comprised a two-way walk up and down the river bank for approximately 1km in either direction from the release point. Section lengths varied slightly (02 upper, 1.9km; 02 mid, 2.0km; 05, 2.3km) but were kept constant for each introduction and river section. Censuses were mostly undertaken between 10.00-13.00 hrs and took about two hours. Exceptions were afternoon visits following a release on that section in the morning. All birds were located with 10x binoculars and then identified by their colour rings using a 2^2-60x telescope. Their positions and activities were marked on standard field maps.

In most introductions, virtually all introduced birds had left the vicinity of the release point within two weeks and regular censuses were abandoned if two successive visits failed to locate any. Thereafter, surveys of the River Devon were undertaken at approximately monthly intervals for up to 10km in either direction from the upstream and downstream ends of the overall release area (length 7.7km). A released bird was considered to have an autumn home range if it was seen on two or more occasions less than one kilometre apart following the cessation of short- term monitoring. In all cases, birds establishing autumn home ranges survived a minimum of four weeks post-release. In the spring following release, March to May, thorough searches of main rivers and hill burns within approximately 20km of the release points were made to locate breeding territories. Identification of nesting pairs yielded data on overwinter survival and recruitment of the introduced birds. One or two visits to initial capture roosts were made between January and March to check for the return of introduced birds that could not be located in the vicinity of the study area.

7.3. RESULTS

7.3.1. Short-term Behaviour of Introduced Birds

Short-term re-sightings of released birds and residents within the 2km core study sections are given in the Appendix (Tables A, B, C, D). Summer released birds (July and August) had the largest apparent residence time within the release section though the median was not significantly different to that of the autumn (September and October) released birds (Mann-Whitney U-test; $U = 268$, $p = 0.068$). Three of 10 summer introduced birds were still in their release section four weeks later, whereas no autumn introduced birds were seen for more than two weeks.

Within autumn introductions, birds released on section 05 (in 1986) had longer residence times than those released on 02 (upper, in 1987). The former were seen for up to 12 days (September release) and five days for the October release. The latter had all disappeared (departed or died) within two days in both September and October. However, median residence times for the two release sections were not significantly different (Mann-Whitney U-test; $U = 129.5$, $p = 0.070$). The single batch of December released birds on 02 (mid) also disappeared very rapidly with none seen four days post-release.

In summary, two short-term trends emerged: earlier released birds tended to disappear from the release area at a slower rate than those released in autumn and winter. Also, birds introduced to river section 05 were sighted more frequently than those released on the 02 sections.

Table 7.1 summarises sighting rates of introduced birds in each experiment and compares them with prior residents. The latter comprises adults that had some or all of their home range within the study section, and birds of the year fledged in, dispersing through, or recently arrived and attempting to settle in, the study section. The percentages in this table are pooled for adult males, adult females, juveniles and introduced birds; the latter were mostly juveniles (83%, $n = 36$). Individuals within resident cohorts had very variable sighting rates. The two extremes were: year-round territorial adults that would be seen in each census irrespective of time of day and season in roughly the same place, and on the other hand, naturally dispersing juveniles that would be seen once or twice but not necessarily in the same vicinity. However, overall sighting rates of the three resident cohorts were always higher than those of introduced birds (Table 7.2., $X^2 = 81.46$, 1 d.f., $p<0.001$). Those released on section 05 had higher sighting rates than those released on 02.

Table 7.1. Sighting rates of resident cohorts and released birds: Dipper introductions, River Devon 1986-87.

Year	Age/sex of bird	Overall study period[*1]			Post 1st release observations			Post 2nd release observations		
		No.of birds	Number of observation days	Sighting rate[**2]	No.of birds	Number of observation days	Sighting rate[**2]	No.of birds	Number of observation days	Sighting rate[**2]
1986	Adult male	5	14	74.3%	5	12	71.7%	5	6	63.3%
	Adult female	8	14	62.2%	8	12	61.5%	8	6	60.4%
	All juveniles	8	14	42.6%	8	12	42.7%	7	6	50.0%
	1st release (1)				5	12	22.5%	-	-	-
	2nd release (2)							5	6	23.3%
	Adult male	7	5	51.4%	7	3	52.4%			
	Adult female	5	5	60.0%	5	3	53.3%			
	All juveniles	7	5	37.1%	5	3	53.3%			
	3rd release (3)				6	3	16.7%			
1987	Adult male	5	19	47.4%	5	17	47.1%	4	8	62.5%
	Adult female	7	19	45.9%	7	17	46.2%	7	8	51.8%
	All juveniles	11	19	33.5%	8	17	43.4%	7	8	41.4%
	1st release (4)				5	17	28.2%	-	-	-
	2nd release (5)							5	8	25.0%
	Adult male	3	13	51.3%	2	11	77.3%	2	4	87.5%
	Adult female	5	13	44.6%	4	11	52.3%	3	4	91.7%
	All juveniles	10	13	36.5%	10	11	34.1%	7	4	42.9%
	3rd release (6)				5	11	10.9%	-	-	-
	4th release (7)							5	4	15.0%

Notes:

[*1] The overall study period includes pre-release censuses and mist-netting sessions.

[**2] The sighting rate is derived from Appendix tables A, B, C & D as follows:

the summed number of sightings of birds of that age/sex cohort is divided by the number of census days x the number of birds of that cohort (released or resident) presumed to be on that river section.

Table 7.2. Differences in sighting rates: Dipper introductions, River Devon 1986-1987.

Year	Introduction	Residents birds v. introduced birds	Resident adults v. resident juveniles	Resident juveniles v. introduced birds
1986	1st release (1)	21.62 ***	15.38 ***	6.07 *
	2nd release (2)	11.21 ***	1.49 n.s.	5.24 *
	3rd release (3)	7.12 **	<0.01 n.s.	4.95 *
1987	1st release (4)	8.13 **	0.33 n.s.	5.12 *
	2nd release (5)	7.92 **	2.92 n.s.	2.67 n.s.
	3rd release (6)	19.63 ***	12.19 ***	9.83 **
	4th release (7)	12.75 ***	11.06 ***	4.21 *
Overall (releases 1-7)		81.46 ***	7.23 **	33.12 ***

Note: Values given as X^2 statistic; n.s. = not significant, * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.

Adults were always sighted more regularly than resident juveniles (Table 7.2., $X^2 = 7.23$, 1 d.f., $p<0.01$) though the difference between these two groups was least in July and August. During this period adults were in active wing moult and became very skulking in their habits and were often hard to locate. The only occasion when resident adults and juveniles were sighted equally was during the post-release period in the December 1986 experiment.

7.3.2. Overwinter Survival of Residents and Introduced Birds

Very few of the introduced birds recruited to the study river sections, and thus comparisons are made between survival rates of resident adults (that bred mostly within the study sections) and both introduced and resident juveniles irrespective of their eventual breeding location (Table 7.3). Overwinter survival was highest in adults (61-83%) and lowest in the introduced birds (0-50%). Un-manipulated juveniles that had been present on study sections during the introduction experiments had intermediate survival rates (27-70%).

Recruitment of introduced and un-manipulated juveniles was equal on only one occasion (1986, experiments 1 and 2 combined). However, in this case the fate of all introduced birds was not determined until after the 1987 breeding season: the 1987 breeding sites of two birds were not located but they returned to overwinter on parts of the main river not far from their initial release point. Their breeding sites were located in Spring 1988; thus the survival rate of 1987 introduced birds are presumably minimal estimates as they have only been followed for one breeding season. Resident birds on river section 02 had higher overwinter survival rates than those on 05, probably reflecting both greater nest site availability and a better autumn/winter food resource. After the failure of any December 1986 introduced birds to recruit, no further winter releases were conducted.

Table 7.3. Overwinter survival and breeding success of resident cohorts and introduced birds, River Devon 1986-87.

Year	Age/Sex of Bird	Total no.of birds	OWS (%)	Fate during breeding season (nos)		
				Successful	Fail/die	Unknown
1986 Sept & Oct	Adult male	5	61.5	1	1	1
	Adult female	8	61.5	1	2	2
	All juveniles	8	50.0	3	1	-
	Introduced birds	10	50.0	2	1	2
1986 Dec	Adult male	7	83.3	4	1	1
	Adult female	5	83.3	2	1	1
	All juveniles	7	57.1	1	1	2
	Introduced birds	6	0.0	-	-	-
1987 July & Aug	Adult male	5	66.7	3	1	-
	Adult female	7	66.7	2	1	1
	All juveniles	11	27.3	-	1	2
	Introduced birds	10	10.0	-	1	-
1987 Sept & Oct	Adult male	3	75.0	2	1	-
	Adult female	5	75.0	1	2	-
	All juveniles	10	70.0	2	4	1
	Introduced birds	8(-10)*	12.5 (-30.0)	-	1	-
Total 1986 -87 Note 1	Adult male	20	71.1	10	4	2
	Adult female	25	71.1	6	6	4
	All juveniles	36	50.0	6	7	5
	Introduced birds	34	20.6	2	3	2
1987 Note 2	Adult male	9	69.2	2	2	1
	Adult female	4	69.2	2	2	-
	All juveniles	10	50.0	2	3	-

Notes:

* Two autumn mist-netting casualties included as potential overwinter survivors.

(1) This is the total for all combined experiments carried out during 1986-87.

(2) This is the sample of resident birds tested in the laboratory for dominance.

Abbreviations used:

OWS = birds that survived overwinter.

Overall, highest survivorship was recorded in autumn released birds: presumably some of the summer released birds were still vulnerable to post-fledging predation due to inexperience or may have dispersed to sites outwith the western Ochils/River Devon catchment.

7.3.3. The Effect of Introductions on Autumn Numbers and Breeding Density

All autumn and summer introductions comprised two releases on the same river section and resulted in a temporary increase in local population density by 10 birds over a period of between two and four weeks. Figures 7.1. to 7.4. show the short-term impact of these introductions on the number of birds recorded during the censuses. The number of birds plotted on the figures do not always tally directly with those on Appendix Tables A, B, C and D as they include some birds that were not identified by means of their colour rings.

Both releases in autumn 1986 elevated the local population to the expected level (Figure 7.1). The constant population (of about 20 individuals) recorded after the September release, however, was the result of the natural arrival of dispersing juveniles and departing introduced birds. However, both this "plateau" and the population peak following the October release had decayed to pre-release levels within 10 days of the introductions. The winter and spring carrying capacity of this section appears to be stable at about eight birds from which two to four pairs attempted to breed (Table 7.4). Thus, the introductions had no effect on local autumn/winter or breeding population densities.

Summer releases on the same stretch of river in 1987 also temporarily raised the census counts, though the fluctuations apparent in Figure 7.2. were as much the result of secretive moulting adults as they were of dispersing juveniles. Although the final census on

Table 7.4. Dipper introductions: pre- and post-introduction number of breeding territories in the study area, middle reaches of the River Devon.

River section	Length of section (km)	Number of breeding season territories			
		1985	1986	1987	1988
02	5.4	9-11	9-11	8-12	10-11
05	2.3	3-4	3	2	3-4
06	1.6	2-4	3-4	3	2
Total	9.3	14-19	15-18	13-17	15-17

Note:

Lower numbers refer to the number of definite nesting attempts, whereas the higher figure includes unmated individuals and pairs that used the river occasionally but had nests elsewhere.

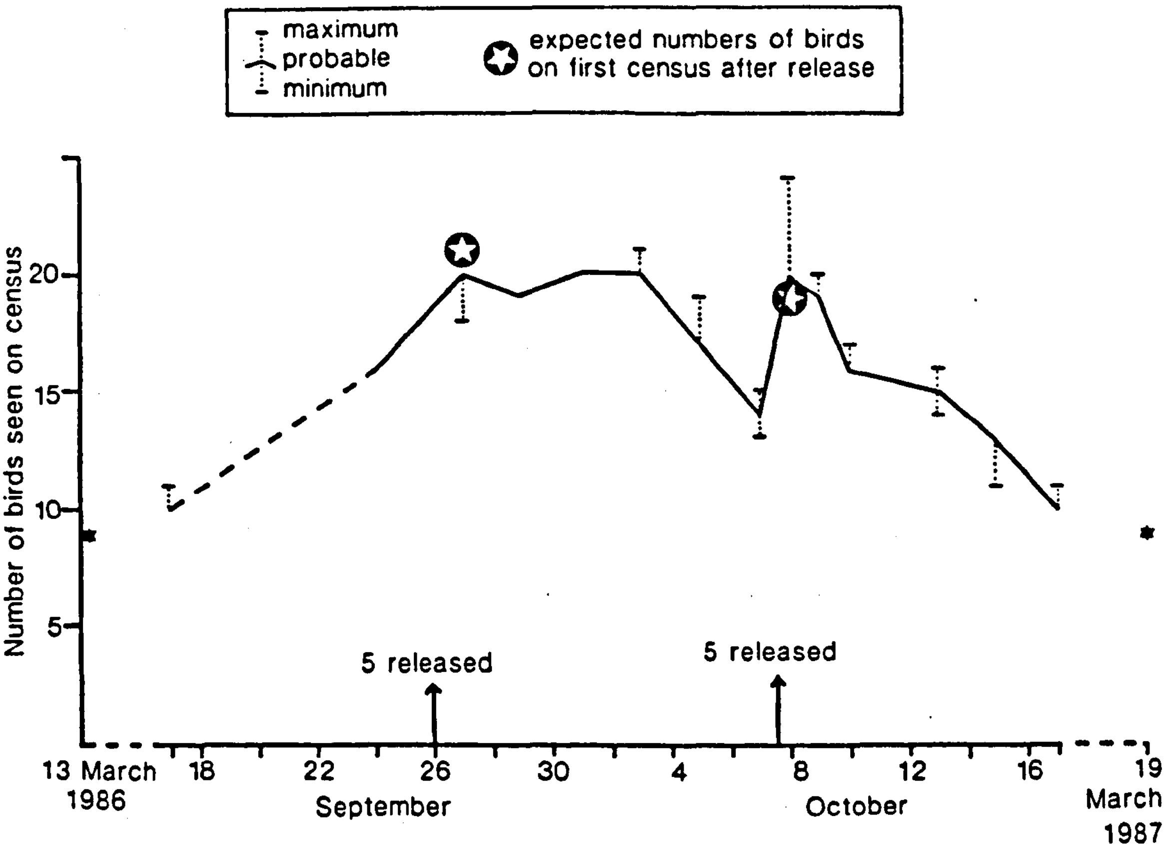


FIG. 7.1 Number of Dippers located on river section 05 after autumn introductions, 1986

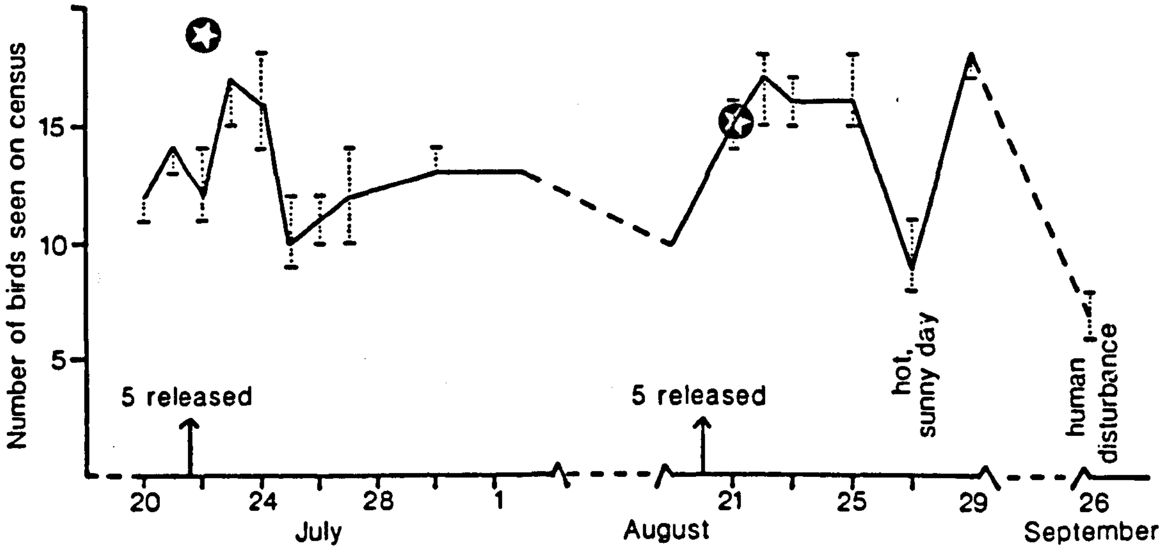


FIG. 7.2 Number of Dippers located on river section 05 after late summer introductions, 1987

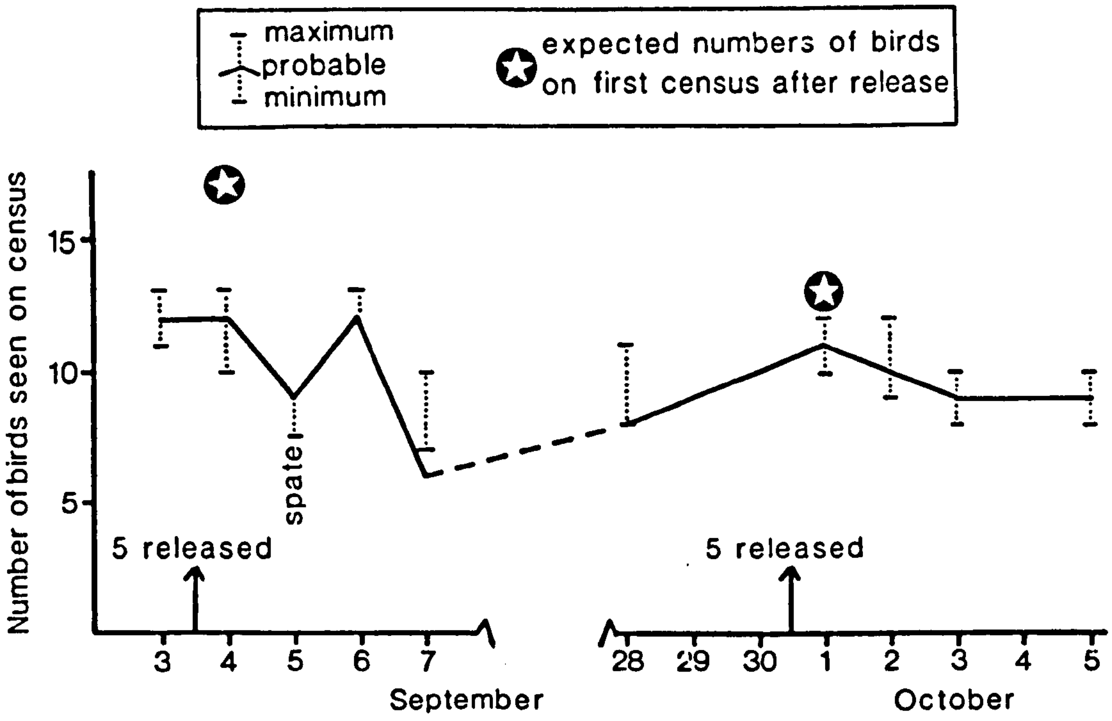


FIG. 7.3 Number of Dippers located on river section 02 (upper) after autumn introductions, 1987.

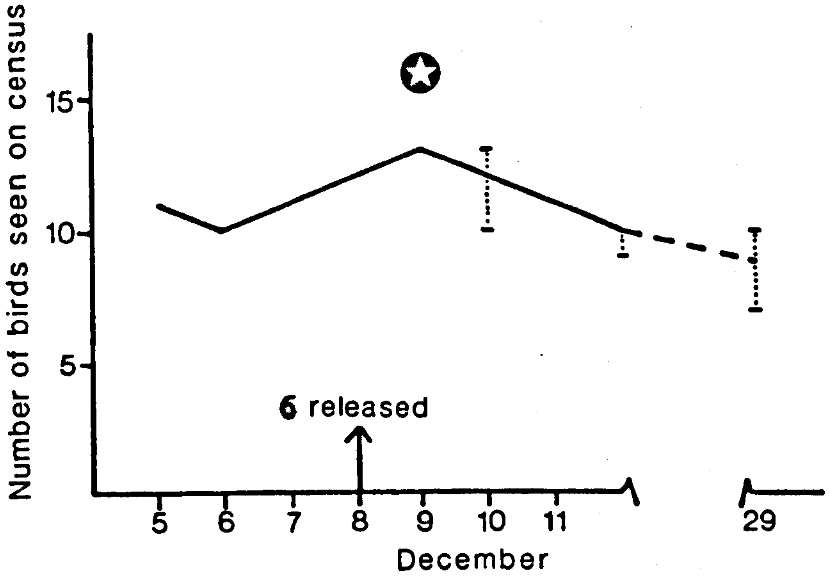


FIG. 7.4 Number of Dippers located on river section 02 (mid) after winter introductions, 1986.

September 26 was disturbed by human disturbance (potato picking in surrounding fields) it seems reasonable to assume that the autumn carrying capacity was in the region of 10 to 15 birds, much the same as the previous year. Late autumn and winter mortality combined with early spring emigration of some individuals to other (upland ?) breeding sites regulates the local breeding population to a maximum of four pairs.

Autumn releases on river section 02 appeared to have no effect on numbers using the main river or lower reaches of side burns in the immediate vicinity of the release point (Figure 7.3). Introduced birds were presumably rapidly chased off by residents and if any time was spent within the study section by these birds then they were probably trying to escape detection by using side burns. A total of nine to 12 birds seems to be the autumn carrying capacity of this section and this number equates with the eventual spring breeding density.

The six birds released in early December slightly further downstream also had a negligible effect on the local population density (Figure 7.4). Whether or not the birds were chased off by residents, rapidly succumbed or made early and determined efforts to return to their original home range is not known.

In summary, the evidence from all introduction experiments strongly suggests that the most suitable Dipper habitat, outwith the breeding season, has a consistent carrying capacity. It appears that density dependent mortality and/or emigration soon regulates any excesses in the late summer/early autumn population pool. The number of breeding territories in the 9.3km of River Devon downstream of the Castlehill Reservoir Dam (incorporating all three sections) are given in Table 7.4. The number of nesting attempts, both pre- and post-introduction experiments, has remained nearly

Table 7.5. Dipper introductions: composition of 7 releases with estimates of dominance, moult stage, number of days survived and distances moved to autumn home ranges and breeding territories.

Time of introduction	Ring no.	Age	Sex	MS	DA	DB	Min S	DM	EAHR	SBS	BTL	BT	Notes
1986	05047	j	m	5	1	D	12	311u					
Late Sept.	05048	j	m	5	2	D	>187	1780d	(+)	+	1780d	3	Apparently settled autumn and breeding territory 1987/88
Release 1	05049	j	m	5	4	I	37	5173u	+				
	05050	j	m	5	5	S	>187	3000u	+	+	12375u	13	
	05260	j	m	5	3	I	>187	2210u	+	+	6100d	9	
1986	05258	j	m	5	2=	I	0	0					
Early Oct.	05261	j	m	5	2=	S	>175	3439u	+	+	2084u	1	
	05268	j	f	5	2=	I	5	35u					
Release 2	05269	j	m	5	1	D	>175	3660u	+	+	6210u	8	
	05270	j	f	5	5	S	3	22d					
1986	05277	a	f	-	1	I	0	0					
Mid Dec.	05278	a	m	-	4=	S	0	0					
	05279	j	m	-	4=	S	2	386d					
Release 3	05280	a	m	-	2	D	0	0					
	05281	j	f	-	4=	S	1	238d					
	55170	a	m	-	3	I	0	0					
1987	05227	j	f	3	5	S	8	61d					
Mid July	93536	j	m	2	2	I	4	42d					
	93656	j	m	4	3=	I	121	125d	+				
Release 4	93657	j	m	4	1	D	38	341u	+				
	93658	j	f	0	3=	S	<1	500d					
1987	93647	j	m	2	1	D	0	0					
Mid August	93665	j	f	1	4	S	4	776u					
	93666	j	m	5	2	D	7	107d					
Release 5	93667	j	m	5	5	S	92	3003u	?				
	93668	j	f	2	3	I	>225	488u	+	+	970u	1	
1987	28467	a	f	-	5	I	<1	113u					
Early Sept.	93661	j	f	5	3	I	<1	100d					
	93670	j	f	5	1=	I	>210	3557d	+	+	3200d	4	
Release 6	93671	j	m	4	1=	D	>49^{+}	6320u	¥				+ mist-netting casualty, ¥ returned to initial capture location
	93672	j	f	5	3=	I	1	840d					
1987	93534	j	m	5	1	D	>47^{+}	1945d	?				+ mist netting casualty
Early Oct.	93678	a	f	-	3	S	55	3160d	+				
	93679	j	m	5	5	S	48	328d	?				
Release 7	93680	j	f	5	4	I	2	585d					
	93681	j	m	5	2	D	0	0					

ABBREVIATIONS:

Age: adult (a), juvenile (j).

Sex: male (m), female (f).

Moult stage (MS): 0 = speckled fledgling, 5 = adult-like.

Dominance A (DA): based on the number of qualitative wins: 1 top-ranking (dominant), 5 low-ranking (subordinate).

Dominance B (DB): 3 point ranking based on percentage interactions won, *viz.*

D = dominant (≥66.7% wins),
I = intermediate (66.7% - 33.3% wins),
S = subordinate (<33.3% wins).

Minimum survival (Min S): days from release to last sighting, with maximum set at April 1st of following spring.

Distance moved (DM): most frequently sighted at about this distance (metres) from the release point (upstream = u, downstream = d).

Established autumn home range (EAHR): seen on ≥ 2 occasions at about this point, ? indicates a single observation or bird known to move around.

Survived to breeding season (SBS).

Breeding territory location (BTL).

Number of breeding territories (BT): number of breeding territories crossed; underlined value indicates good site.

constant throughout the course of this study and manipulation of local population density did not increase the rate of recruitment.

7.3.4. Establishment of Autumn Home Ranges by Introduced Birds

Although the majority of autumn introduced birds failed to settle within the study sections, 55% (11/20) did manage to establish a home range within the overall study area (Table 7.5). Most of these birds moved to a relatively poorly defended stretch of river, which was immediately upstream of section 05 and downstream of, but incorporating part of, section 02 (mid). In this area the river is at its widest and shallowest and thus provides a large area of potential feeding riffles with open visibility (Figure 7.5).

More summer released birds (3/4) established home ranges within study section 05; the remaining bird moved to the same general area as autumn birds. All birds failing to establish were last sighted on release or within one kilometre of the release point, presumably indicating rapid mortality or prolonged emigration. No winter released birds managed to establish themselves locally in the December experiment.

Overall, 50% (15/30) of summer and autumn released birds managed to survive a minimum of one month and most had established a home range. The majority of these birds were juvenile males (12 out of 18 released) with much fewer juvenile females (2/10) and a single adult female (1/2). The former included a single bird (ring number 93671) that had managed to return to the proximity of its initial capture. It was one of the three transported the shortest distance before introduction and as it was not seen on the study section after release day it was presumed to have homed rapidly.

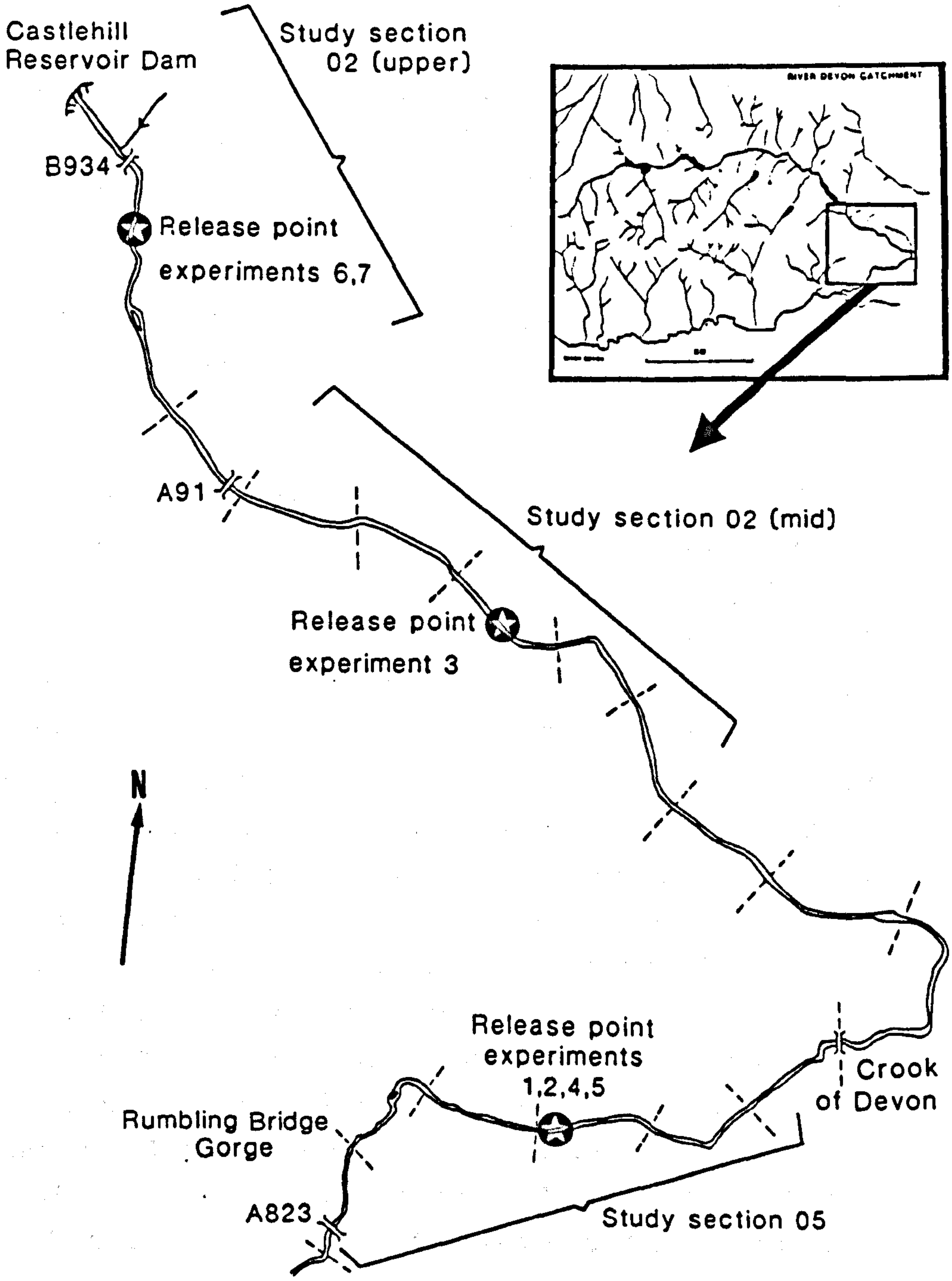


FIG. 7.5 Location of introduction experiment study areas, central River Devon.

There were significant positive Spearman rank correlations between tarsus length and the distance moved from release point (MDIST, mean of short-term sightings or centre of autumn home range), and the minimum number of days survived (NDAYS) and wing length in females (Table 7.6). Tarsus is generally a poor predictor of body size in Dippers so the correlation may be spurious, but the latter relationship may indicate that larger introduced females did survive longer. Conversely, in males the distance moved and number of days survived were negatively correlated with wing length and plumage brightness index (COLOUR). Thus smaller and duller plumaged males appeared to survive longer and move further from the release point (Figure 7.6a, b).

7.3.5. Recruitment of Introduced Birds

Only seven birds out of a possible maximum of 34 survived over winter and presumably attempted to breed in April or May. Five juvenile males from autumn 1986 experiments (maximum possible 17) and two juvenile females from late summer/autumn 1987 introductions (maximum possible 11) recruited. The six adults, mostly released in December, all failed to recruit locally or to return successfully to their original home ranges. The relative importance of age and date of release in determining this outcome cannot be established from the data available. The breeding territories of two males (ring numbers 05048 and 05260) were not located until spring 1988 but it is likely, at least in the latter case, that similar sites were used in 1987. Three males (05050, 05260 and 05269) dispersed away from their autumn/winter home range in spring to establish breeding territories elsewhere.

Two of these movements involved distances in excess of 8km (Table 7.4). However, of the spring dispersers, two subsequently established non-breeding season home ranges in the vicinity of their nest sites and one (05260) returned to the autumn range used the preceding

Table 7.6. Dipper introductions: Spearman rank correlation coefficients between distance moved, number of days survived and dominance estimates & body size of introduced birds.

	PNQUALW	PNTOR	PNFWON	MASS	WING	KEEL	TARSUS	HEAD + BILL	COLOUR
<u>FEMALES:</u>									
MDIST (Distance moved from release point)	0.207 n=14 n.s.	0.222 n=14 n.s.	-0.159 n=14 n.s.	0.222 n=14 n.s.	0.301 n=14 n.s.	0.267 n=14 n.s.	0.625 n=14 **	0.235 n=14 n.s.	-0.024 n=10 n.s.
NDAYS (Number of days survived post-release)	0.112 n=14 n.s.	0.144 n=14 n.s.	-0.221 n=14 n.s.	0.201 n=14 n.s.	0.509 n=14 *	0.098 n=14 n.s.	-0.200 n=14 n.s.	0.135 n=14 n.s.	0.052 n=10 n.s.
<u>MALES</u>									
MDIST (Distance moved from release point)	-0.137 n=22 n.s.	-0.129 n=22 n.s.	-0.096 n=22 n.s.	-0.096 n=22 n.s.	-0.497 n=22 **	-0.139 n=22 n.s.	-0.208 n=22 n.s.	0.036 n=22 n.s.	-0.456 n=18 *
NDAYS (Number of days survived post-release)	-0.179 n=22 n.s.	-0.234 n=22 n.s.	-0.164 n=22 n.s.	-0.098 n=22 n.s.	-0.603 n=22 **	-0.093 n=22 n.s.	-0.294 n=22 n.s.	0.184 n=22 n.s.	-0.565 n=18 **

Notes: PNQUALW, PNTOR, PNFWON are laboratory measures of dominance; PNQUALW is the proportion of qualitative wins, PNTOR is the proportion of time on perch, PNFWON is the proportion of disputes won. COLOUR is defined as: (2 x AREA) + RICH.

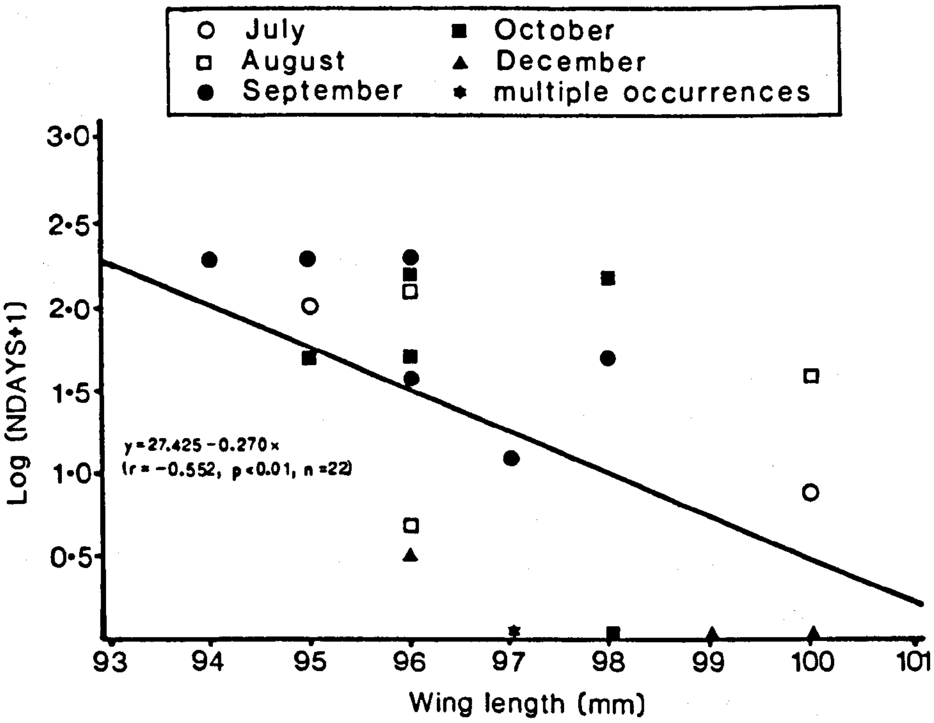


FIG. 7.6a Relationship between minimum number of days survived post-release (NDAYS) and wing length of introduced male Dippers.

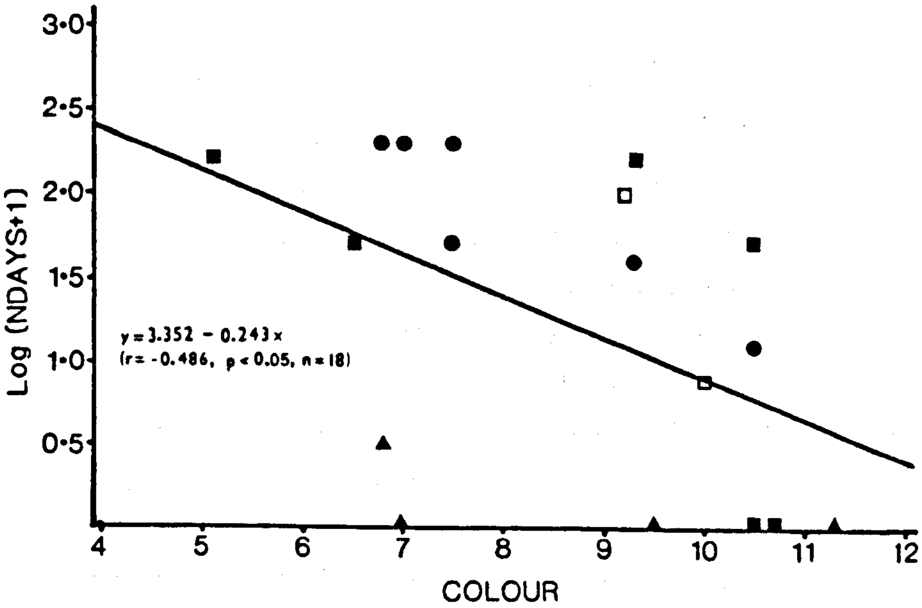


FIG. 7.6b Relationship between minimum number of days survived post-release (NDAYS) and plumage brightness index (COLOUR) of introduced male Dippers.

winter. The two females and the remaining male (05261) acquired nest sites more or less within their autumn/winter home ranges. The number of breeding territories crossed by these recruits ranged from one to 13 (Table 7.5). Breeding success of introduced birds was not closely monitored, although it was similar to that of other un-manipulated juveniles but below that of adults (Table 7.3).

7.3.6. The Effect of Relative Age on Post-release Behaviour

All September and October released birds, bar one, had completed their post-juvenile moult (score = 5) and so their relative ages could not be determined. However, July and August released birds included a wide variety of relative ages. Table 7.7. summarises the performance of different groups and broadly classifies them into predominantly fledgling-like (scores = 0 to 2) and adult-like (scores = 3 to 5). Overall, 14 (61%) of adult-like juveniles established autumn home ranges in contrast to only a single fledgling-like bird (20%), but this difference was not significant (one-tailed Fisher exact test, $p>0.109$).

7.3.7. Relationships Between Laboratory Estimates of Dominance and Post-release Performance

Using the three-point scale of DOMINANCE B, the 15 juveniles that acquired autumn home ranges came equally from the dominant, intermediate and subordinate classes (5 in each, $X^2 = 0.490$, $p>>0.05$). Furthermore, the eventual seven recruits were also almost equally distributed between these classes: two dominants, three intermediates and two subordinates.

Table 7.8 presents overwinter survival data for introduced birds as well as residents using the above three-point classification. Overall survivorship of residents was almost three times as great as that for introduced birds ($X^2 = 9.57$, $p<0.01$). However, amongst residents, intermediate ranking birds performed best

Table 7.7. Dipper introductions: acquisition of autumn home ranges by introduced juveniles in relation to moult stage at release.

	Stages of post-juvenile moult <———>					
	Completely speckled					Moult finished
Moult stage	0	1	2	3	4	5
Number released	1	1	3	1	3	19
Number acquiring autumn home ranges	0	0	1	0	3	11
% acquiring home ranges	20			61		

Table 7.8. Dipper introductions: comparison of the overwinter survival of residents versus introduced birds in relation to dominance status.

Status	Resident population		Introduced birds	
	Autumn numbers	Overwinter survivors (%)	Numbers released	Overwinter survivors (%)
Dominant	9	6 (66.7)	8-10	2-4* (25.0-40.0)
Intermediate	6	5 (83.3)	14	3 (21.4)
Subordinate	8	3 (37.5)	12	2 (16.7)
Total	23	14 (60.9)	34-36	7-9 (20.6-25.0)

NOTE: * two autumn mist-netting casualties included as potential overwinter survivors.

and subordinates poorest. Differences in survivorship between classes were not so pronounced for the introduced birds, though again subordinates survived least well. Pooling the intermediates in turn with dominants, then subordinates, failed to detect any significant differences between higher and lower ranked birds in both the resident and introduced sub-populations (Fisher exact tests, $p >> 0.10$). The two mist-netting casualties were introduced dominant males. Their inclusion as potential overwinter survivors did not result in a significant bias towards enhanced recruitment of dominant birds (Fisher exact tests, $p >> 0.10$).

Correlations (Spearman rank) between laboratory dominance measures, PNQUALW, PNTOR, PNFWON (see derivations in Chapter 5) and distance moved (MDIST) and minimum number of days survived post-release (NDAYS) were weak and non-significant in both sexes (Table 7.6). Further, analyses of variance failed to identify any significant differences in MDIST and NDAYS between the three DOMINANCE B classes for juveniles excluding the two December released birds (males and females separated, one-way ANOVAs, $p >> 0.05$). Controlling for season, (summer or autumn released) also failed to identify any differences (two-way ANOVAs, $p >> 0.05$, sexes separated). Finally, there were no significant differences in PNQUALW, PNTOR and PNFWON between those that acquired autumn home ranges and those that disappeared during the intensive census period (sexes combined, one-way ANOVA, $p >> 0.05$).

Transformation of dominance measures PNQUALW, PNFWON and PNTOR (Arcsin) and MDIST and NDAYS (log) for summer and autumn released females produced significant, positive correlations between MDIST and PNQUALW (Pearson correlation coefficient $r_{12} = 0.634$, $p < 0.05$, one-tailed test), PNTOR ($r_{12} = 0.600$, $p < 0.05$), but not PNFWON ($r_{12} = 0.059$, $p = 0.428$, n.s.). Similarly NDAYS and PNQUALW ($r_{12} = 0.634$, $p < 0.05$), PNTOR ($r_{12} = 0.534$,

$p < 0.05$) but not PNFWON ($r_{12} = 0.070$, $p = 0.414$, n.s.) were correlated. These data are plotted in Figures 7.7 a, b, c and 7.8 a, b, c respectively. To summarise, dominant birds moved further from release points and tended to survive longer than subordinate birds but the ability to win individual disputes (PNFWON) appeared to have little influence on females.

There was no systematic pattern in the relationship between number of territories crossed and nest site quality for recruits from different DOMINANCE B categories. High quality nests were those that produced fledged young each year: dominant male 05269 acquired a very secure nest site on Castlehill Reservoir Dam having crossed eight potential breeding territories since release; intermediate male 05260 also moved a considerable distance downstream of his autumn home range to recruit to a secure side burn territory and though his paternity of the 1987 brood could not be proven, in 1988 he reared an exceptional brood of six young. The subordinate male 05261 moved the least distance, only crossing a single breeding territory, and he managed to produce a single brood in 1987 and was double-brooded in 1988. On the other hand, failed recruits included the remaining two males: a dominant that moved a short distance to a poor site (probable tree-nest) and a subordinate moving 12km upstream. The two females remained close to release points (1 to 3km) but neither acquired good territories or bred successfully. The evidence presented here suggests that released dominants may range widely to find a good, vacant or acquirable site/mate whereas subordinates either try and stay and use sub-optimal but local resources to their best advantage, or are forced into exploring distant upland sites.

7.4. DISCUSSION

The main aim of the introductions was to compare the settlement pattern, movements, survival and recruitment of groups of naive juveniles by standardising time of

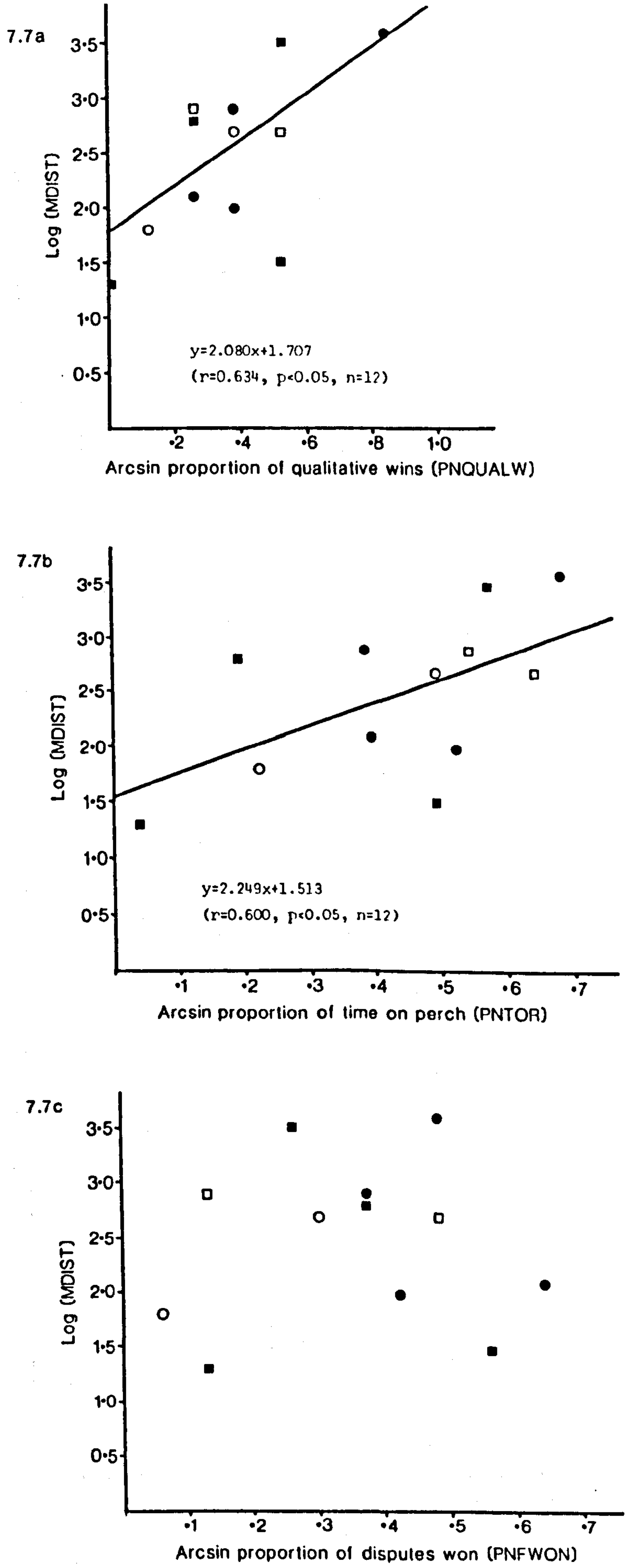


FIG. 7.7a,b,c Relationships between distance moved from release-point (MDIST) and laboratory measures of dominance (PNQUALW, PNTOR, PNFWON) of introduced female Dippers. Key as for Fig. 7.6

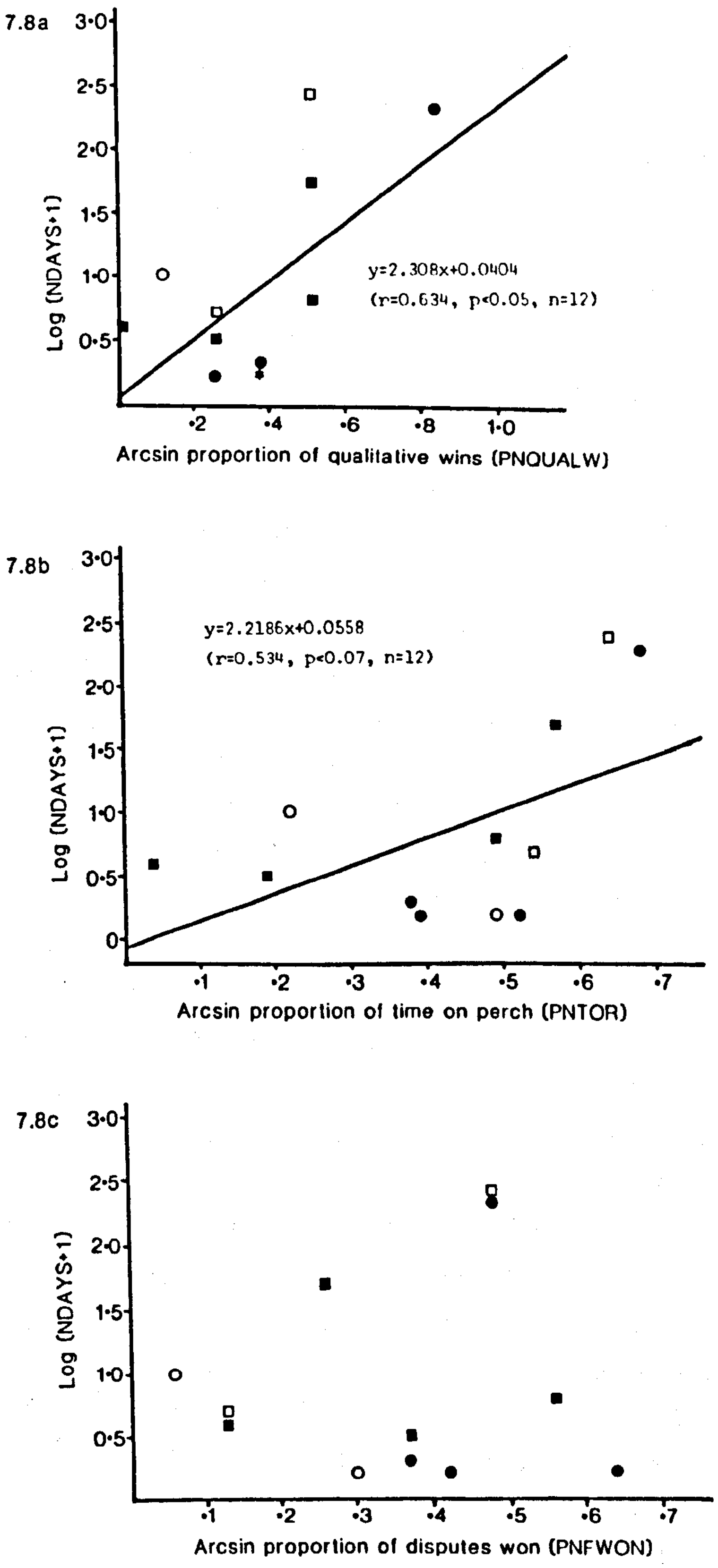


FIG. 7.8a,b,c Relationships between minimum number of days survived post-release and laboratory measures of dominance (PNQUALW, PNTOR, PNFWON) of introduced female Dippers. Key as for Fig. 7.6

arrival at a specific site. Conditions in the vicinity of the release points were therefore equal for all introduced birds in terms of habitat quality and the number and status of resident conspecifics. This allowed the relative importance of sex, size, age, plumage brightness and dominance status in the recruitment process to be assessed for these birds. Small samples necessitated more emphasis on component processes of recruitment than recruitment itself.

Short-term re-sighting frequency was highest in the July and August released juveniles. At this time, recently independent fledglings often dispersed away from their natal territories (Chapter 6), so introduced birds could be expected to move away rapidly from a release point. However, the proximate mechanisms behind dispersal are poorly understood though perhaps the process may be driven by intraspecific competition (Waser 1985). If fledglings are able to satisfy their daily needs with little interference at a site then there may be little incentive to move. The retiring habits of adult Dippers during the moult may permit fledglings to settle and allow access to resources in the short-term, yet the same adults may drive them away later in the autumn. One other factor likely to influence residence time is the availability of roost sites. Fledglings often roost in riverside bushes and trees (Chapter 6) and the longer flights, typical of adults, to more secure cliff and bridge sites probably do not occur. The more rapid turnover of autumn released juveniles was probably due to a wider ranging behaviour whilst looking for secure roost sites. In the process, foraging sites closer to roosts would be discovered and this would reduce the likelihood of a bird returning to the proximity of its release point.

At the time of the earliest summer introduction experiment in July, the study sections were already occupied by juveniles of the year that had probably completed their initial dispersal phase. Their overwinter survivorship and recruitment rate was considerably higher than that of the introduced birds. This implies that site familiarity and prior residence is important to Dippers and accords well with the findings of Stamp (1987) and Harper (1984).

Introductions failed to increase the local breeding population. The evidence presented here implies a near "perfect" density dependence, with food resources ultimately limiting autumn densities and home range acquisition. Nilsson (1987) has described a density-dependent relationship between recruitment to the autumn population and current food supply in Nuthatches *Sitta europaea*. Suitable Dipper habitat within the study area was presumably already saturated at the time of the introductions and the majority of breeding recruits came from resident adults and early established juveniles. Those introduced birds that did recruit, successfully competed for vacancies arising due to adult mortality at high quality sites (05269, 05260) or risked nesting failure by occupying poorer sites (05050, 05269, 93668 and 93670).

In this study, sex was the most important factor determining the acquisition of an autumn home range. Females are both smaller than and generally subordinate to males and were thus less able to compete against residents, and no doubt introduced males, for the limited resources within the study area. The fate of most introduced females remains unknown: both death and emigration to marginal sites outwith the region are likely. Future replication of experiments such as these should be undertaken with radio-marked birds to remove reliance on chance colour-ring sightings and to provide data on the fate of the non-recruiting birds.

One of the introduced juvenile Dippers did manage to return to its initial capture location but this was attributable to poor experimental technique as this exceptional bird had only been transported 5km. In non-manipulated conditions, some birds may travel this distance to roost on a regular basis. The introduced female Pied Flycatchers studied by Slagsvold *et al.* (1988) showed a much more developed ability to "home" than was demonstrated by the Dippers in this study. In the flycatcher experiment, all experimental plots were within 10km of one another and, further, a migratory species would be expected to have a wider knowledge of local topography. Settlement rates of introduced female Pied Flycatchers were much higher on study sites in which all previously resident females had been removed than on those in which some females were present and had already mated. Although only six adults were introduced in the Dipper experiments, only one acquired an autumn home range and none apparently survived. This was probably attributable to them making a sustained effort to return to their original sites, but becoming disoriented in the process. Winter introduced juveniles did not leave the study area immediately on release, and probably did not survive long due to a combination of short days and unfamiliar terrain.

Several authors have confirmed the importance of relative age in juveniles. Earlier fledged Robins *Erithacus rubecula* (Harper 1984) and Nuthatches (Matthysen 1987) were more likely to acquire autumn territories than younger birds. Arcese & Smith (1985) have shown that dominance status was a good predictor of overwinter survival and of settlement in a territory, and that most dominant juveniles came from the earliest hatched broods.

Laboratory estimates of dominance were not always reliable predictors of post-release behaviour and survivorship in introduced Dippers. This finding is not consistent with the higher survivorship of dominant and intermediate ranked residents. It is possible that performance in laboratory tests had little relevance in the field and further, such measures of dominance are always relative to the status of the birds with which they were tested. If five males are tested, then one or two will inevitably end up as subordinates; if the latter were matched against females then there would be a reasonable chance of them being classed as dominants. Such a scenario may have confounded the findings presented here and much larger sample sizes would be necessary to unravel the costs and benefits of dominance in resident and introduced Dippers.

Elsewhere (Chapter 5), it is shown that dominant males tended to be larger (juveniles only) and have brighter plumage (both adults and juveniles) than subordinates. The negative correlations identified here between wing length, COLOUR index and post-release survival imply there may be costs associated with being a big and bright male without a home range. Röskaft *et al.* (1986) and Hogstad (1987) have demonstrated that dominant Great Tits, Pied Flycatchers and Willow Tits *Parus montanus* have higher metabolic rates. These birds usually have higher overwinter survival prospects and acquire better quality territories but these benefits must be set against increased energetic costs. In the male Dipper, defending a year-round territory or stable autumn home range may be energetically economic, but with acquisition much more costly. Clearly, further research into this topic is needed and this could be achieved by the field application of the doubly-labelled water ($D_2{}^{18}O$) technique in conjunction with introduction experiments.

CHAPTER EIGHT

BODY COMPOSITION OF SMALL BIRDS: STUDIES OF DIPPERS & CANARIES

8.1. INTRODUCTION

Many authors have found correlations between expressions (often ratios) of body mass and body size and the composition of carcasses of shot or sacrificed birds. Such relationships are usually expressed as "condition indices" in which lipid content is given as a proportion of live, dry or lean dry mass of the whole bird. These indices have mainly arisen from work on wildfowl (Anatidae) and waders (Charadridae, Scolopacidae) that are known to carry large lipid stores for use during migration and reproduction (Ankney and MacInnes 1978, Campbell and Leatherland 1980, Iverson and Vohs 1982, Johnson *et al.* 1985, Krapu 1981, Moser and Rusch 1988, Raveling 1979, Ringelman and Szymczak 1985, Wishart 1979). Condition indices have seldom been investigated systematically in small birds despite Fretwell (1968) demonstrating that "good condition" was advantageous in overwinter survival.

The phenomenon of winter fattening has been described by Newton (1969) and Evans (1969) in resident, temperate passerines; much of the stored lipid is accumulated through the day for use overnight whilst roosting. The annual cycles of body mass for Dippers *Cinclus cinclus* in Britain presented by Bryant and Tatner (1988) and Ormerod *et al.* (1986) do not show any significant increase in mass in midwinter and thus any seasonal storage would apparently have to be made at the expense of other body components. In Finland, the migratory Dippers studied by Lehikoinen and Hakala (1988) did show a slight rise in body mass in midwinter and they attributed this to fat deposition.

In this chapter, the potential use of size-adjusted masses derived from standard biometric measurements made in the field is explored, and also, the use of the non-intrusive ultrasonic flaw detector with the Dipper and laboratory-maintained Canaries *Serinus canaria*. I also present body composition data on a sample of Dipper carcasses for birds taken between early autumn and spring.

8.2. MATERIALS AND METHODS

A small group of Canaries was maintained in the laboratory between September 1987 and April 1988. The group comprised six birds housed in two or three cages and fed *ad lib* with canary seed and millet. Some of the birds died during the course of the experiment and were replaced so that data are available for eight individuals. At approximately monthly intervals the birds were weighed and measured at midday (± 2 hours) and an assessment of pectoralis muscle thickness was made using the ultrasound technique.

The physical principles behind this technique have already been described by Baldassarre *et al.* (1980) in their study of subcutaneous and omental fat in Mallard *Anas platyrhynchos* and Sears (1988) in her study of breast muscle thickness in the Mute Swan *Cygnus olor*. In this study, a portable Krautkrämer instrument (model number USK7) powered by six rechargeable Ni-Cd cells (NCA2-6) was used (Figure 8.1a). The transducer comprises a small cylindrical probe (Alpha 2 Aerotech, 10MHz) with a diameter of 9mm and height of 11mm. The sound emitting face of the transducer was applied to the pectoralis muscles (Figure 8.1b), feathers brushed to one side, at three standard locations on either side of the keel: near the anterior and posterior edges of the muscle block and in the middle (Figure 8.2). The face of the probe was wetted with water or alcohol to achieve full contact. The instrument's span and zero were checked for constancy using a stepped perspex block. Arbitrary "ultrasound units" were measured off the grid overlying the cathode ray tube (CRT) display as the interval on the x-axis to the first reflection.

Fig. 8.1a Field application of ultrasonic flaw detector for measurement pectoralis muscle thickness in a Dipper.

Fig. 8.1b Close-up of ultrasound probe positioned on anterior part of a Dipper's breast (R1).

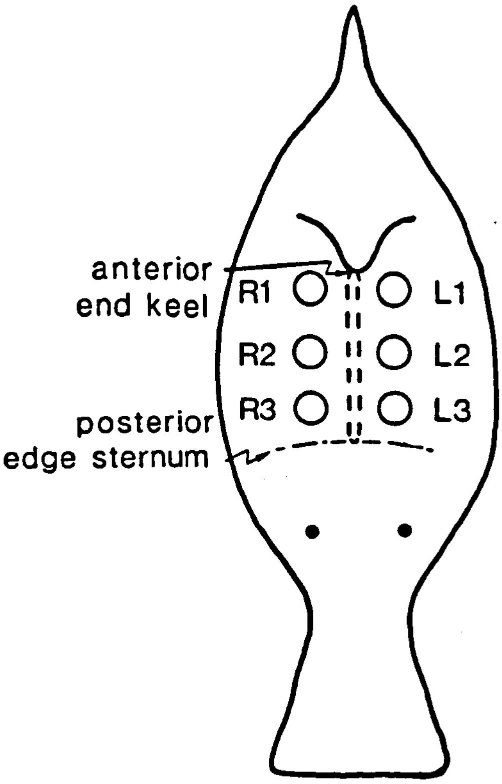


Fig. 8.2a Location of ultrasound probe for assessment of pectoralis muscle thickness.

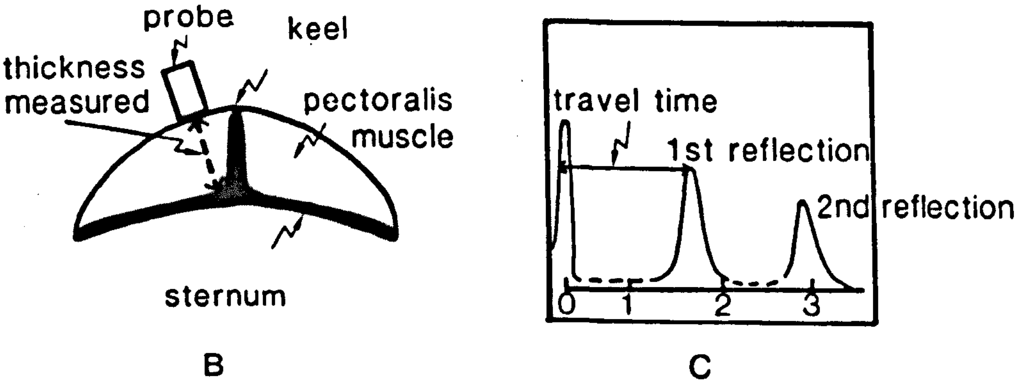


Fig. 8.2b,c Relationship between muscle thickness (b) and signal travel time displayed on ultrasound detector CRT (c).

This distance represents the return travel time of a sound pulse between probe and the muscle: sternum bone interface and is directly proportional to the intervening thickness of tissue (Figure 8.2). The pressure at which the probe was applied to the skin was kept constant and its long axis was kept parallel to the keel so that the reflections from the keel itself did not arise (Figure 8.2). Usually, several readings were taken at each location until a "clean" reflection peak at constant position along the x-axis was achieved. During this procedure, birds lay across the palm of the left hand with neck and head only restrained by index and middle finger.

Those Canaries that had not died naturally or from disease, or subordinates that had apparently starved, were killed by ether inhalation at the end of the experiment. Carcasses were deep frozen immediately after death.

The sample of Dipper carcasses was derived from autumn mist-netting fatalities between 1983-1987. These birds had usually, but not always, drowned in the bottom panel of the net before they could be reached for extraction and were supplemented by birds taken under licence from the Nature Conservancy Council during midwinter and early spring. The latter were killed by ether inhalation. Data are available for 15 fledged Dippers. All carcasses were weighed, measured and pectoralis thicknesses assessed using ultrasound before being stored frozen.

Both Dipper and Canary carcasses were allowed to thaw at room temperature and further determinations of pectoralis thickness were made using the ultrasound device. A direct measurement of muscle thickness was then made at the same six locations on the breast by the insertion of a 0.45 x 10mm hypodermic needle. A visual estimation of the transverse pectoralis profile was made using a four-point scale based on the prominence of the keel (Village 1983) (a score of 1 = keel very prominent, 4 = breast muscle uniformly rounded and convex). The birds were then dissected into 20 components as follows: flight feathers (primaries and secondaries), tail feathers, skin and contour (body) feathers (including most subcutaneous lipid), wings, legs, head, neck, left and right pectoralis major and minor (= supracoracoideus) muscles, tracheal (= tracheal plus clavicle-coracoid fat body of McGreal & Farner 1956, King & Farner 1965) lipid depot, gizzard and oesophagus, intestine, heart, lungs, liver, kidneys, gonads and the residue comprising the body shell. Wet masses (WM) were recorded for the four pectoralis muscles as soon as they were excised. Four further skeletal measurements were taken, A, B, C and D of Evans & Smith (1975) and Piersma *et al.* (1984) to enable calculation of standard muscle volume (SMV). All components were freeze dried to constant mass over seven or eight days and were then weighed to give dry masses (DM).

Lipids were extracted from all components in a Soxhlet apparatus for 40 hours using a 5:1 mixture of diethyl ether and chloroform as solvent. After allowing the solvent to evaporate, lean components were freeze dried for a further two days before weighing (LDM). Lipid mass (LiM) and water content (WC) were derived by subtraction. All masses were measured to 0.001g.

A sample of carcasses (4 Dippers and 4 Canaries) representing as wide a range of body size as possible were reduced to ash in a muffle furnace at 550-600°C for 24 hours to generate ash masses (AM). For this purpose, components were aggregated into six units: body shell, head and neck, skin and contour feathers, flight and tail feathers, pectoralis muscles and guts. Ash-free lean dry masses (ALDM) were calculated by subtraction (LDM - AM). Ash masses for the remainder of birds were estimated from those of the nearest sex and size category for Dippers and from those of the same cause of death in Canaries. A starved/diseased bird was one which had lost more than a third of its normal body mass before death.

The above measures were used to generate several indices for components and whole birds:

lipid index (LiI) = LiM/LDM
water index (WI) = WC (g)/LDM
ash index (AI) = AM/LDM

Pectoralis lean dry mass deviation (PLDMD) was calculated for Dippers following Jones (1987).

$$\text{PLDM} = \frac{\text{observed pectoralis lean dry mass}}{\text{expected pectoralis lean dry mass as a function of keel length}}$$

A value of 1 for this index indicates that the pectoralis lean dry mass of an individual corresponds exactly with that expected for a bird of that size derived for the regression of observed PLDM on keel length:

$$\text{PLDM} = -5.761 + (0.300 \times \text{keel length in mm})$$
$$(r = 0.865,\ n = 15,\ p < 0.001).$$

8.3. RESULTS

8.3.1 Validation of Ultrasound Readings as Measures of Pectoralis Muscle Thickness

Correlations of arbitrary "ultrasound thickness units" and measured thickness (by hypodermic needle) proved highly significant in both Dippers (Figure 8.3, r_{102} = 0.954, p<0.001) and Canaries (r_{66} = 0.950, p<0.001). The relationship is most precise at muscle thicknesses exceeding 5mm, with less scatter around the regression

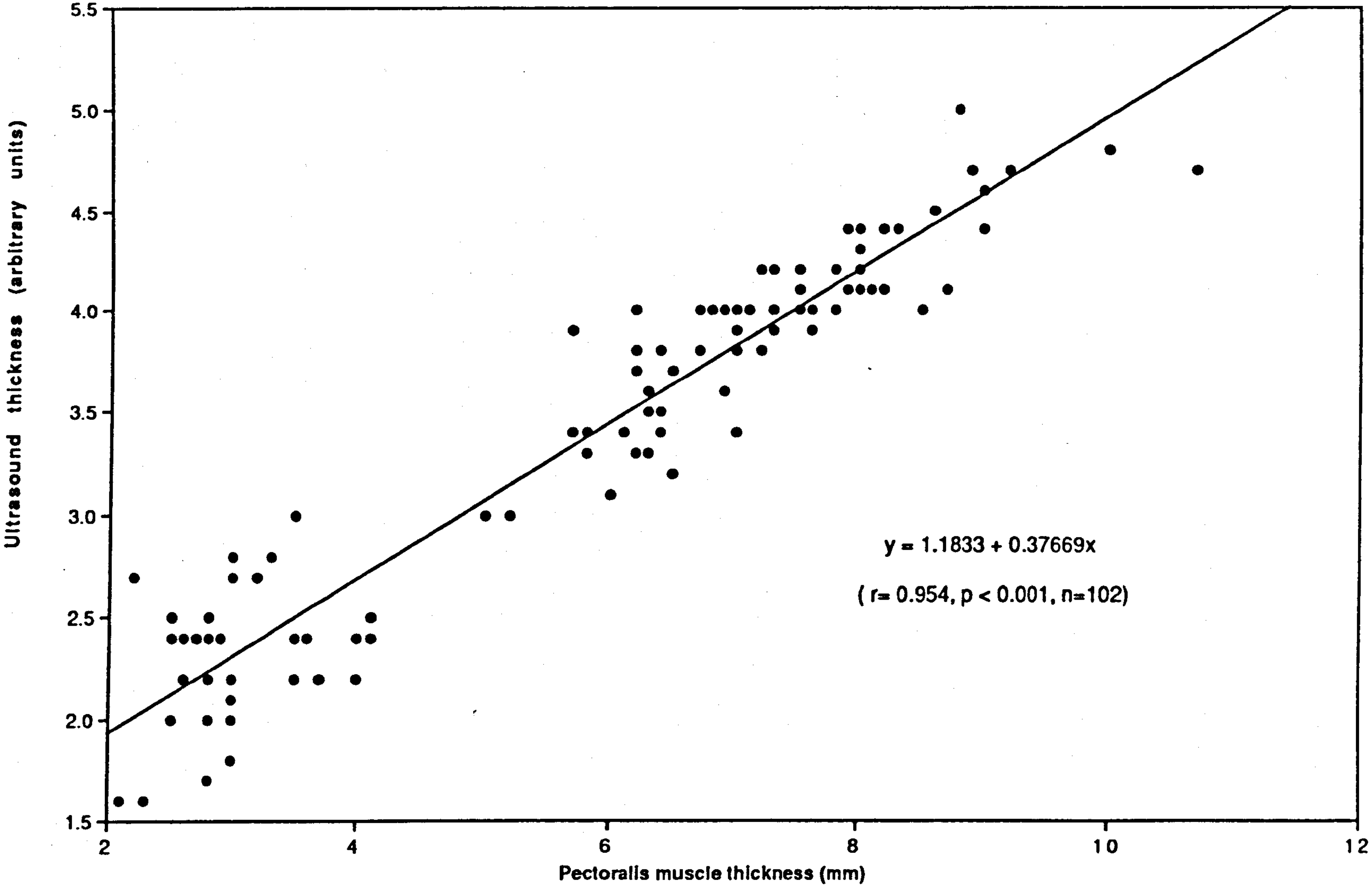


FIG. 8.3 Correlation of pectoralis muscle thickness with ultrasound readings.

line. The following regression equations enabled arbitrary ultrasound thickness units to be expressed in millimetres:

Dipper:

$$\text{mm thickness} = \frac{\text{ultrasound CRT readings} - 1.18334}{0.37669}$$

Canary:

$$\text{mm thickness} = \frac{\text{ultrasound CRT readings} - 0.54157}{0.41219}$$

In any ensuing manipulations involving pectoralis thickness, measurements are expressed in mm.

8.3.2. Variation in Body Mass and Pectoralis Muscle Thickness in Live Canaries

Total body mass may increase by up to 10g without significant change in pectoralis muscle thickness (Figure 8.4). However, any mass loss exceeding two grams was always accompanied by a reduction in pectoralis muscle thickness. In 16 out of 23 cases (70%) body mass and pectoralis thickness changed in the same direction. Mass change and thickness change (sum of the measurements at the 6 probe locations) between handlings were correlated ($r = 0.475$, $p<0.05$) but the r^2 value of 0.23 indicated changes in other body components were also occurring. Visible tracheal lipid depots varied markedly and presumably these accounted for most of the residual mass changes.

8.3.3. Whole Body Composition

8.3.3.1. Canaries

Body composition data are available for seven Canaries. These varied considerably in size (see range in Table 8.1) and could be assigned to one of three categories depending on the circumstances of death: apparently healthy, sacrificed at the end of the experiment (3 birds); lost condition markedly before dying during the experiment (2 birds) and dying "naturally" (2 birds).

Table 8.1. Biometrics and whole-body composition of Canaries. (Mean values ± standard deviation).

	Taken	Died naturally	Starved	All birds (range)
Live mass (g)	24.70 ± 8.15	22.45 ± 0.35	13.55 ± 3.47	20.87 (11.1-29.8)
Wing length (mm)	87.33 ± 7.57	88.50 ± 3.54	80.50 ± 0.71	85.71 (80.0-96.0)
Keel length (mm)	21.03 ± 2.11	20.50 ± 0.71	19.20 ± 2.69	20.36 (17.3-22.4)
Tarsus length (mm)	19.23 ± 2.53	20.05 ± 1.20	16.43 ± 1.28	18.66 (15.52-21.50)
Head & bill length (mm)	28.39 ± 1.76	28.68 ± 0.42	27.52 ± 0.99	28.22 (26.56-30.06)
Wet mass (g)	24.600 ± 7.977	22.100 ± 0.141	13.500 ± 3.394	20.714 ± 6.977
Dry mass (g)	10.289 ± 3.504	8.862 ± 0.169	5.126 ± 1.044	8.406 ± 3.116
Water content (g)	14.311 ± 4.496	13.238 ± 0.027	8.374 ± 2.350	12.308 ± 3.887
Lean dry mass (g)	7.486 ± 1.859	7.569 ± 0.295	4.830 ± 1.113	6.751 ± 1.760
Lipid mass (g)	2.803 ± 1.888	1.293 ± 0.126	0.300 ± 0.074	1.656 ± 1.583
Ash-free lean dry mass(g)	6.558 ± 1.626	6.676 ± 0.255	3.969 ± 0.904	5.852 ± 1.639
Ash mass (g)	0.928 ± 0.234	0.893 ± 0.040	0.856 ± 0.215	0.898 ± 0.165
Lipid index	0.353 ± 0.207	0.172 ± 0.023	0.066 ± 0.030	0.219 ± 0.179
Water index	1.888 ± 0.194	1.751 ± 0.071	1.726 ± 0.087	1.802 ± 0.145
Ash index	0.124 ± 0.003	0.118 ± 0.000	0.178 ± 0.004	0.137 ± 0.028
Sample size	3	2	2	7

Table 8.2. Whole-body lipid, water and ash indices for 7 canaries.

Bird Number	Lipid Index	Water Index	Ash index
01 (taken) 03 (taken) 05 (taken)	0.575 0.320 0.164	2.077 1.896 1.690	0.121 0.126 0.124
04 (died 07 naturally)	0.155 0.188	1.700 1.801	0.118 0.118
02 (starved/ 06 diseased)	0.044 0.087	1.787 1.664	0.180 0.175

Note: Bird numbers correspond with those in Figure 8.4.

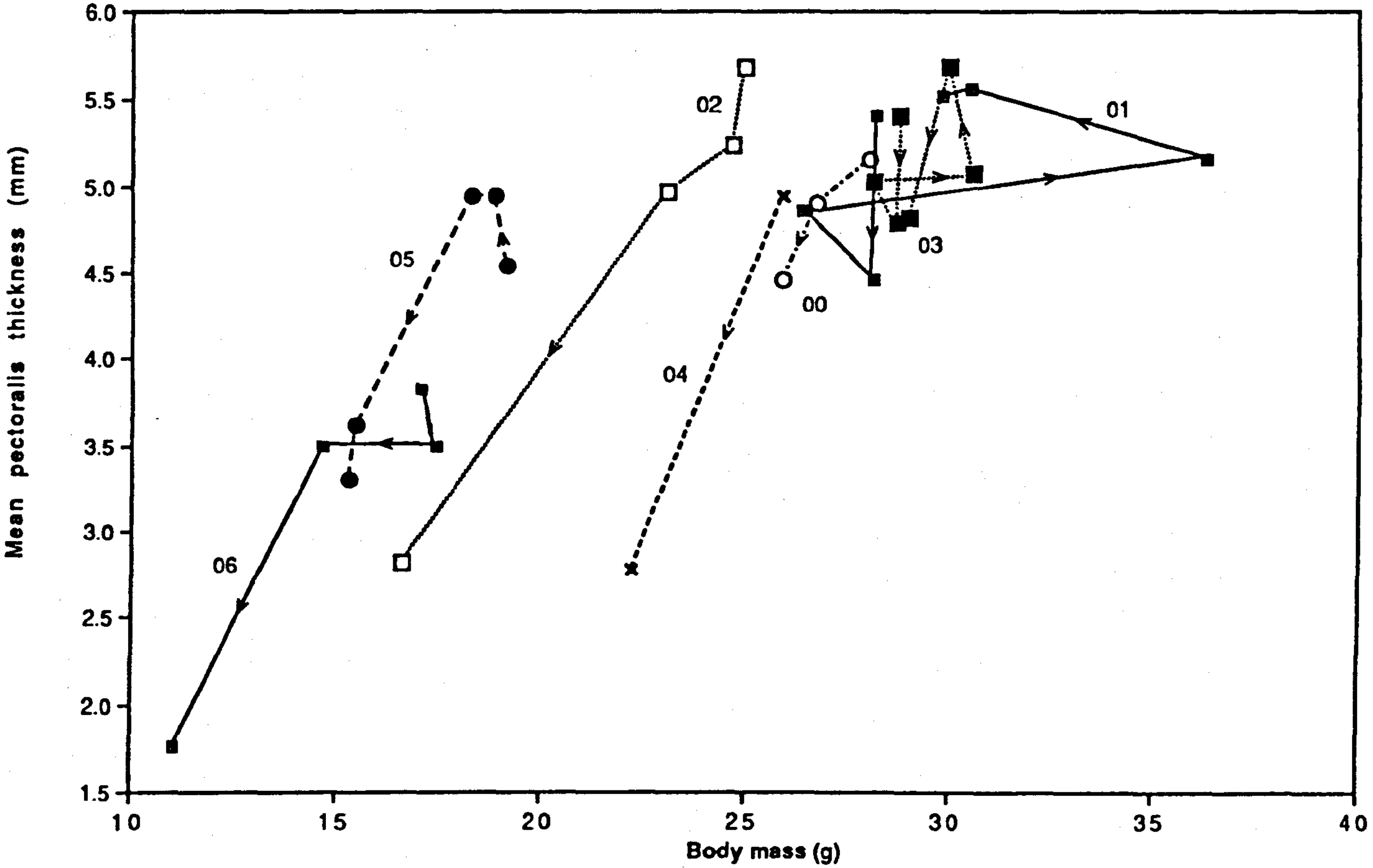


Fig. 8.4 Monthly variation in body mass and pectoralis change for 7 canaries.

In most cases the Canaries could not be sexed reliably as gonads were indistinct after freezing and thawing. Biometrics and whole- body composition are given in Table 8.1.

In the small sample of Canaries, lipid and water indices were highest in those birds taken at the end of the experiment; two had lipid indices exceeding 0.3, indicating a considerable lipid store (Table 8.2). The indices of the third bird (No.5) were more akin to birds that had died in the course of the ultrasound experiment. This bird was one of the smallest and had lost 18% of its initial body mass the month before it was taken. Temporarily removing this bird from the "healthy" category resulted in significantly higher lipid and water indices for the two birds in good condition over the remaining five birds ($p<0.05$, t-test). Ash indices were significantly higher in those birds that had starved to death than in those taken ($p<0.001$, t-test) and those dying naturally ($p<0.01$, t-test). Considerable loss of lean mass, especially from the pectoralis muscles, accounted for much of this difference.

8.3.3.2. Dippers

The Dippers comprised a rather random sample of 15 birds, mostly from the non-breeding season between September and early April. No adult females were taken (Table 8.3). Biometrics and whole body composition are broken down by sex and season in Table 8.4. Whole body lipid indices in the Dipper varied between seasons: they were highest in the winter, lowest in the spring and intermediate during the autumn (Figure 8.5). Between season differences were significant for sexes combined: autumn and winter ($p<0.05$, t-test), autumn and spring ($p<0.05$, t-test), winter and spring ($p<0.05$, t-test) and autumn/winter combined against spring ($p<0.05$, t-test). Females, the smaller sex in this dimorphic species, showed a tendency towards having higher lipid indices in autumn and winter than males

Table 8.3. Seasonal distribution of Dipper carcasses.

Month	Season	Dipper carcass type
July	Summer	1 fledgling female
September	Autumn	4 juvenile females
October	Autumn	2 juvenile males
November	Autumn	1 juvenile male
December	Winter	1 adult male, 1 juvenile male, 1 juvenile female
March	Spring	1 adult male
April	Spring	2 adult males, 1 juvenile male (2 pre-breeding, 1 failed breeder respectively)

Table 8.4. Biometrics and whole-body composition of Dippers. (Mean values ± standard deviation).

	All females	All males	Autumn/winter females	Autumn/Winter males	Spring males
Live mass (g)	57.35 ± 3.69	70.49 ± 3.90	58.58 ± 2.18	70.32 ± 3.87	70.70 ± 4.53
Wing length (mm)	90.17 ± 2.71	97.22 ± 1.99	90.20 ± 3.03	97.00 ± 1.58	97.50 ± 2.65
Keel length (mm)	28.07 ± 1.12	31.40 ± 1.05	28.40 ± 0.86	31.64 ± 1.19	31.10 ± 0.90
Tarsus length (mm)	27.02 ± 0.77	29.40 ± 0.87	27.33 ± 0.19	29.54 ± 1.08	29.22 ± 0.62
Head & bill length (mm)	45.18 ± 1.43	47.48 ± 0.68	45.81 ± 0.31	47.67 ± 0.28	47.15 ± 1.09
Wet mass (g)	55.467 ± 5.602	68.378 ± 4.898	57.580 ± 2.395	68.020 ± 5.286	68.750 ± 5.139
Dry mass (g)	20.688 ± 2.095	24.510 ± 2.070	21.414 ± 1.237	25.405 ± 1.897	23.391 ± 1.903
Water content (g)	34.779 ± 4.445	43.868 ± 3.927	36.166 ± 3.205	42.675 ± 3.908	45.359 ± 3.928
Lean dry mass (g)	17.416 ± 1.641	21.985 ± 1.484	18.078 ± 0.287	21.993 ± 1.803	21.976 ± 1.240
Lipid mass (g)	3.271 ± 1.025	2.524 ± 1.533	3.336 ± 1.132	3.412 ± 1.437	1.415 ± 0.751
Ash-free lean dry mass (g)	15.337 ± 1.481	18.884 ± 1.279	15.932 ± 0.289	18.871 ± 1.547	18.900 ± 1.081
Ash mass (g)	2.080 ± 0.166	3.101 ± 0.234	2.146 ± 0.038	3.122 ± 0.279	3.076 ± 0.200
Lipid index	0.189 ± 0.057	0.116 ± 0.075	0.184 ± 0.063	0.158 ± 0.075	0.063 ± 0.030
Water index	1.998 ± 0.188	2.002 ± 0.214	2.003 ± 0.210	1.950 ± 0.239	2.067 ± 0.190
Ash index	0.120 ± 0.003	0.141 ± 0.005	0.119 ± 0.003	0.142 ± 0.004	0.140 ± 0.005
Sample size	6	9	5	5	4

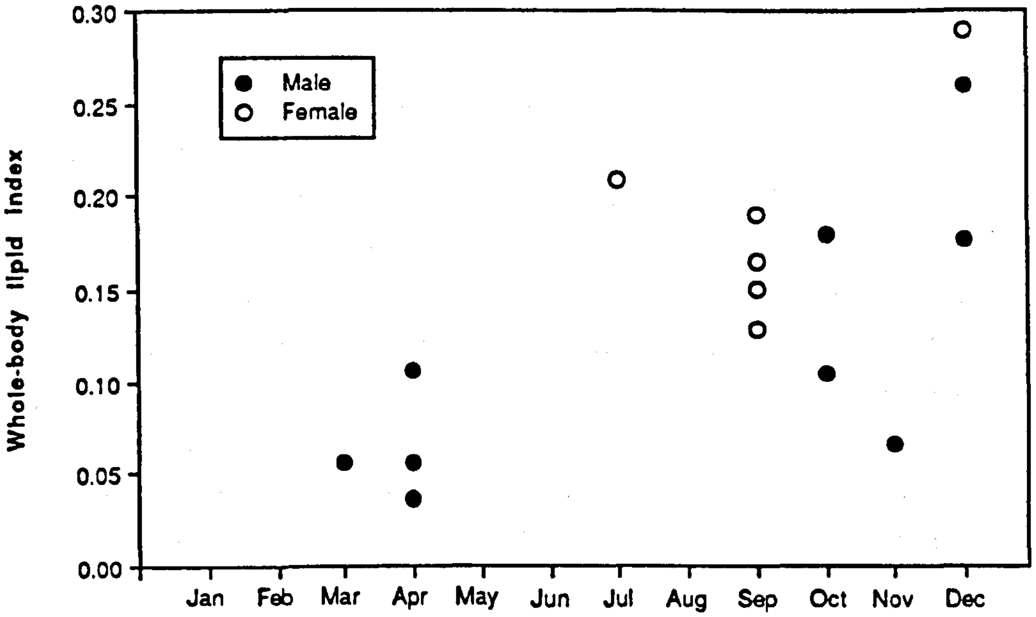


Fig. 8.5 Seasonal variation in whole-body lipid indices for 15 Dippers

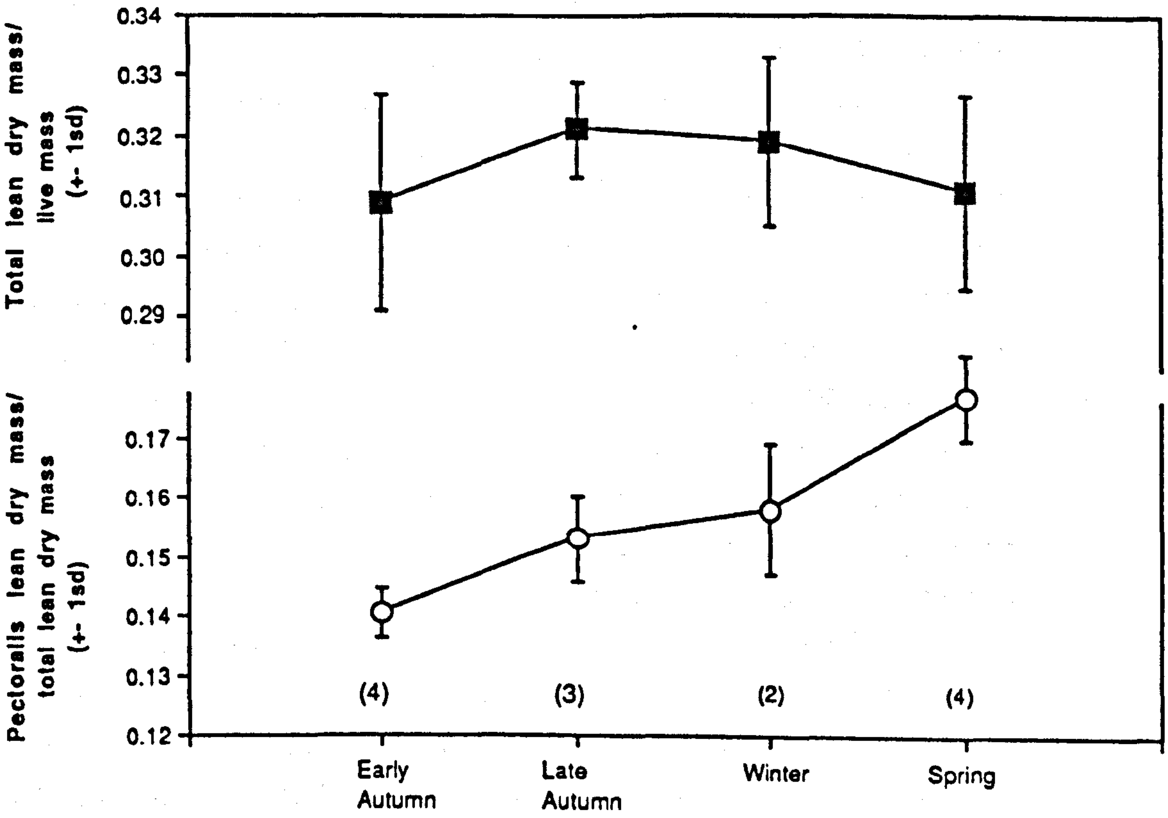


Fig. 8.6 Variation in pectoralis lean dry mass as a proportion of total lean dry mass with season in the Dipper. (sample sizes in parentheses)

during the same time period. Water and ash indices showed no seasonal trend but the latter were consistently higher in the males ($p<0.001$, t-test) indicating a larger, or denser, skeleton per unit mass.

8.3.4. Distribution and Variation of Lipid Mass

8.3.4.1. Canaries

Tables 8.5-8.8 summarise dry masses, lean dry masses and lipid indices of Canaries for dissected components. Breakdowns are given for all birds combined and various sub-groupings based on the circumstances of death. Tracheal lipid was not analysed as a separate component as it tended to come away with the skin and contour feathers or remain on the neck when the birds were dissected. As the sample of Canaries was very heterogeneous in body size, comparisons between lipid indices are most useful. In the "healthy" birds 86.4% of total lipid mass was in the body shell, skin and contour feathers, head, neck, wings and legs with most located in the former two (59.5%). These six components accounted for 84.8% of total lipid in the "naturally dying" birds although only 45.6% was in the body shell and skin and contour feathers. Most of this lipid was subcutaneous and would be readily mobilisable as an energy source. Birds dying from starvation had almost totally depleted their lipid stores, though of what little remained, 75.0% was in the above six components including 42.7% in body shell and skin and contour feathers. Thus, it appears probable that lipid is drawn evenly from depots around the body in times of severe nutritional stress. Only two other components held significant amounts of lipid, the intestine and liver; some of the former may have been in undigested food. The pectoralis muscles were characterised by exceedingly low lipid indices, though they were slightly higher in the healthy birds. Most of this lipid is presumably structural and is not usually mobilisable as an energy source.

Table 8.5. Dry masses, lean dry masses and lipid indices of Canary body components. (Mean values ± standard deviation, n = 7)

	Dry mass (g)	Lean dry mass mass (g)	Lipid index
Body shell	1.236 ± 0.636	0.852 ± 0.257	0.385 ± 0.347
Skin & contour feathers	2.402 ± 1.044	1.867 ± 0.544	0.256 ± 0.285
Flight feathers	0.320 ± 0.035	0.318 ± 0.034	0.005 ± 0.007
Tail feathers	0.117 ± 0.022	0.113 ± 0.021	0.006 ± 0.007
Head	0.729 ± 0.133	0.593 ± 0.081	0.223 ± 0.085
Neck	0.262 ± 0.136	0.178 ± 0.049	0.415 ± 0.469
Wings	0.625 ± 0.226	0.505 ± 0.148	0.218 ± 0.146
Legs	0.726 ± 0.259	0.606 ± 0.153	0.233 ± 0.151
Pectoralis major (right)	0.335 ± 0.174	0.311 ± 0.156	0.070 ± 0.034
Pectoralis minor (right)	0.044 ± 0.021	0.041 ± 0.019	0.062 ± 0.032
Pectoralis major (left)	0.347 ± 0.180	0.322 ± 0.162	0.072 ± 0.035
Pectoralis minor (left)	0.047 ± 0.020	0.044 ± 0.018	0.057 ± 0.033
Gizzard & oesophagus	0.441 ± 0.162	0.384 ± 0.114	0.130 ± 0.135
Intestine	0.345 ± 0.136	0.263 ± 0.094	0.307 ± 0.296
Heart	0.088 ± 0.027	0.079 ± 0.025	0.124 ± 0.075
Lungs	0.083 ± 0.031	0.075 ± 0.028	0.100 ± 0.083
Liver	0.141 ± 0.092	0.124 ± 0.081	0.168 ± 0.085
Kidney	0.073 ± 0.059	0.066 ± 0.055	0.136 ± 0.070
Gonads	0.010 ± 0.013	0.009 ± 0.012	0.103 ± 0.164

Table 8.6. Dry masses, lean dry masses and lipid indices of Canaries taken in relatively healthy condition, broken down by dissected body components. (Mean values ± standard deviation, n=3)

	Dry mass (g)	Lean dry mass(g)	Lipid index
Body shell	1.671 ± 0.768	0.972 ± 0.322	0.659 ± 0.387
Skin & contour feathers	2.919 ± 1.288	1.950 ± 0.509	0.452 ± 0.367
Flight feathers	0.307 ± 0.029	0.306 ± 0.031	0.003 ± 0.006
Tail feathers	0.107 ± 0.012	0.106 ± 0.011	0.002 ± 0.003
Head	0.800 ± 0.121	0.624 ± 0.084	0.281 ± 0.077
Neck	0.350 ± 0.168	0.197 ± 0.058	0.731 ± 0.608
Wings	0.784 ± 0.225	0.599 ± 0.172	0.307 ± 0.026
Legs	0.904 ± 0.258	0.662 ± 0.154	0.351 ± 0.089
Pectoralis major (right)	0.461 ± 0.181	0.420 ± 0.165	0.097 ± 0.024
Pectoralis minor (right)	0.057 ± 0.024	0.052 ± 0.022	0.083 ± 0.024
Pectoralis major (left)	0.475 ± 0.187	0.433 ± 0.170	0.094 ± 0.027
Pectoralis minor (left)	0.060 ± 0.016	0.056 ± 0.014	0.078 ± 0.034
Gizzard & oesophagus	0.528 ± 0.173	0.429 ± 0.104	0.216 ± 0.185
Intestine	0.381 ± 0.135	0.254 ± 0.056	0.487 ± 0.418
Heart	0.094 ± 0.001	0.081 ± 0.007	0.171 ± 0.100
Lungs	0.093 ± 0.023	0.083 ± 0.012	0.116 ± 0.116
Liver	0.216 ± 0.075	0.188 ± 0.062	0.147 ± 0.029
Kidney	0.064 ± 0.009	0.057 ± 0.006	0.119 ± 0.030
Gonads	0.019 ± 0.014	0.016 ± 0.014	0.236 ± 0.184

Table 8.7. Dry masses, lean dry masses and lipid indices of naturally dying Canary body components. (Mean values ± standard deviation, n=2).

	Dry mass (g)	Lean dry mass(g)	Lipid index
Body shell	1.143 ± 0.050	0.906 ± 0.060	0.262 ± 0.028
Skin & contour feathers	2.601 ± 0.645	2.248 ± 0.614	0.161 ± 0.030
Flight feathers	0.355 ± 0.019	0.352 ± 0.014	0.009 ± 0.013
Tail feathers	0.139 ± 0.015	0.135 ± 0.021	0.006 ± 0.008
Head	0.774 ± 0.059	0.626 ± 0.032	0.235 ± 0.033
Neck	0.251 ± 0.028	0.194 ± 0.021	0.296 ± 0.008
Wings	0.633 ± 0.004	0.497 ± 0.046	0.281 ± 0.128
Legs	0.846 ± 0.006	0.680 ± 0.044	0.246 ± 0.072
Pectoralis major (right)	0.319 ± 0.014	0.301 ± 0.016	0.060 ± 0.011
Pectoralis minor (right)	0.044 ± 0.003	0.041 ± 0.003	0.066 ± 0.006
Pectoralis major (left)	0.337 ± 0.040	0.316 ± 0.045	0.069 ± 0.024
Pectoralis minor (left)	0.050 ± 0.011	0.047 ± 0.011	0.061 ± 0.022
Gizzard & oesophagus	0.481 ± 0.113	0.422 ± 0.103	0.088 ± 0.001
Intestine	0.436 ± 0.108	0.368 ± 0.085	0.182 ± 0.021
Heart	0.117 ± 0.007	0.106 ± 0.009	0.102 ± 0.026
Lungs	0.106 ± 0.004	0.100 ± 0.009	0.059 ± 0.057
Liver	0.108 ± 0.066	0.097 ± 0.070	0.182 ± 0.174
Kidney	0.122 ± 0.113	0.112 ± 0.106	0.108 ± 0.035
Gonads	<0.001 -	<0.001 -	---

Table 8.8. Dry masses, lean dry masses and lipid indices of Canaries apparently dying of starvation, broken down by dissected body components. (Mean values ± standard deviation, n = 2).

	Dry mass (g)	Lean dry mass(g)	Lipid index
Body shell	0.677 ± 0.188	0.616 ± 0.161	0.097 ± 0.018
Skin & contour feathers	1.428 ± 0.160	1.361 ± 0.241	0.055 ± 0.069
Flight feathers	0.303 ± 0.039	0.302 ± 0.041	0.005 ± 0.006
Tail feathers	0.109 ± 0.031	0.104 ± 0.026	0.011 ± 0.010
Head	0.578 ± 0.090	0.514 ± 0.082	0.124 ± 0.005
Neck	0.141 ± 0.044	0.133 ± 0.043	0.060 ± 0.010
Wings	0.378 ± 0.084	0.371 ± 0.089	0.021 ± 0.018
Legs	0.466 ± 0.143	0.448 ± 0.143	0.042 ± 0.015
Pectoralis major (right)	0.160 ± 0.086	0.156 ± 0.089	0.039 ± 0.040
Pectoralis minor (right)	0.024 ± 0.013	0.024 ± 0.013	0.026 ± 0.033
Pectoralis major (left)	0.165 ± 0.086	0.160 ± 0.089	0.043 ± 0.045
Pectoralis minor (left)	0.024 ± 0.013	0.024 ± 0.013	0.024 ± 0.016
Gizzard & oesophagus	0.270 ± 0.029	0.259 ± 0.030	0.043 ± 0.009
Intestine	0.199 ± 0.017	0.171 ± 0.002	0.162 ± 0.087
Heart	0.052 ± 0.005	0.048 ± 0.006	0.075 ± 0.016
Lungs	0.044 ± 0.015	0.040 ± 0.016	0.116 ± 0.078
Liver	0.063 ± 0.064	0.055 ± 0.058	0.118 ± 0.093
Kidney	0.038 ± 0.021	0.033 ± 0.022	0.189 ± 0.136
Gonads	0.008 ± 0.011	0.007 ± 0.010	0.060 ± 0.084

8.3.4.2. Dippers

Dry masses, lean dry masses and lipid indices of Dipper components are given for several age, sex and seasonal groupings in Tables 8.9-8.13. Male lipid indices for most components were usually lower than for females, a difference probably attributable to the lack of females in the spring sample. The difference for pectoralis muscles was significant ($p<0.05$, t-test). Around 77-78% of total lipid mass was located in the body shell, skin and contour feathers, head, neck, wings and legs in the autumn and winter groupings of both sexes with a further 5.2-5.5% in the tracheal depot. The proportions in the spring sampled males were 71.7% and 4.1% respectively. The mass of lipid in these seven depots fell from a mean of 0.181g to 0.058g in spring. Lipid in body shell and skin and contour feathers comprised 51.8% and 49.5% of total body lipid in autumn/winter females and males respectively and was 34.0% in spring males. A tracheal pit lipid depot was recorded in most birds irrespective of season or sex; two exceptions were the November juvenile male and one of the April adult males. The other spring adult male had only a negligible reserve in this depot. The visible location of lipid during dissection conformed closely with the distribution indicated by Soxhlet extraction: common depots, tracheal aside, were in the sub-alar region at the base of the wing, around the knee joint and along the posterior edge of the sternum. Unfortunately, unlike most other passerines, it is not possible to fat-score live Dippers due to a thick covering of down. The pectoralis muscle water index of spring birds was significantly higher than the autumn/winter sample ($p<0.05$, t-test).

8.3.5. Relationships Between Whole-body and Pectoralis Composition

Tables 8.14-8.15 and 8.16-8.17 give correlation matrices of biometrics, whole-body and pectoralis composition for Canaries and Dippers respectively. The

Table 8.9 Dry masses, lean dry masses and lipid indices of female Dipper body components. (Mean Values ± Standard Deviation, n=6).

	Dry mass (g)	Lean dry mass(g)	Lipid index
Body shell	3.456 ± 0.272	2.778 ± 0.139	0.245 ± 0.094
Skin & contour feathers	5.119 ± 0.823	4.045 ± 0.801	0.281 ± 0.128
Flight feathers	0.465 ± 0.034	0.463 ± 0.035	0.004 ± 0.010
Tail feathers	0.148 ± 0.014	0.146 ± 0.015	0.002 ± 0.005
Head	1.172 ± 0.181	1.023 ± 0.141	0.142 ± 0.031
Neck	0.760 ± 0.073	0.637 ± 0.061	0.198 ± 0.123
Wings	1.448 ± 0.104	1.234 ± 0.072	0.173 ± 0.057
Legs	2.251 ± 0.222	1.935 ± 0.159	0.163 ± 0.044
Pectoralis major (right)	1.148 ± 0.137	1.055 ± 0.115	0.087 ± 0.039
Pectoralis minor (right)	0.184 ± 0.022	0.175 ± 0.019	0.053 ± 0.020
Pectoralis major (left)	1.165 ± 0.140	1.074 ± 0.108	0.083 ± 0.042
Pectoralis minor (left)	0.178 ± 0.020	0.170 ± 0.016	0.047 ± 0.026
Gizzard & oesophagus	0.469 ± 0.091	0.437 ± 0.079	0.072 ± 0.031
Intestine	0.856 ± 0.135	0.726 ± 0.122	0.185 ± 0.125
Heart	0.299 ± 0.083	0.270 ± 0.073	0.106 ± 0.019
Lungs	0.255 ± 0.074	0.234 ± 0.058	0.082 ± 0.039
Liver	0.885 ± 0.132	0.766 ± 0.090	0.153 ± 0.064
Kidney	0.228 ± 0.041	0.203 ± 0.035	0.122 ± 0.039
Gonads	0.014 ± 0.019	0.011 ± 0.014	0.131 ± 0.159
Tracheal fat	0.204 ± 0.078	0.024 ± 0.007	7.626 ± 2.711

Table 8.10. Dry masses, lean dry masses and lipid indices of male Dipper body components. (Mean Value ± Standard Deviation, n=9)

	Dry mass (g)	Lean dry mass(g)	Lipid index
Body shell	4.063 ± 0.369	3.530 ± 0.251	0.155 ± 0.130
Skin & contour feathers	5.034 ± 0.695	4.414 ± 0.419	0.143 ± 0.140
Flight feathers	0.587 ± 0.024	0.585 ± 0.024	0.003 ± 0.006
Tail feathers	0.202 ± 0.011	0.200 ± 0.012	0.001 ± 0.002
Head	1.458 ± 0.053	1.285 ± 0.036	0.135 ± 0.023
Neck	0.856 ± 0.137	0.751 ± 0.075	0.135 ± 0.100
Wings	1.908 ± 0.122	1.692 ± 0.128	0.130 ± 0.059
Legs	2.952 ± 0.164	2.688 ± 0.143	0.099 ± 0.043
Pectoralis major (right)	1.734 ± 0.138	1.634 ± 0.135	0.061 ± 0.012
Pectoralis minor (right)	0.232 ± 0.011	0.223 ± 0.011	0.042 ± 0.010
Pectoralis major (left)	1.748 ± 0.135	1.648 ± 0.131	0.061 ± 0.015
Pectoralis minor (left)	0.232 ± 0.013	0.223 ± 0.011	0.042 ± 0.011
Gizzard & oesophagus	0.525 ± 0.210	0.493 ± 0.194	0.061 ± 0.078
Intestine	0.762 ± 0.325	0.680 ± 0.309	0.156 ± 0.201
Heart	0.439 ± 0.114	0.413 ± 0.101	0.061 ± 0.026
Lungs	0.374 ± 0.114	0.359 ± 0.112	0.048 ± 0.037
Liver	0.922 ± 0.172	0.833 ± 0.136	0.105 ± 0.081
Kidney	0.292 ± 0.039	0.273 ± 0.039	0.068 ± 0.021
Gonads	0.016 ± 0.021	0.015 ± 0.021	0.268 ± 0.378
Tracheal fat	0.147 ± 0.128	0.016 ± 0.015	3.940 ± 3.562

Table 8.11. Dry masses, lean dry masses and lipid indices of female Dippers collected in autumn and winter, broken down by dissected body components. (Mean Value ± Standard Deviation, n=5).

	Dry mass (g)	Lean dry mass(g)	Lipid index
Body shell	3.492 ± 0.288	2.822 ± 0.097	0.238 ± 0.103
Skin & contour feathers	5.403 ± 0.489	4.349 ± 0.335	0.244 ± 0.103
Flight feathers	0.467 ± 0.037	0.465 ± 0.039	0.005 ± 0.011
Tail feathers	0.150 ± 0.014	0.148 ± 0.016	0.002 ± 0.005
Head	1.246 ± 0.009	1.080 ± 0.015	0.153 ± 0.016
Neck	0.751 ± 0.078	0.623 ± 0.057	0.210 ± 0.134
Wings	1.480 ± 0.076	1.251 ± 0.067	0.185 ± 0.055
Legs	2.324 ± 0.147	1.991 ± 0.088	0.167 ± 0.048
Pectoralis major (right)	1.207 ± 0.046	1.103 ± 0.048	0.095 ± 0.041
Pectoralis minor (right)	0.194 ± 0.009	0.183 ± 0.010	0.061 ± 0.012
Pectoralis major (left)	1.221 ± 0.067	1.119 ± 0.047	0.092 ± 0.043
Pectoralis minor (left)	0.186 ± 0.008	0.176 ± 0.006	0.057 ± 0.016
Gizzard & oesophagus	0.494 ± 0.075	0.460 ± 0.061	0.071 ± 0.034
Intestine	0.877 ± 0.139	0.744 ± 0.126	0.185 ± 0.140
Heart	0.314 ± 0.084	0.284 ± 0.072	0.103 ± 0.019
Lungs	0.269 ± 0.073	0.246 ± 0.056	0.086 ± 0.042
Liver	0.926 ± 0.095	0.797 ± 0.054	0.161 ± 0.068
Kidney	0.239 ± 0.035	0.213 ± 0.028	0.119 ± 0.042
Gonads	0.010 ± 0.017	0.008 ± 0.013	0.085 ± 0.125
Tracheal fat	0.213 ± 0.087	0.025 ± 0.007	7.551 ± 3.124

Table 8.12. Dry masses, lean dry masses and lipid indices of male Dippers collected in autumn and winter, broken down by dissected body components. (Mean Value ± Standard Deviation, n = 5).

	Dry mass (g)	Lean dry mass(g)	Lipid index
Body shell	4.210 ± 0.336	3.473 ± 0.297	0.219 ± 0.145
Skin & contour feathers	5.442 ± 0.666	4.490 ± 0.575	0.220 ± 0.144
Flight feathers	0.580 ± 0.027	0.578 ± 0.028	0.004 ± 0.008
Tail feathers	0.203 ± 0.015	0.201 ± 0.017	0.002 ± 0.002
Head	1.457 ± 0.039	1.272 ± 0.017	0.146 ± 0.020
Neck	0.908 ± 0.125	0.759 ± 0.058	0.193 ± 0.093
Wings	1.904 ± 0.145	1.633 ± 0.142	0.168 ± 0.047
Legs	2.968 ± 0.181	2.636 ± 0.156	0.127 ± 0.034
Pectoralis major (right)	1.663 ± 0.103	1.561 ± 0.108	0.066 ± 0.010
Pectoralis minor (right)	0.227 ± 0.006	0.217 ± 0.007	0.045 ± 0.007
Pectoralis major (left)	1.685 ± 0.108	1.577 ± 0.108	0.068 ± 0.011
Pectoralis minor (left)	0.228 ± 0.008	0.218 ± 0.009	0.043 ± 0.009
Gizzard & oesophagus	0.642 ± 0.217	0.592 ± 0.213	0.091 ± 0.098
Intestine	0.833 ± 0.339	0.716 ± 0.342	0.228 ± 0.254
Heart	0.464 ± 0.141	0.432 ± 0.128	0.073 ± 0.024
Lungs	0.375 ± 0.102	0.356 ± 0.094	0.052 ± 0.042
Liver	1.023 ± 0.118	0.892 ± 0.104	0.150 ± 0.083
Kidney	0.312 ± 0.029	0.293 ± 0.030	0.068 ± 0.025
Gonads	0.002 ± 0.003	0.002 ± 0.003	0.383 ± 0.431
Tracheal fat	0.189 ± 0.135	0.015 ± 0.016	5.418 ± 3.856

Table 8.13. Dry masses, lean dry masses and lipid indices of male Dippers collected in spring, broken down by dissected body components. (Mean Value ± Standard Deviation, n = 4).

	Dry mass (g)	Lean dry mass(g)	Lipid index
Body shell	3.879 ± 0.362	3.602 ± 0.195	0.075 ± 0.041
Skin & contour feathers	4.524 ± 0.272	4.320 ± 0.083	0.047 ± 0.050
Flight feathers	0.594 ± 0.019	0.594 ± 0.018	0.001 ± 0.003
Tail feathers	0.200 ± 0.003	0.200 ± 0.003	<0.001 ± 0.001
Head	1.460 ± 0.074	1.302 ± 0.049	0.121 ± 0.021
Neck	0.792 ± 0.138	0.742 ± 0.102	0.062 ± 0.050
Wings	1.913 ± 0.107	1.765 ± 0.063	0.083 ± 0.035
Legs	2.932 ± 0.165	2.754 ± 0.109	0.065 ± 0.024
Pectoralis major (right)	1.828 ± 0.132	1.731 ± 0.112	0.056 ± 0.013
Pectoralis minor (right)	0.239 ± 0.013	0.230 ± 0.012	0.037 ± 0.013
Pectoralis major (left)	1.833 ± 0.134	1.743 ± 0.104	0.051 ± 0.016
Pectoralis minor (left)	0.238 ± 0.018	0.229 ± 0.013	0.040 ± 0.016
Gizzard & oesophagus	0.378 ± 0.057	0.369 ± 0.053	0.025 ± 0.013
Intestine	0.674 ± 0.329	0.635 ± 0.307	0.064 ± 0.035
Heart	0.407 ± 0.077	0.389 ± 0.065	0.045 ± 0.021
Lungs	0.374 ± 0.145	0.362 ± 0.148	0.043 ± 0.036
Liver	0.797 ± 0.150	0.761 ± 0.149	0.050 ± 0.026
Kidney	0.265 ± 0.037	0.249 ± 0.038	0.068 ± 0.017
Gonads	0.044 ± 0.003	0.043 ± 0.003	0.039 ± 0.002
Tracheal fat	0.076 ± 0.094	0.017 ± 0.016	2.956 ± 2.304

Table 8.14. Correlation matrix of Canary biometrics and whole-body composition (n=7).

	Wing	Keel	Tarsus	Head + bill	Keel diss	SMV	TWM	TDM	TWC	TLDM	TLiM	TALDM	TAM	TLiI	TWI	TAI
Live mass (g)	0.598 ns	0.872 **	0.898 **	0.824 *	0.836 *	0.902 **	0.999 ***	0.994 ***	0.997 ***	0.966 ***	0.882 **	0.963 ***	0.750 *	0.825 *	0.822 *	-0.683 *
Wing length (mm)	--	0.533 ns	0.821 *	0.766 *	0.497 ns	0.709 *	0.593 ns	0.555 ns	0.619 ns	0.751 *	0.256 ns	0.752 *	0.542 ns	0.166 ns	0.090 ns	-0.576 ns
Keel length (mm)		--	0.842 **	0.885 **	0.972 ***	0.917 **	0.869 **	0.833 *	0.892 **	0.873 **	0.669 ns	0.844 **	0.935 **	0.583 ns	0.749 *	-0.381 ns
Tarsus (mm)			--	0.931 **	0.856 **	0.978 ***	0.890 **	0.858 **	0.909 **	0.972 ***	0.606 ns	0.967 ***	0.772 *	0.518 ns	0.516 ns	-0.665 ns
Head & bill length (mm)				--	0.892 **	0.938 **	0.817 *	0.767 *	0.852 **	0.893 **	0.516 ns	0.866 **	0.928 **	0.404 ns	0.536 ns	-0.372 ns
Dissected keel length (mm) **					--	0.941 **	0.828 *	0.792 *	0.852 **	0.847 **	0.616 ns	0.818 *	0.916 **	0.582 ns	0.686 *	-0.341 ns
Standard muscle volume (SMV)						--	0.894 **	0.858 **	0.916 **	0.957 ***	0.623 ns	0.945 **	0.840 **	0.534 ns	0.595 ns	-0.580 ns
Total wet mass (g) (TWM)							--	0.995 ***	0.997 ***	0.962 ***	0.888 **	0.959 ***	0.747 *	0.832 *	0.829 *	-0.682 *
Total dry mass (g) (TDM)								--	0.985 ***	0.939 **	0.923 **	0.939 **	0.695 *	0.877 **	0.844 **	-0.697 *
Total water (g) content (TWC)									--	0.975 ***	0.854 **	0.969 ***	0.783 *	0.790 *	0.812 *	-0.666 ns
Total lean dry mass (g) (TLDM)										--	0.735 *	0.998 ***	0.766 *	0.661 ns	0.663 ns	-0.725 *
Total lipid mass (g) (TLiM)											--	0.738 *	0.515 ns	0.992 ***	0.923 **	-0.564 ns
Total ash-free lean dry mass (TALDM) (g)												--	0.723 *	0.669 ns	0.647 ns	-0.767 *
Total ash mass (g) (TAM)													--	0.406 ns	0.650 ns	-0.124 ns
Total lipid index (TLiI)														--	0.901 **	-0.567 ns
Total water index (TWI)															--	-0.329 ns

NOTE: Values are Pearson Correlation Coefficients; ns = not significant; * = p < 0.05; ** = p < 0.01; *** = p < 0.001; ** Keel length after dissection.

Table 8.15. Correlation matrix of Canary pectoralis muscle composition and some whole-body parameters (n=7).

	PDM	PWC	PLDM	PLiM	PALDM	PAM	PLiI	PWI	PAI	TWM	TDM	TLDM	Keel	SMV	TLiI
Pectoralis wet mass (g)	0.998 ***	1.000 ***	0.998 ***	0.877 **	0.997 ***	0.774 *	0.493 ns	-0.419 ns	-0.623 ns	0.958 ***	0.951 **	0.909 **	0.841 **	0.797 *	0.801 *
Pectoralis dry mass (g) (PDM)	--	0.996 ***	0.998 ***	0.894 **	0.999 ***	0.746 *	0.531 ns	-0.457 ns	-0.654 ns	0.967 ***	0.962 ***	0.921 **	0.838 **	0.810 *	0.813 *
Pectoralis water content (g) (PWC)		--	0.997 ***	0.869 **	0.996 ***	0.784 *	0.477 ns	-0.403 ns	-0.610 ns	0.953 ***	0.945 **	0.903 **	0.842 **	0.791 *	0.796 *
Pectoralis lean dry mass(g)(PLDM)			--	0.867 **	1.000 ***	0.763 *	0.484 ns	-0.465 ns	-0.646 ns	0.962 ***	0.952 ***	0.927 **	0.849 **	0.820 *	0.780 *
Pectoralis lipid mass (g) (PLiM)				--	0.873 **	0.528 ns	0.833 *	-0.343 ns	-0.640 ns	0.893 **	0.930 **	0.766 *	0.655 ns	0.638 ns	0.969 ***
Pectoralis ash-free lean dry mass (g) (PALDM)					--	0.743 *	0.501 ns	-0.477 ns	-0.667 ns	0.964 ***	0.956 ***	0.931 **	0.839 **	0.819 *	0.786 *
Pectoralis ash mass (g) (PAM)						--	0.004 ns	-0.089 ns	-0.043 ns	0.674 *	0.637 ns	0.626 ns	0.856 **	0.637 ns	0.469 ns
Pectoralis lipid index (PLiI)							--	-0.242 ns	-0.598 ns	0.557 ns	0.632 ns	0.415 ns	0.179 ns	0.267 ns	0.828 *
Pectoralis water index (PWI)								--	0.783 *	-0.522 ns	-0.500 ns	-0.677 *	-0.508 ns	-0.690 *	-0.193 ns
Pectoralis ash index (PAI)									--	-0.679 *	-0.691 *	-0.722 *	-0.393 ns	-0.571 ns	-0.560 ns

NOTE: Values are Pearson correlation coefficients; ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Table 8.16. Correlation matrix of Dipper biometrics and whole-body composition (adults and juveniles, n=15).

	Wing	Keel	Tarsus	Head+ Bill	Keel Diss	SMV	TWM	TDM	TWC	TLDM	TLiM	TALDM	TAM	TLiI	TWI	TAI
Live mass (g)	0.786 ***	0.827 ***	0.802 ***	0.894 ***	0.880 ***	0.927 ***	0.981 ***	0.820 ***	0.951 ***	0.897 ***	-0.134 ns	0.880 ***	0.921 ***	-0.387 ns	0.232 ns	0.820 ***
Wing length (mm)	--	0.839 ***	0.703 **	0.632 *	0.826 ***	0.752 **	0.742 **	0.603 **	0.727 **	0.738 **	-0.258 ns	0.705 **	0.836 ***	-0.450 *	0.106 ns	0.855 ***
Keel length (mm)		--	0.893 ***	0.808 ***	0.920 ***	0.865 ***	0.809 ***	0.743 **	0.753 **	0.806 ***	-0.110 ns	0.779 ***	0.876 ***	-0.354 ns	0.066 ns	0.848 ***
Tarsus (mm)			--	0.820 ***	0.928 ***	0.915 ***	0.763 **	0.778 **	0.675 **	0.911 ***	-0.248 ns	0.898 ***	0.915 ***	-0.503 *	-0.199 ns	0.776 ***
Head & bill length (mm)				--	0.894 ***	0.926 ***	0.910 ***	0.903 ***	0.867 ***	0.887 ***	0.006 ns	0.886 ***	0.847 ***	-0.283 ns	0.116 ns	0.671 **
Dissected keel length (g)					--	0.962 ***	0.850 ***	0.839 ***	0.815 **	0.929 ***	-0.246 ns	0.917 ***	0.939 ***	-0.547 *	-0.219 ns	0.836 ns
Standard muscle volume (SMV)						--	0.890 ***	0.814 **	0.884 ***	0.956 ***	-0.368 ns	0.950 ***	0.941 ***	-0.652 *	-0.088 ns	0.805 **
Total wet mass (g) (TWM)							--	0.837 ***	0.968 ***	0.872 ***	-0.050 ns	0.862 ***	0.872 ***	-0.311 ns	0.293 ns	0.740 **
Total dry mass (g) (TDM)								--	0.674 **	0.879 ***	0.269 ns	0.878 ***	0.841 ***	-0.022 ns	-0.174 ns	0.640 **
Total water (g) content (TWC)									--	0.777 ***	-0.191 ns	0.763 ***	0.794 ***	-0.410 ns	0.476 *	0.707 **
Total lean dry mass (g) (TLDM)										--	-0.223 ns	0.998 ***	0.961 ***	-0.495 *	-0.182 ns	0.744 **
Total lipid (g) mass (TLiM)											--	-0.221 ns	-0.221 ns	0.954 ***	0.012 ns	-0.194 ns
Total ash-free lean dry mass (g) (TALDM)												--	0.939 ***	-0.492 *	-0.201 ns	0.696 **
Total ash mass (g) (TAM)													--	-0.482 *	-0.098 ns	0.899 ***
Total lipid index (TLiI)														--	0.046 ns	-0.393 ns
Total water index (TWI)															--	0.072 ns

NOTE: Values are Pearson correlation coefficients; ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Table 8.17. Correlation matrix of Dipper pectoralis muscle composition and some whole-body parameters (n=15).

	PDM	PWC	PLDM	PLiM	PALDM	PAM	PLiI	PWI	PAI	TWM	TDM	TLDM	Keel	SMV	TLiI
Pectoralis wet mass (g)	0.978 ***	0.996 ***	0.980 ***	0.312 ns	0.981 ***	0.910 ***	-0.364 ns	0.169 ns	0.692 **	0.930 ***	0.745 **	0.893 ***	0.846 ***	0.923 ***	-0.511 *
Pectoralis dry mass (g) (PDM)	--	0.956 ***	0.996 ***	0.388 ns	0.996 ***	0.939 ***	-0.298 ns	-0.026 ns	0.732 **	0.886 ***	0.756 **	0.858 ***	0.880 ***	0.918 ***	-0.416 ns
Pectoralis water content (g) (PWC)		--	0.961 ***	0.277 ns	0.963 ***	0.886 ***	-0.386 ns	0.247 ns	0.667 **	0.936 ***	0.731 **	0.896 ***	0.821 ***	0.918 ***	-0.543 *
Pectoralis lean dry mass(g)(PLDM)			--	0.306 ns	0.999 ***	0.945 ***	-0.378 ns	-0.023 ns	0.744 **	0.880 ***	0.747 **	0.859 ***	0.865 ***	0.904 ***	-0.430 ns
Pectoralis lipid mass (g) (PLiM)				--	0.309 ns	0.258 ns	0.740 **	-0.034 ns	0.121 ns	0.370 ns	0.350 ns	0.288 ns	0.459 *	0.379 ns	0.011 ns
Pectoralis ash-free lean dry mass (g) (PALDM)					--	0.933 ***	-0.373 ns	-0.013 ns	0.720 **	0.878 ***	0.741 **	0.856 ***	0.856 ***	0.900 ***	-0.434 ns
Pectoralis ash mass (g) (PAM)						--	-0.408 ns	-0.120 ns	0.918 ***	0.839 ***	0.757 **	0.836 ***	0.899 ***	0.878 ***	-0.369 ns
Pectoralis lipid index (PLiI)							--	-0.024 ns	-0.426 ns	-0.257 ns	-0.159 ns	-0.281 ns	-0.138 ns	-0.219 ns	0.269 ns
Pectoralis water index (PWI)								--	-0.238 ns	0.316 ns	0.044 ns	0.216 ns	-0.023 ns	0.444 ns	-0.404 ns
Pectoralis ash index (PAI)									--	0.646 **	0.629 **	0.679 **	0.689 **	0.696 **	-0.274 ns

Note: Values are Pearson Correlation Coefficients; ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Canaries represent a sample of passerines varying little in structural size but markedly in mass and "condition" whereas the Dippers show more body size and structural variation, partly due to their sexual size dimorphism and were all presumably healthy (in good "condition") at the time of death. Most body size parameters correlate positively and significantly with whole body composition in both Canaries and Dippers (Tables 8.14, 8.16) but in the former case some coefficients may be misleading in that the largest birds in the sample fell into the "healthy" category and the smallest into the "starved to death" category. However, few whole-body composition or body size measures correlate closely with the lipid, water or ash indices. Notable exceptions were the ash indices of the Dipper (noted above) and the expected relationship between lipid index and total lipid mass. The significant negative correlations between lipid index and some biometrics (wing length, tarsus and dissected keel length) in the Dipper were probably due to the lack of small birds, specifically females, in the spring sample when lipid indices of males were very low.

Total lean dry mass of both Dippers and Canaries gave significant and positive correlations with most body size parameters including live and wet mass. However, lipid mass showed no relationship with any body mass measures in the Dipper though it gave significant correlations with live, wet, dry and lean dry mass in the Canary. Short term variation in body mass may thus represent parallel changes in lipid stores in healthy Canaries but not in the Dipper.

On the whole, pectoralis compositional indices showed little relationship to whole body masses, keel length, standard muscle volume and total lipid index (Tables 8.15 and 8.17). Pectoralis wet, dry and lean dry masses all correlated positively and significantly ($p<0.01$) with total wet, dry and lean dry masses, keel length and standard muscle volume (Dipper only). Consequently, accurate measurement of pectoralis muscle thickness in the field may enable the potential protein reserves of a bird to be estimated in relation to body size.

Pectoralis ash indices of starved Canaries were significantly higher than those of both healthy birds ($p<0.001$, t-test) and naturally dying birds ($p<0.01$, t-test), indicating considerable net catabolism of lean material (protein) prior to death. In Dippers, pectoralis ash indices of the male sample were higher than those of the females ($p<0.001$, t-test).

8.3.6. Derivation of Pectoralis Protein Reserve Indices

Jones (1987) used "pectoralis lean dry mass deviation" (PLDMD) to assess whether potential protein reserves of Sand Martins *Riparia riparia* were above or below that expected for an individual of a specific size (keel length). In this study, PLDMD was not computed for Canaries as there were too few healthy birds to derive a reliable regression equation describing the relationship between pectoralis lean dry mass and keel length. However, several other indices have been generated using combinations of carcass analysis data, dissected skeletal measures and pectoralis thicknesses derived from ultrasound measurements:

1. Standard Muscle Index (SMI) is the total lean dry mass of the pectoralis (PLDM) expressed as a proportion of standard muscle volume.

$$\mathrm{SMI} = \frac{\mathrm{PLDM}}{2\mathrm{SMV}} \times 1000$$

2. Ultrasound Volume (USVOL) is an absolute measure (not adjusted for body size) of pectoralis muscle tissue present.

$$\mathrm{USVOL} = \frac{(R1 + R2 + R3 + L1 + L2 + L3)}{1000} \times \text{keel length}$$

[where R1 = ultrasound thickness (mm) measurement, anterior right side of bird etc.]

3. Ultrasound Index 1 (USI1) is the sum of six pectoralis thickness measurements expressed as a proportion of standard muscle volume.

$$USI1 = \frac{(R1 + R2 + R3 + L1 + L2 + L3)}{2 \times SMV} \times 100$$

4. Ultrasound Index 2 (USI2) is a measure of pectoralis muscle tissue present per unit length of keel.

$$USI2 = \frac{(R1 + R2 + R3 + L1 + L2 + L3)}{\text{keel length}}$$

5. Ultrasound Index 3 (USI3) expresses USVOL as a proportion of standard muscle volume.

$$USI3 = \frac{(R1 + R2 + R3 + L1 + L2 + L3)}{2 \times SMV} \times 10(\text{keel length})$$

In the above equations, all multiplicands and divisors in base 10 (i.e. 10, 100, 1000) are used to ensure indices fall within the range 0-10 for ease of comparison. Also, SMV was computed for a single side of the keel only; thus 2 x SMV is used to equate with ultrasound measurements taken for both sides of the keel.

Additionally, USVOL and USI2 were computed using the sum of the anterior four ultrasound thicknesses only (R1 + R2 + L1 + L2) as the instrument showed less reliability at thicknesses of less than 4mm. These are given as USVOLAnt and USI2Ant below and in tables. Four size-adjusted masses were also calculated from standard biometrics:

6. SIZE1 = Live mass / Wing length
7. SIZE2 = Live mass / Keel length
8. SIZE3 = Live mass / Head and bill length
9. SIZE4 = Maximum recorded live mass / Keel length (Canaries only)

8.3.6.1. Canaries

The computed values for each of these indices are given for individual Canaries in Table 8.18 and correlation coefficients between them and pectoralis and whole-body masses in Table 8.19 and lastly between the indices themselves in Table 8.20.

Duplicate indices (USVOLAnt and USI2Ant) derived from the anterior four ultrasound thicknesses in Canaries did not improve correlations with the pectoralis and whole-body masses listed in Table 8.19 compared with those using all six measurements. Thus, the latter combination was used in computing all indices involving ultrasound in Table 8.18.

The Canaries comprised a cross-section of birds in very different condition and most of the above indices were highest in the healthy birds, lowest in those that had died from starvation and intermediate in the natural deaths (Table 8.18). Bird number 5, as noted previously, was the main anomaly to this pattern. She appeared to be losing condition according to the SMI and USI2 but was apparently healthy if USI1 and USI3 were considered. Both deductions were in part consistent as she had lost some of her pectoralis protein reserve a month before she was killed but then her condition remained stable until death. "Traditional" size-adjusted masses SIZE1 to SIZE4 gave positive correlations with most pectoralis condition indices (Table 8.20). However the scores themselves tended to reflect differences in body mass only as

Table 8.18. Pectoralis condition and body size indices for Canaries.

Bird No.	Size	Sex	Mode of death	Visual pectoral condition	SMI	USVOL	USI1	USI2	USI3	SIZE1	SIZE2	SIZE3	SIZE4
1	L	(?M)	H,T	4	0.34	0.62	0.90	1.28	1.98	0.36	1.35	1.04	1.64
3	L	M	H,T	4	0.37	0.65	0.86	1.30	1.93	0.30	1.29	0.96	1.37
5	S	F	?H,T	2	0.26	0.37	0.95	1.07	1.77	0.18	0.82	0.58	1.03
7	M	F	ND	3	0.27	0.40	0.70	1.00	1.40	0.26	1.11	0.78	1.40
4	M	(?)	ND	2	0.20	0.34	0.49	0.77	1.02	0.25	1.08	0.78	1.23
2	M	(?)	St	1	0.19	0.30	0.55	0.68	1.16	0.20	0.76	0.57	1.18
6	S	(?F)	St	1	0.12	0.17	0.55	0.58	0.95	0.14	0.64	0.41	1.01

KEY: Size: L = large, M = medium, S = small.
Sex: M = male, F = female.
Mode of death: H = healthy, T = taken, ND = natural death, St = starvation/disease.

Note: Indices defined and other abbreviations are given in text.

Table 8.19. Correlation matrix for Canaries: indices of body size, pectoralis ultrasound condition and body composition (n=7).

	Live mass	TWM	TDM	TLDM	TLiM	TLiI	Dipper SMV	Wader SMV	PWM	PDM	PLDM	PLiM	PLiI	SIZE 1	SIZE 2	SIZE 3
SIZE1 (= Live mass/wing)			0.982 ***	0.901 **	0.929 **				0.914 **	0.922 **	0.910 **	0.902 **				
SIZE2 (= Live mass/keel)			0.990 ***	0.959 ***	0.882 **				0.936 **	0.948 **	0.941 **	0.891 **				
SIZE3 (= Live mass/head+bill)			0.997 ***	0.951 **	0.903 **				0.945 **	0.956 ***	0.948 **	0.905 **				
SIZE4 (= Max. live mass/keel)			0.900 **	0.802 *	0.878 **				0.820 *	0.817 *	0.807 *	0.798 *				
FMRL (Sum of anterior ultrasound thicknesses	0.885 **	0.895 **	0.903 **	0.813 *	0.872 **	0.841 **	0.719 *	0.657 n.s.	0.967 ***	0.967 ***	0.960 ***	0.902 **	0.579 n.s.	0.867 **	0.880 **	0.893 **
TOTRL (Sum of 6 ultrasound thicknesses	0.889 **	0.898 **	0.908 **	0.818 *	0.877 **	0.847 **	0.711 *	0.656 n.s.	0.967 ***	0.967 ***	0.960 ***	0.908 **	0.595 n.s.	0.871 **	0.888 **	0.898 **
USVOLAnt (See text)	0.920 **	0.928 **	0.931 **	0.851 **	0.885 **	0.842 **	0.791 *	0.724 *	0.987 ***	0.985 ***	0.980 ***	0.907 **	0.548 n.s.	0.899 **	0.901 **	0.921 **
USI2Ant (See text)	0.800 *	0.811 *	0.829 *	0.725 *	0.824 *	0.813 *	0.580 n.s.	0.527 n.s.	0.904 **	0.905 **	0.896 **	0.867 **	0.613 n.s.	0.786 *	0.814 *	0.817 *
USVOL (See text)	0.925 **	0.932 **	0.936 **	0.855 **	0.891 **	0.849 **	0.785 *	0.724 *	0.988 ***	0.987 ***	0.982 ***	0.913 **	0.563 n.s.	0.903 **	0.910 **	0.926 **
USI2 (See text)	0.803 *	0.814 *	0.833 *	0.728 *	0.828 *	0.819 *	0.571 n.s.	0.526 n.s.	0.902 **	0.904 **	0.894 **	0.871 **	0.629 n.s.	0.789 *	0.821 *	0.821 *

Values are Pearson Correlation Coefficients; n.s. = not significant; * = p<0.05; ** = p<0.01; *** = p<0.001.

Table 8.20. Correlation matrix of Canary pectoralis ultrasound condition and body size indices, (n=7).

	USVOL	USI1	USI2	USI3	SIZE1	SIZE2	SIZE3	SIZE4
SMI	0.976 ***	0.798 *	0.979 ***	0.933 **	0.830 *	0.856 **	0.864 **	0.725 *
USVOL	--	0.704 *	0.943 **	0.884 **	0.903 **	0.910 **	0.926 **	0.800 *
USI1		--	0.879 **	0.950 **	0.451 ns	0.463 ns	0.469 ns	0.353 ns
USI2			--	0.966 ***	0.789 *	0.821 *	0.821 *	0.679 *
USI3				--	0.677 *	0.674 *	0.692 *	0.573 ns
SIZE1					--	0.970 ***	0.987 ***	0.960 ***
SIZE2						--	0.993 ***	0.896 **
SIZE3							--	0.914 **

NOTE: Values are Pearson Correlation Coefficients; ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Index abbreviations given in text.

there was relatively little variation in wing, keel and head and bill lengths amongst the sample.

Data from carcass analysis demonstrates that as Canaries lost condition, the pectoralis protein reserve was drawn on heavily (Table 8.21). Pectoralis lean dry mass expressed as a proportion of total lean dry mass in starved birds was considerably lower than in healthy birds whereas the proportion of lean dry mass in wings and legs combined remained more or less constant.

Table 8.22 shows significant differences between the pectoralis condition indices of healthy Canaries tested against the two dying cohorts.

8.3.6.2. Dippers

Pectoralis condition and body-size indices of 15 Dippers are given in Table 8.23. Correlations between ultrasound indices computed using the anterior four thicknesses and the complete suite of six are given in Table 8.24. The index USVOL gives slightly higher correlations with pectoralis masses than USVOLAnt and thus the six measurements are used in the calculation of all indices in Table 8.23. Size-adjusted masses did not vary between seasons; for example the means of the SIZE1 index for autumn, winter and spring males were 0.72, 0.73 and 0.73 respectively. SIZE1 and SIZE3 showed a similar constancy. Although these indices correlate well amongst themselves (Table 8.25) there are too few significant correlations with pectoralis condition indices (assessed from ultrasound) for them to be used as reliable indicators of potential protein reserves.

The five pectoralis condition indices appear to fall into two groupings. USI1 and USI3 were highest in mid winter and spring, lowest in late autumn and intermediate in early autumn. This may be interpreted as a slight loss of condition (pectoralis protein reserve utilisation) from late summer through to the

Table 8.21. Proportions of whole-body lean dry mass held in pectoralis muscles and wings/legs in Canaries.

	Healthy birds (n = 3)	Naturally dying birds (n = 2)	Starved birds^{++} (n = 2)
Total lean dry mass/live mass	30.31%	33.71%	35.65%
Pectoralis lean dry mass/total lean dry mass	12.84%	9.31%	7.54%
Wings and legs lean dry mass/ total lean dry mass	16.84%	15.55%	16.96%

Table 8.22. Significant differences in pectoralis condition indices of canaries dying in different circumstances.

	Naturally dying birds (n=2)	Starved birds^{++} (n=2)	Both dying groups (n=4)
Healthy (n= 3)	USI1 * USI2 *	SMI * USI1 ** USI3 **	SMI * USVOL * USI1 ** USI3 ***
Naturally dying birds (n=2)	------------	Not significant	(No test)

Note: $^{++}$ includes both starved and diseased birds; USI2 and SIZE1 to 4 not entered as variables; * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, all t-tests.

Table 8.23. Pectoralis condition and body size indices for Dippers.

Bird No.	Age	Sex	Month	PLDMD	SMI	USVOL	USI1	USI2	USI3	SIZE1	SIZE2	SIZE3
19	Fl	F	July	0.95	0.50	0.84	0.78	1.21	2.07	0.57	1.94	1.20
21	Juv	F	Sept	0.86	--	--	--	--	--	0.68	2.13	--
12	Juv	F	Sept	1.08	0.47	0.91	0.62	1.24	1.68	0.68	2.15	1.27
13	Juv	F	Sept	0.86	0.46	0.92	0.58	1.09	1.68	0.65	2.01	1.27
14	Juv	F	Sept	0.89	0.48	0.87	0.57	1.06	1.64	0.60	1.95	1.24
15	Juv	M	Oct	1.05	0.51	1.06	0.48	1.12	1.47	0.77	2.45	1.57
16	Juv	M	Oct	0.94	0.49	1.09	0.52	1.13	1.61	0.72	2.26	1.46
17	Juv	M	Nov	0.94	0.48	1.07	0.48	1.08	1.50	0.68	2.04	1.35
22	Juv	M	Dec	1.09	--	--	--	--	--	0.74	2.27	1.49
9	Juv	F	Dec	1.01	0.56	0.95	0.69	1.20	1.94	0.66	2.07	1.27
8	Ad	M	Dec	0.89	0.57	1.21	0.53	1.06	1.78	0.72	2.11	1.50
23	Ad	M	Mar	0.96	--	--	--	--	--	0.71	2.20	--
10	Ad	M	Apr	1.14	0.61	1.27	0.62	1.33	1.92	0.73	2.20	1.46
11	Ad	M	Apr	1.13	0.59	1.13	0.60	1.26	1.81	0.67	2.22	1.44
18	Juv	M	Apr	1.14	0.55	1.18	0.51	1.21	1.60	0.79	2.47	1.59

Note: Indices are defined and abbreviations are given in text.

Abbreviations: Fl = fledgling, Juv = juvenile, Ad = adult, M = male, F = female.

Table 8.24. Correlation matrix for Dippers including body size and ultrasound condition indices.

	Live Mass	TWM	TDM	TLDM	TLiM	TLI	Dipper SMV	Wader SMV	PWM	PDM	PLDM	PLM	PLI	SIZE1	SIZE2	SIZE3
SIZE1 (n=15)			0.801 ***	0.838 ***	-0.056 ns				0.893 ***	0.835 ***	0.842 ***	0.223 ns				
SIZE2 (n=15)			0.668 **	0.737 **	-0.124 ns				0.788 ***	0.694 **	0.708 **	0.093 ns				
SIZE3 (n=13)			0.850 ***	0.893 ***	-0.117 ns				0.947 ***	0.914 ***	0.923 ***	0.120 ns				
FMRL (n=11)	0.730 **	0.705 **	0.496 ns	0.677 *	-0.333 ns	-0.440 ns	0.541 *	0.607 *	0.854 ***	0.816 **	0.845 ***	-0.316 ns	-0.741 **	0.742 **	0.632 *	0.745 **
TOTRL (n=11)	0.643 *	0.608 *	0.361 ns	0.643 *	-0.504 ns	-0.590 *	0.477 ns	0.556 *	0.838 **	0.811 **	0.847 **	-0.386 ns	-0.755 **	0.654 *	0.560 *	0.682 *
USVOLAnt (n=11)	0.836 **	0.800 **	0.688 *	0.840 **	-0.287 ns	-0.456 ns	0.768 **	0.785 **	0.924 ***	0.936 ***	0.946 ***	-0.130 ns	-0.644 *	0.761 **	0.561 *	0.840 **
USI2Ant (n=11)	0.238 ns	0.246 ns	-0.038 ns	0.108 ns	-0.255 ns	-0.212 ns	-0.083 ns	0.035 ns	0.372 ns	0.263 ns	0.315 ns	-0.526 *	-0.617 *	0.504 ns	0.487 ns	0.265 ns
USVOL (n=11)	0.788 **	0.745 **	0.607 *	0.828 **	-0.405 ns	-0.561 *	0.734 **	0.759 **	0.927 ***	0.947 ***	0.963 ***	-0.180 ns	-0.663 *	0.709 **	0.516 ns	0.809 **
USI2 (n=11)	0.131 ns	0.127 ns	-0.185 ns	0.067 ns	-0.436 ns	-0.373 ns	-0.144 ns	-0.018 ns	0.334 ns	0.243 ns	0.299 ns	-0.571 *	-0.597 *	0.289 ns	0.386 ns	0.184 ns

Notes:

1. Values are Pearson Correlation Coefficients; n.s. = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$.

2. Size1 = live mass/wing; Size2 = live mass/keel; Size3 = live mass/head + bill; FMRL = sum of anterior 4 ultrasound thicknesses; TOTRL = sum of 6 ultrasound thicknesses. For the definitions of USVOLAnt, USI2Ant, USVOL and USI2, see text.

Table 8.25. Correlation matrix of Dipper pectoralis ultrasound condition and body size indices.

	SMI	USVOL	USI1	USI2	USI3	SIZE1	SIZE2	SIZE3
PLDMD (n=14)	0.568 *	0.451 ns	0.230 ns	0.848 ***	0.235 ns	0.539 *	0.648 **	0.476 ns
SMI (n=11)	--	0.778 **	0.289 ns	0.592 *	0.676 *	0.382 ns	0.308 ns	0.499 ns
USVOL (n=11)		--	-0.284 ns	0.379 ns	0.191 ns	0.709 **	0.516 ns	0.809 **
USI1 (n=11)			--	0.540 *	0.851 ***	-0.481 ns	-0.382 ns	-0.566 *
USI2 (n=11)				--	0.541 *	0.289 ns	0.386 ns	0.184 ns
USI3 (n=11)					--	-0.241 ns	-0.288 ns	-0.227 ns
SIZE1 (n=14)						--	0.910 ***	0.929 ***
SIZE2 (n=14)							--	0.865 ***

Note: Values are Pearson Correlation Coefficients; ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Index abbreviations are given in text.

onset of winter, followed by a relatively rapid build-up of protein reserves in December that are held to the onset of the breeding season. Bird 18, a juvenile male, was not collected until late in April and it was known to have failed in an early breeding attempt, perhaps accounting for the slightly lower indices compared with the two early April pre-breeding males.

PLDMD, SMI and USI2 all seemed to increase gradually from early autumn up to the onset of the breeding season, without a noticeable loss of condition in late autumn. The most significant correlations between indices fitted this pattern: USI1 with USI3 (r_{11} = 0.851, $p<0.001$) and PLDMD with USI2 (r_{11} = 0.898, $p<0.001$). Three indices, PLDMD, SMI and USI3 were tested for age, sex and seasonal differences (Table 8.26). The significant difference between adults and juveniles probably arose out of the uneven distribution of age classes through the seasons: wholly juveniles in autumn and predominantly adults in spring.

Although USVOL is not strictly an index, it seemed to follow the same trend (in both sexes) as PLDMD, SMI and USI2, rising through autumn and winter to peak levels in spring. Assuming no major biases in the body size distribution with season, then this "index" also implied a steady build-up of pectoralis protein and possibly body protein reserves in general, as the breeding season is approached.

8.4. DISCUSSION & CONCLUSIONS

8.4.1. Potential Application of Ultrasound

Many bird species and families, notably waders, show considerable increases in body mass immediately prior to migration, both in spring (to breeding sites) and in autumn (between staging or moulting and wintering sites). Clear examples are seen in the Dunlin *Calidris alpina* (Pienkowski *et al.* 1979), the Curlew Sandpiper *C.ferruginea* in autumn (Stanley and Minton 1972) and in the boreal spring exodus of Palearctic breeding waders

Table 8.26 Differences in pectoralis condition indices of Dippers (t-tests, n = 14).

Adults v juveniles	$t_{SMI} = 3.89$, $p<0.01$
Males v females	no significant differences
Autumn v winter	$t_{SMI} = 6.75$, $p<0.01$ $t_{USI3} = 3.39$, $p<0.05$
Autumn v spring	$t_{SMI} = 7.02$, $p<0.001$ $t_{PLDMD} = 2.64$, $p<0.05$
Autumn v winter v spring	$t_{SMI} = 3.16$, $p<0.05$ $t_{PLDMD} = 2.46$, $p<0.05$
Winter v spring	no significant differences

from southern Africa (Summers & Waltner 1979). Much of this mass increase is attributable to lipid storage but changes in the lean components cannot be ruled out. Evans and Smith (1975) have shown increases in pectoralis muscle protein during spring in both adult and juvenile Bar-tailed Godwits *Limosa lapponica*. In juveniles, some of this may be attributable to continuing growth but this is unlikely in the case of the adults. Unfortunately, distinguishing between increases in lipid and lean components has usually only been feasible when the bird has been taken for carcass analysis.

Thus the development of non-intrusive and non-destructive techniques for measuring lean components are likely to lead to a considerable advance in the understanding of seasonal mass dynamics in population and behavioural ecology. Several techniques have recently been demonstrated: neutron activation analysis (NAA) for measuring body protein (Preston *et al.* 1985), nuclear magnetic resonance (NMR) for measuring water and fat content, and thus protein by subtraction (Lewis *et al.* 1986), and finally electromagnetic induction for fat determination (Walsberg 1988). Of these only the latter has potential in routine field use, but in this case the animals had to be anaesthetised and allowances had to be made for variations in temperature and humidity. None of these methods could be targeted at specific protein or lipid stores. Elsewhere in this thesis (see Chapter 9) the use of the ultrasonic flaw detector in the field is demonstrated; in the present chapter it has been shown how these "direct" measures of pectoralis size can be easily transformed into condition indices with minimal processing of instrument readings. Davidson (1979) has developed modified callipers for estimating pectoralis muscle size in a medium-sized bird such as the Redshank *Tringa totanus*. Such devices are probably not suitable for use with small passerines. Abundant down in the Dipper would prevent clean contact with the pectoralis muscles and all birds examined so far have a more or less uniformly broad and convex profile across the breast.

Although the first application of the ultrasonic flaw detector to avian biology was to assess lipid deposits in wintering Mallard (Baldassarre *et al.* 1980), I have shown that the instrument has the potential to measure small scale changes in the thickness of pectoralis muscles and hence give an estimate of potential protein reserves in small passerines. Fretwell (1968) was one of the first researchers to show that fatter passerines were more likely to survive the winter. More recently Haramis *et al.* (1986) similarly demonstrated that Canvasbacks *Aythya valisineria* with higher body masses in early winter had both higher overwinter and annual survival probabilities. Subtle differences in protein reserves between conspecifics in an autumn population of resident passerines showing little variation in body mass may help in the explanation of differential overwinter survival and recruitment to the breeding population.

In conclusion, it is hoped that the pessimism of Sibly *et al.* (1987) "It is probable that only extremes of protein condition can be predicted from live birds and more accurate assessments require carcass analysis" can be overcome with the more widespread use of techniques such as that described here.

8.4.2. Seasonal Variation in Condition in the Dipper

Winter fattening has been well documented in resident, temperate passerines such as the Yellowhammer *Emberiza citrinella* (Evans 1969) and Bullfinch *Pyrrhula pyrrhula* (Newton 1969). Lipid stores are built up through daylight hours to serve primarily as an overnight energy source. In this study of Dippers, lipid indices were highest during midwinter with a mean of 0.242 compared with 0.326 in the Yellowhammer (Evans 1969). As the Dipper is territorial in winter (defends a relatively predictable food reserve), is well insulated by a thick layer of down, and roosts in very sheltered niches, its dependence on lipid stores for overnight survival is probably reduced in comparison to the more nomadic habits of winter flocking and relatively open-roosting finches and buntings.

The sample of Dippers in this study is too small to draw conclusions about seasonal and diurnal changes in lipid levels. However there is an indication that Dippers may deplete their lipid store overnight to some extent: the lipid indices of the two birds taken immediately after dawn were amongst the lowest recorded (Figure 8.5, November juvenile male and March adult male). Also, birds caught at roost in the early evening possibly had higher lipid indices than those caught during the middle of the day, before lipid stores were fully replenished.

In House Sparrows *Passer domesticus*, Jones (1980) postulated that the overnight loss in lean dry mass from the protein reserve of the pectoralis muscles was mainly to replace body proteins catabolised during the day. There is insufficient evidence from the Dippers to demonstrate this, though birds kept overnight in the laboratory may lose up to 5g of body mass (for a large male). Much of this is thought to be digestion of the crop contents and water loss, though future research using the ultrasound technique should identify the extent, if any, of utilisation of the potential protein reserves in the pectoralis muscles as opposed to lipid metabolism.

The importance of the pectoralis as a protein reserve in the breeding season has been stressed by several authors (Kendall *et al.* 1973, Jones and Ward 1976) and here it is shown that Dippers may start building up these reserves from winter onwards. The build-up demonstrated by the ultrasound condition indices is in close accord with data from carcass analysis.

Pectoralis lean dry mass expressed as a proportion of whole-body lean dry mass is shown alongside whole-body lean dry mass expressed as a proportion of live mass in Figure 8.6.

Several of the ultrasound-derived condition indices (USI1 and USI3) show slight troughs in pectoralis protein mass/volume in October and November. Regular invertebrate sampling throughout the year on part of the study area has shown the total biomass of potential Dipper prey to be at its lowest at this time of year (Bryant, unpubl.data, see also Hynes 1970).

Males appear to be in peak condition in the early breeding season, though pectoralis condition is perhaps acquired at the expense of other lean components (Figure 8.6). Bryant and Tatner (1988) have shown that the observed rates of energy gain were highest in the immediate pre-breeding period (when my samples were taken) and also in midwinter. Thus, it seems that Dippers normally have little difficulty in maintaining pectoralis condition at these times and that such potential protein reserves may be utilised if river spates or other perturbations prevent sufficient food intake when mate-guarding and territorial disputes feature prominently in the daily time/activity budget. Large lipid stores are not needed for overnight survival in this season of shortening and warmer nights. The condition of the females at this time is unknown though their body mass is often 10g above the annual mean (Bryant and Tatner *loc.cit.*). Some of this increase is attributable to development of ovaries and eggs, and although incubating birds handled at this time are very oedematous, they presumably also have enhanced protein reserves or lipid stores. The use of the ultrasound technique in pre-breeding females should be given high priority in future research.

CHAPTER NINE

THE INFLUENCE OF BODY CONDITION ON OVERWINTER SURVIVAL IN THE DIPPER

9.1. INTRODUCTION

"Reserves" and "condition" are two concepts frequently discussed in the ornithological literature in studies of breeding biology, migration and survival (Wishart 1979, Marcström & Kenward 1981, Murphy 1986, Jenni & Jenni-Eiermann 1987, Krementz & Ankney 1988, Moser & Rusch 1988). More rarely are they precisely defined or directly measured in studies of wild, live birds. King & Murphy (1985) have done much to clarify the confusion by distinguishing nutrient stores and nutrient reserves. Nutrient stores, for example, include the build-up of lipid depots in wading and other birds before migration (Summers & Waltner 1979), whereas nutrient reserves comprise, for example, an existing mass or volume of skeletal muscle protein that can be catabolised for a variety of purposes including energy metabolism or egg production (Kendall *et al.* 1973). These parameters can be measured directly by carcass analysis but are usually derived in live birds from body mass data (Crick & Fry 1986, Lehikoinen 1986a) or body mass divided by a skeletal or related body size parameter (Slagsvold 1982, Summers *et al.* 1987, Rienecke & Shaiffer 1988).

Assessment of "condition" is usually more subjective but Owen & Cook (1977) propose a working definition: "the fitness of a bird to cope with its present or future needs". Good condition therefore implies an enhanced survival probability. In this chapter the application of ultrasound techniques to measure variation in the thickness of pectoralis muscles as an indicator of condition (potential protein reserves) and hence survival prospects of a wild population of Dippers is described. This data set is then used to generate some condition indices and these are evaluated as predictors of overwinter survival and compared in this respect with body mass data.

9.2. METHODS

9.2.1. Field Methods

Dippers were caught by mist-netting during daytime and in hand nets at roosts in the hours of night during a 39 day period between 19 October and 27 November 1987. Standard measurements, including mass, wing length, keel length and head and bill were taken for all birds at their first capture; retrapped birds were weighed and processed with ultrasound only. The majority of birds had been ringed at an earlier date with individually identifiable combinations of colour rings; the remainder were given unique combinations. Birds were usually processed immediately after capture, either on the river bank or in a car if vehicular access was feasible. Six measurements of pectoralis muscle thickness were made with ultrasound at the standard positions outlined in Chapter 8. To permit full contact between probe and skin, the downy feathers of the breast were wetted with methanol and could then be pushed to one side. Biometrics and ultrasound procedures took around 10 minutes for each individual. They were then kept in cloth bags for a further 10-20 minutes to allow feathers to dry out completely prior to release.

The experiment was restricted to central parts of the main River Devon study area (sections 1 to 8), though four birds caught in the lower reaches of some of the tributary hill burns were incorporated in the sample. During spring (late March onwards) a thorough search was made of the whole study area for these birds. In most cases birds could be identified by means of colour rings and did not need to be retrapped. However, a few females were caught in hand nets at the nest to allow identification during incubation. Mates and nest sites were located as soon as possible and breeding success was monitored up to the end of May. Thus, each bird could be allocated to one of ten classes:

0 = recovered dead.
1 = inferred dead.
2 = known to be alive (in hindsight).
3 = present in study area during breeding season, status unknown.
4 = makes nesting attempt but fails to rear young.
5 = makes nesting attempt but outcome unknown.
6 = probably successful in fledging young.
7 = bred successfully after initial failure (loss of first nest or clutch).
8 = successfully fledged first brood.
9 = successfully reared two broods.

In some of the following analyses, these classes have been recoded into two or three groups: non-recruits/non-survivors (0 + 1), recruits but failing to rear young (2 + 3 + 4 + 5), successful recruits (6 + 7 + 8 + 9) and survivors (2 + 3 + 4 + 5 + 6 + 7 + 8 + 9).

9.2.2. Computation of Condition Indices

Ultrasound thickness (arbitrary units) was transformed into millimetres using the regression equations given in Chapter 8. The sum of the six pectoralis thicknesses (TOTMM) is the basic measure from which most condition indices were calculated. A check for seasonal trends in mass and TOTMM during the field data collection period was undertaken by regressing these variables on date, for both sexes separately. Data for birds caught on two or more occasions were, for the purpose of this analysis, presumed to represent independent cases.

For females, mass was positively correlated with date ($r_{52} = 0.269$) but the result just failed to be statistically significant ($p = 0.053$, two-tailed test). There was no correlation between male mass and date. TOTMM was significantly correlated with date in females

(r_{52} = -0.306, $p<0.05$, two-tailed test) but not in males (Figures 9.1 and 9.2). Thus, in the following analyses of survival in females, TOTMM was standardised to a reference date (November 1) using the regression equation:

$$\text{TOTMMA} = (-\ 0.0824 \times \text{TOTDAY}) + 148.181$$

where TOTMMA is the adjusted sum of ultrasound thicknesses and TOTDAY is a day number (January 1 = 1, December 31 = 365). Figure 9.2 shows that a curve may best describe the relationship between TOTMM and date in males; however, no significant quadratic equation could be determined for the data set and male condition indices were therefore calculated from unadjusted thicknesses.

The seven size-adjusted masses and condition indices presented in Chapter 8 were calculated for all birds tested with ultrasound in this study; those abbreviations followed by an "A" indicate the use of standardised ultrasound in females, (i.e. USVOLA, USI1A, USI2A, UISI3A). Estimated standard muscle volume (ESMV) was required for two indices, USI1(A) and USI3(A) and was computed from regression of SMV on keel length (r_{11} = 0.808, p = <0.01, two-tailed test) and total head length (r_{11} = 0.908, $p<0.001$, two-tailed test) using measurements obtained from carcass analysis. The mean of the keel- and total head length-generated SMV estimates was used.

9.3. RESULTS

9.3.1. Age and Sex Composition of Sample

A total of 112 captures/handlings was made of 93 individuals. Handling frequency and age/sex breakdowns are given in Tables 9.1 and 9.2. Most birds were handled on a single occasion only, though some birds were caught and processed three times. Age and sex ratios were approximately equal though there was a slight preponderance of adults over juveniles in males,

Table 9.1. Handling frequency of Dippers caught for ultrasound condition assessment.

Number of birds		x 1	x 2	x 3	Total
Whole sample	93	77	13	3	112
Excluding 3 individuals (mist-netting casualties)	90	76	11	3	107

Table 9.2. Age and sex breakdown of Dippers caught for ultrasound condition assessment.

Sample	Adult male	Juvenile male	Adult female	Juvenile female
All individuals	26	22	20	25
Excluding 3 mist-netting casualties	26	19	20	25
Numbers surviving to spring	16	6	11	10
% surviving to spring	61.5	31.6	55.0	40.0

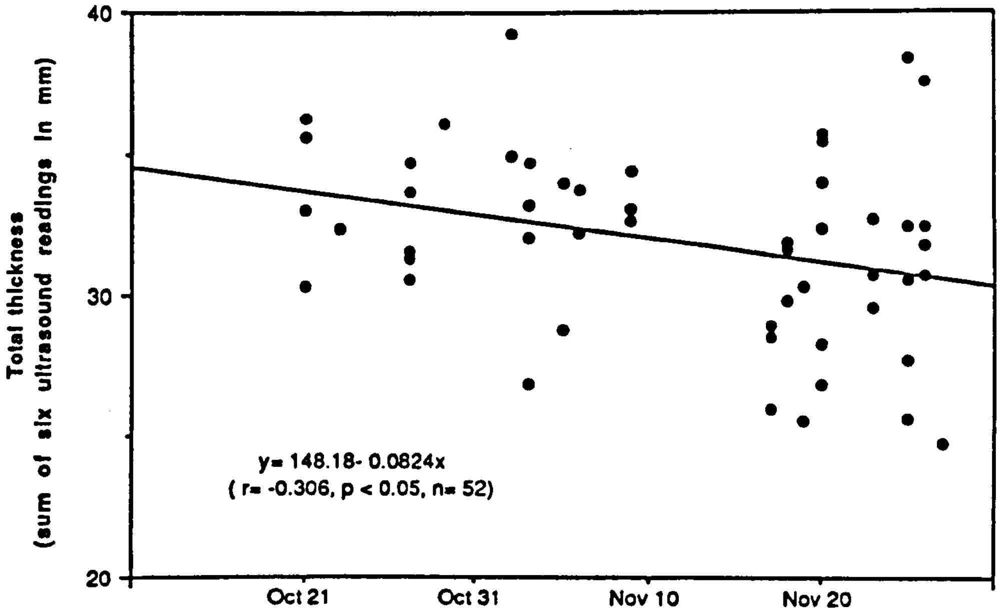


Fig. 9.1 Seasonal change in pectoralis muscle thickness (females).

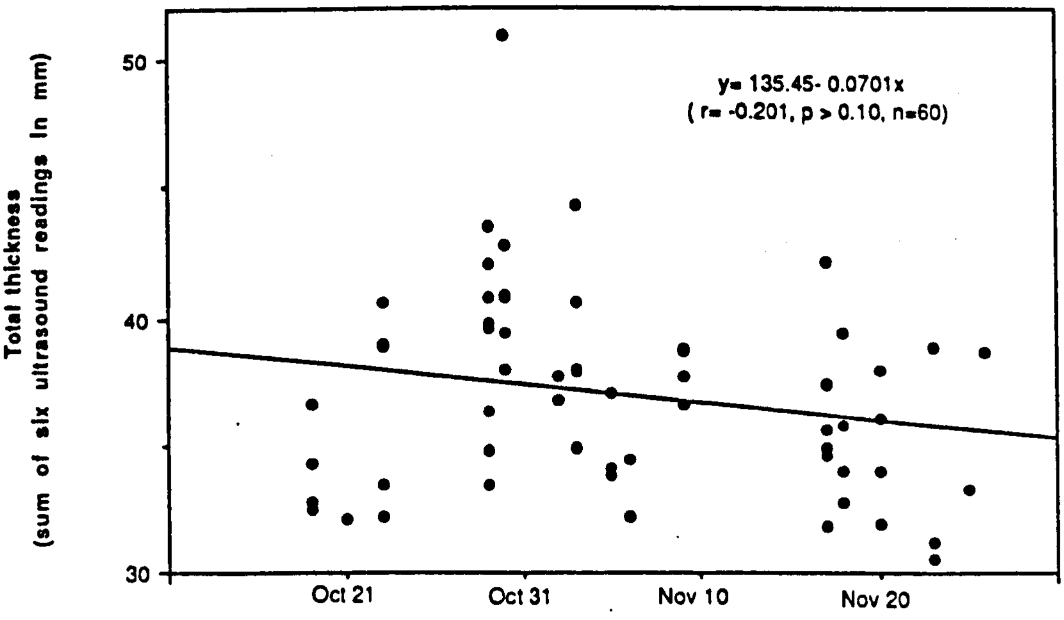


Fig. 9.2 Seasonal change in pectoralis muscle thickness (males).

and juveniles over adults in females. Overwinter survival rates were higher in adults than juveniles (Table 9.2) and overall 47.8% of the autumn population survived to make breeding attempts within the study area. Successful breeding was more frequently recorded in adults (Table 9.3).

9.3.2. Biometrics and Ultrasound Measurements

Summaries of mean body size measurements, pectoralis muscle thicknesses, size-adjusted masses and pectoralis condition indices are given in Tables 9.4-9.6. The latter two are subdivided by age and survivorship class. In males all body size measures were larger, masses higher and pectoralis muscle thicknesses greater in the overwinter survivors than in the non-surviving cohort (ages combined, first capture of each bird only, Table 9.4). The body size differences disappeared when multiple handlings were included in the means though body mass and pectoralis muscle thicknesses remained higher in the survivors in both adults and juveniles (Table 9.5).

Body mass, wing and head and bill lengths were greater in the overwinter surviving females but keel length and pectoralis muscle thicknesses were comparable in the two cohorts (ages combined, first handling of each bird only, Table 9.4). However, juvenile overwinter surviving females followed the overall male pattern and were noticeably larger than non-survivors in all measures. Adult female survivors had shorter keels and, in contrast to the other age/sex cohorts, pectoralis muscle thicknesses were less that those of the non-survivors (Table 9.6).

9.3.3. Seasonal Trends in Body Size and Pectoralis Condition Indices

The relationships between mass and TOTMM with date are given in methods section of this chapter. All computed size-adjusted masses and pectoralis muscle condition indices were regressed against handling date and

Table 9.3. Overwinter survival and breeding success of 90 Dippers caught for ultrasound condition assessment in autumn. (NOTE: ** See text for details).

Class **		Adult male	Juvenile male	Adult female	Juvenile female
Probably dead	0,1	10	13	9	15
Failed recruits	2				
	3	3	1		
	4	4	2	3	5
	5	1	1	3	
Successful recruits	6	1			1
	7	1		1	
	8	4	2	3	3
	9	2		1	
% overwinter survivors breeding successfully		50.0	33.3	45.5	40.0

Table 9.4. Mean biometrics, size-adjusted masses and pectoralis muscle condition indices for all autumn caught Dippers (± standard deviation).

	All males	Male overwinter survivors	Non-surviving males	All females	Female over-winter survivors	Non-surviving females
Mass (g)	68.50 ± 3.96	69.33 ± 3.36	67.29 ± 4.18	57.54 ± 2.96	58.41 ± 2.93	56.75 ± 3.12
Wing length (mm)	97.07 ± 2.07	97.36 ± 2.01	96.65 ± 1.87	89.96 ± 1.79	90.43 ± 1.54	89.29 ± 1.97
Keel length (mm)	31.44 ± 0.94	31.65 ± 0.96	31.29 ± 1.05	27.55 ± 0.95	27.58 ± 0.84	27.60 ± 1.05
Head & bill (mm)	47.61 ± 0.80	47.62 ± 0.88	47.58 ± 0.76	45.96 ± 0.88	46.12 ± 0.61	45.72 ± 1.02
TOTMM	36.96 ± 3.83	38.50 ± 4.36	35.52 ± 3.30	31.90 ± 3.30	32.01 ± 2.95	31.78 ± 4.01
TOTMMA	-----------	------------	------------	32.74 ± 3.14	32.81 ± 2.70	32.64 ± 3.81
R1 (mm)	7.92 ± 0.71	8.21 ± 0.79	7.63 ± 0.42	6.91 ± 0.60	6.90 ± 0.52	6.87 ± 0.72
R2 (mm)	6.79 ± 0.77	7.14 ± 0.89	6.60 ± 0.59	5.91 ± 0.68	5.91 ± 0.63	5.90 ± 0.79
R3 (mm)	3.69 ± 1.03	3.74 ± 1.12	3.48 ± 1.05	3.13 ± 0.77	3.17 ± 0.86	3.13 ± 0.79
L1 (mm)	8.06 ± 0.65	8.37 ± 0.66	7.82 ± 0.53	7.07 ± 0.57	7.06 ± 0.50	7.04 ± 0.68
L2 (mm)	6.90 ± 0.78	7.25 ± 0.81	6.62 ± 0.69	5.88 ± 0.69	5.92 ± 0.56	5.81 ± 0.83
L3 (mm)	3.61 ± 0.87	3.80 ± 0.88	3.37 ± 0.91	3.00 ± 0.71	3.06 ± 0.71	3.03 ± 0.79
ESMV	3414 ± 221	3437 ± 232	3394 ± 226	2719 ± 228	2754 ± 160	2677 ± 267
SIZE1	0.706 ± 0.039	0.712 ± 0.035	0.696 ± 0.042	0.640 ± 0.031	0.646 ± 0.034	0.635 ± 0.032
SIZE2	2.179 ± 0.108	2.191 ± 0.088	2.151 ± 0.117	2.089 ± 0.100	2.118 ± 0.079	2.057 ± 0.106
SIZE3	1.438 ± 0.072	1.456 ± 0.056	1.414 ± 0.079	1.252 ± 0.059	1.267 ± 0.063	1.241 ± 0.600
USVOL(A)	1.162 ± 0.128	1.219 ± 0.149	1.111 ± 0.108	(0.903 ± 0.101)	(0.905 ± 0.085)	(0.902 ± 0.120)
USI1(A)	0.543 ± 0.065	0.562 ± 0.068	0.526 ± 0.064	(0.605 ± 0.065)	(0.597 ± 0.050)	(0.614 ± 0.082)
USI2(A)	1.176 ± 0.124	1.217 ± 0.136	1.137 ± 0.114	(1.188 ± 0.108)	(1.190 ± 0.095)	(1.183 ± 0.133)
USI3(A)	1.707 ± 0.193	1.776 ± 0.210	1.642 ± 0.178	(1.664 ± 0.168)	(1.645 ± 0.135)	(1.690 ± 0.211)
Sample size	60	22	23	52	21	24
Notes:	All observations	First capture of each bird only		All observations	First capture of each bird only	

Notes:

1. Abbreviations defined in section 8.3.6.
2. Parentheses refer to adjusted indices for females.

Table 9.5. Mean biometrics, size-adjusted masses and pectoralis muscle condition indices of male Dippers (± standard deviation). NOTE: All observations, i.e. including multiple handlings.

	All adult males	Adult overwinter survivors	Non-surviving adults	All juvenile males	Juvenile over-winter survivors	Non-surviving juveniles
Mass (g)	69.96 ± 3.20	70.01 ± 3.36	69.90 ± 3.09	66.71 ± 4.11	67.57 ± 2.54	65.10 ± 4.18
Wing length (mm)	98.12 ± 2.04	98.05 ± 2.12	98.21 ± 2.01	95.78 ± 1.19	96.14 ± 1.07	95.33 ± 1.23
Keel length (mm)	31.86 ± 0.77	31.93 ± 0.81	31.76 ± 0.72	30.93 ± 0.90	30.84 ± 0.86	30.95 ± 1.08
Head & bill (mm)	47.86 ± 0.74	47.82 ± 0.86	47.91 ± 0.56	47.29 ± 0.77	47.09 ± 0.56	47.22 ± 0.91
TOTMM	36.96 ± 3.49	38.33 ± 3.40	35.11 ± 2.75	36.96 ± 4.29	38.30 ± 6.34	36.19 ± 3.38
R1 (mm)	7.99 ± 0.67	8.24 ± 0.69	7.66 ± 0.50	7.83 ± 0.75	8.04 ± 0.95	7.65 ± 0.45
R2 (mm)	6.90 ± 0.72	7.19 ± 0.70	6.51 ± 0.56	6.66 ± 0.82	6.84 ± 1.27	6.62 ± 0.66
R3 (mm)	3.49 ± 0.90	3.59 ± 0.93	3.36 ± 0.87	3.93 ± 1.14	4.26 ± 1.48	3.75 ± 1.11
L1 (mm)	8.15 ± 0.58	8.40 ± 0.56	7.80 ± 0.41	7.95 ± 0.72	8.11 ± 0.86	7.81 ± 0.60
L2 (mm)	6.95 ± 0.71	7.24 ± 0.66	6.56 ± 0.58	6.84 ± 0.87	7.03 ± 1.18	6.74 ± 0.76
L3 (mm)	3.48 ± 0.87	3.67 ± 0.85	3.22 ± 0.85	3.76 ± 0.86	4.01 ± 0.94	3.61 ± 0.87
ESMV	3504 ± 192	3502 ± 218	3505 ± 159	3304 ± 206	3255 ± 151	3292 ± 251
SIZE1	0.713 ± 0.037	0.714 ± 0.037	0.712 ± 0.039	0.696 ± 0.039	0.703 ± 0.025	0.683 ± 0.041
SIZE2	2.195 ± 0.074	2.192 ± 0.079	2.200 ± 0.069	2.158 ± 0.138	2.192 ± 0.106	2.104 ± 0.135
SIZE3	1.462 ± 0.060	1.464 ± 0.056	1.459 ± 0.067	1.410 ± 0.076	1.435 ± 0.051	1.378 ± 0.074
USVOL	1.179 ± 0.124	1.225 ± 0.122	1.116 ± 0.099	1.143 ± 0.133	1.181 ± 0.194	1.120 ± 0.108
USI1	0.529 ± 0.054	0.549 ± 0.054	0.502 ± 0.043	0.561 ± 0.074	0.590 ± 0.101	0.553 ± 0.066
USI2	1.160 ± 0.103	1.200 ± 0.100	1.105 ± 0.081	1.196 ± 0.146	1.243 ± 0.212	1.171 ± 0.118
USI3	1.684 ± 0.176	1.751 ± 0.173	1.593 ± 0.138	1.734 ± 0.213	1.816 ± 0.299	1.708 ± 0.184
Sample size	33	19	14	27	7	15

Note:

Abbreviations defined in section 8.3.6.

Table 9.6. Mean biometrics, size-adjusted masses and pectoralis muscle condition indices of female Dippers (± standard deviation). NOTE: All observations, i.e. including multiple handlings.

	All adult females	Adult overwinter survivors	Non-surviving adults	All juvenile females	Juvenile over-winter survivors	Non-surviving juveniles
Mass (g)	59.03 ± 2.90	59.14 ± 2.75	58.87 ± 3.26	56.45 ± 2.53	57.49 ± 2.51	55.53 ± 2.24
Wing length (mm)	90.82 ± 1.71	91.15 ± 1.52	90.33 ± 1.94	89.33 ± 1.61	90.00 ± 1.18	88.75 ± 1.73
Keel length (mm)	27.75 ± 0.85	27.60 ± 0.75	27.96 ± 0.98	27.41 ± 1.01	27.55 ± 0.94	27.29 ± 1.09
Head & bill (mm)	46.15 ± 0.59	46.20 ± 0.43	46.07 ± 0.78	45.82 ± 1.04	46.24 ± 0.78	45.44 ± 1.11
TOTMM	31.98 ± 3.42	31.59 ± 3.06	32.56 ± 4.01	31.84 ± 3.26	32.49 ± 2.20	31.28 ± 3.95
TOTMMA	32.94±3.37	32.46 ± 2.69	33.64 ± 4.24	32.58 ± 3.01	33.34 ± 2.30	31.92 ± 3.45
R1 (mm)	6.89 ± 0.66	6.86 ± 0.56	6.93 ± 0.82	6.92 ± 0.57	7.04 ± 0.43	6.83 ± 0.66
R2 (mm)	5.87 ± 0.69	5.74 ± 0.55	6.06 ± 0.85	5.94 ± 0.68	6.10 ± 0.61	5.80 ± 0.74
R3 (mm)	3.17 ± 0.82	3.10 ± 0.98	3.27 ± 0.56	3.10 ± 0.74	3.16 ± 0.57	3.04 ± 0.88
L1 (mm)	7.11 ± 0.61	7.05 ± 0.56	7.18 ± 0.70	7.05 ± 0.54	7.11 ± 0.37	6.99 ± 0.67
L2 (mm)	5.88 ± 0.63	5.80 ± 0.45	6.00 ± 0.84	5.87 ± 0.74	6.09 ± 0.62	5.68 ± 0.80
L3 (mm)	3.07 ± 0.84	3.03 ± 0.90	3.12 ± 0.78	2.96 ± 0.61	2.98 ± 0.30	2.94 ± 0.80
ESMV	2775 ± 174	2771 ± 127	2779 ± 235	2679 ± 256	2775 ± 196	2594 ± 278
SIZE1	0.650 ± 0.034	0.649 ± 0.034	0.652 ± 0.036	0.632 ± 0.027	0.639 ± 0.029	0.626 ± 0.024
SIZE2	2.128 ± 0.104	2.143 ± 0.083	2.108 ± 0.132	2.060 ± 0.087	2.088 ± 0.086	2.036 ± 0.082
SIZE3	1.279 ± 0.064	1.280 ± 0.061	1.278 ± 0.073	1.232 ± 0.047	1.243 ± 0.054	1.222 ± 0.039
USVOLA	0.915 ± 0.109	0.896 ± 0.084	0.942 ± 0.139	0.894 ± 0.095	0.919 ± 0.081	0.872 ± 0.104
USI1A	0.594 ± 0.054	0.586 ± 0.046	0.606 ± 0.065	0.612 ± 0.072	0.602 ± 0.042	0.621 ± 0.091
USI2A	1.187 ± 0.109	1.176 ± 0.093	1.202 ± 0.134	1.189 ± 0.109	1.210 ± 0.077	1.171 ± 0.130
USI3A	1.648 ± 0.154	1.617 ± 0.128	1.694 ± 0.184	1.676 ± 0.179	1.658 ± 0.116	1.691 ± 0.224
Sample size	22	13	9	30	14	16

Note:

Abbreviations are defined in section 8.3.6.

significant correlations are given below (two-tailed tests):

Males:	USI1	$r_{60} = -0.268$, $p<0.05$
	USI1	$r_{60} = -0.301$, $p<0.05$
Females:	SIZE1	$r_{52} = +0.365$, $p<0.01$
	USI1	$r_{52} = -0.448$, $p<0.001$
	USI2	$r_{52} = -0.440$, $p<0.01$
	USI3	$r_{52} = -0.362$, $p<0.01$

The negative correlation coefficients for female pectoralis muscle condition indices (non-standardised) were to be expected as the decline in TOTMM with handling date has already been demonstrated. Thus, females appear to draw on the potential protein reserves in their pectoralis muscles as autumn progresses to winter. A similar, but weaker, relationship exists in males (USI1 and USI2 only). The positive correlation between SIZE1 and handling date in females may have been the result of a slight increase in mass through the study period.

Differences in mass, TOTMM and USI2 between early and late capture dates were examined. Birds of both sexes handled in the early part of the study period (before 10 November) showed no significant differences in mass to those in the later part (t-tests). TOTMM and USI2 were significantly different for both sexes; pectoralis muscle indices were higher in early autumn caught birds.

Males:

TOTMM: early caught ($n = 41$) v late caught ($n = 19$),
$t = 2.35$, $p<0.05$.USI2:
early caught ($n = 41$) v late caught ($n = 19$),
$t = 2.71$, $p<0.01$.

Females:

TOTMM: early caught ($n = 25$) v late caught ($n = 27$), $t = 2.66$, $p<0.05$USI2:
early caught ($n = 25$) v late caught ($n = 27$), $t = 3.57$, $p<0.01$.

9.3.4. Diurnal Variation in Mass and Pectoralis Muscle Condition Indices

Most mist-netted birds were caught between 10.00 and 18.00 (GMT) during daylight hours and roost birds caught between 20.00 and 24.00. Mass, TOTMM and USI2 were examined for differences in three time periods: midday (10.00 - 13.59), afternoon (14.00 - 17.59) and evening (20.00 - 23.59). Afternoon caught males ($n = 30$) had significantly thicker pectoralis muscles (TOTMM) and higher USI2 indices than midday captured birds, ($n = 16$, $t = 9.38$, $p<0.05$ and $t = 3.31$, $p<0.01$ respectively). There were no significant differences in all three variables between midday and evening, afternoon and evening, and daytime (midday and afternoon combined) versus evening.

In females, TOTMM and USI2 did not differ significantly between any of the time periods (t-tests) though masses were significantly greater in the afternoon than at midday ($t = 2.65$, $p<0.05$) or in the evening ($t = 3.19$, $p<0.01$). Daytime masses were significantly greater than evening (roosting) masses ($t = 2.30$, $p<0.05$).

The USI2 indices for midday and afternoon periods showed significant negative correlations with date of capture when sexes were combined:

Midday: $r_{36} = -0.492$, $p<0.01$
Afternoon: $r_{49} = 0.403$, $p<0.01$

No significant seasonal decline in pectoralis muscle condition was detected in roosting birds ($r_{26} = -0.266$, $p<0.189$).

9.3.5. Short-term Variation in Mass and Pectoralis Muscle Thicknesses

Sixteen birds were caught on more than one occasion (Table 9.1). In most cases the time interval was less than one week. Figure 9.3 shows mean pectoralis muscle thickness change (TOTMM/6) plotted against mass change between two successive captures. In 11 out of 19 cases (58%), an increase in mass was accompanied by an increase in pectoralis muscle thickness and if mass change over 1.0g are considered, 60% (9/15) showed parallel increases. Correlations for both sexes combined and for females alone were not significant ($r_{19} = 0.423$, $p>0.05$ and $r_7 = 0.195$, $p>0.05$) but mass changes and pectoralis muscle thickness change were significantly correlated in males ($r_{12} = 0.605$, $p<0.05$).

In summary, mass change is not necessarily a good indicator of change in pectoralis muscle condition and must often represent variation in gut content or lipid stores.

9.3.6. Relationships Between Pectoralis Muscle Indices & Size-adjusted Masses

The pectoralis muscle condition indices and size-adjusted masses computed for live birds in this study fell within the range of those taken for carcass analysis (see Table 8.23, Chapter 8). Mean values for various age and sex groupings are given in Tables 9.4-9.6. Such indices and masses can be used for inter-bird, inter-cohort or inter-seasonal comparisons. Correlations between pectoralis muscle condition and size-adjusted masses were generally very poor, especially in females (Table 9.7). The relationships between USVOL and USVOLA and size-adjusted masses were to be expected: muscle volume should increase with increasing size of birds. However, the correlations presented in Table 9.7 show that the potential protein reserves held in pectoralis muscles do not necessarily increase with body size.

Table 9.7. Significant correlations between size-adjusted masses and pectoralis muscle condition indices in autumn caught Dippers.

	Males			Females		
	SIZE1	SIZE2	SIZE3	SIZE1	SIZE2	SIZE3
USVOL	0.560 ***	0.381 **	0.593 ***	-----	-----	-----
USVOLA	------	-----	-----	0.414 **	n.s.	0.361 *
USI1	n.s.	n.s.	n.s.	-----	-----	-----
USI1A	------	-----	-----	n.s.	n.s.	n.s.
USI2	0.334 *	0.428 **	0.392 **	-----	-----	-----
USI2A	------	-----	-----	n.s.	n.s.	n.s.
USI3	n.s.	n.s.	0.372 *	n.s.	n.s.	n.s.
USI3A	------	-----	-----	n.s.	n.s.	n.s.
Sample size	45	45	45	45	45	45

Values given are Pearson correlation coefficients; significance levels (2-tailed): n.s. = not significant, * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.

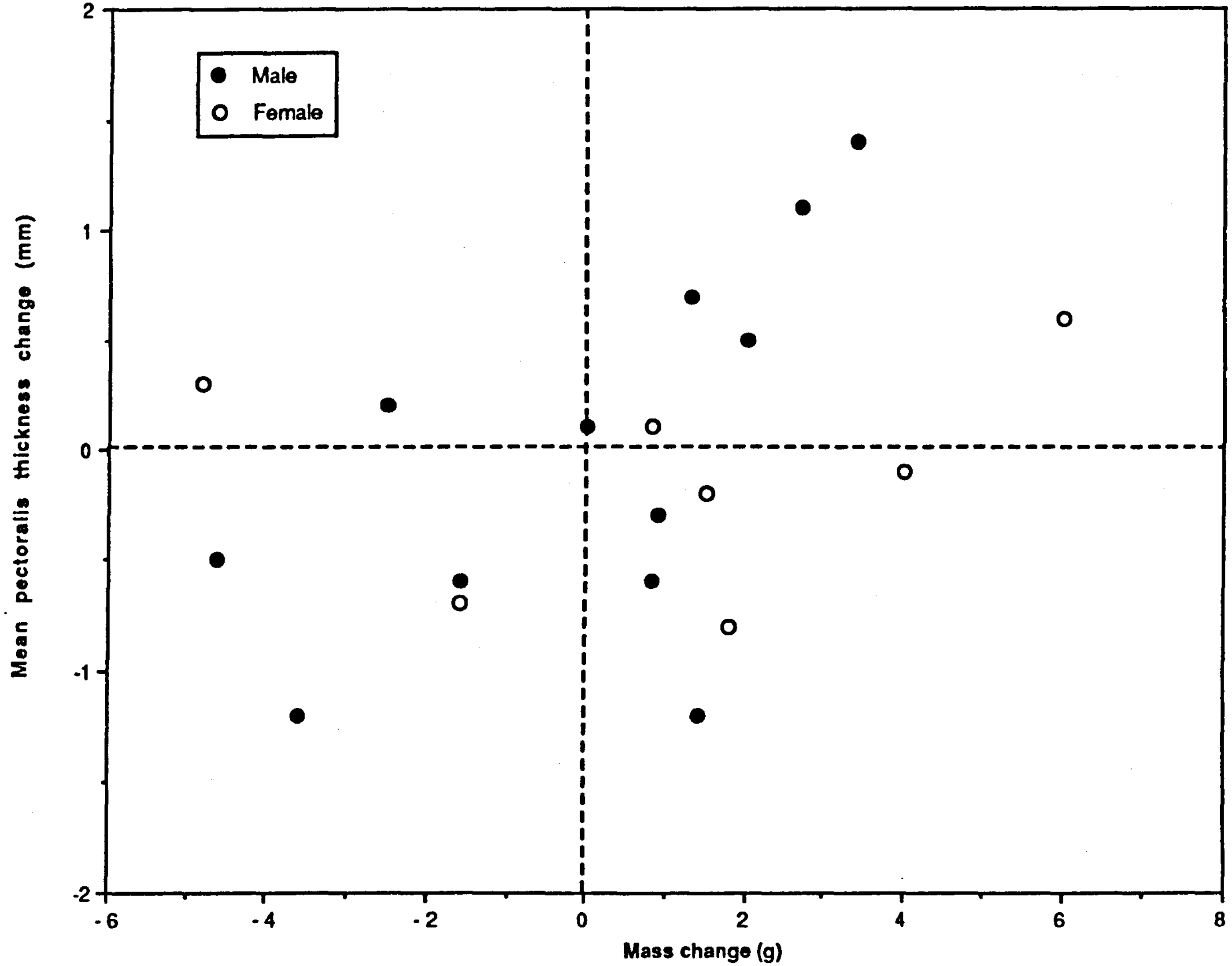


Fig. 9.3 Relationship of mean pectoralis muscle thickness change with change in body mass

9.3.7. Body Size, Pectoralis Muscle Condition Indices & Overwinter Survival

The relationship between "condition indices" and overwinter survival was examined using three-way analyses of variance (ANOVAs). The continuously varying "condition index" was designated the dependent variable and the role of three factors is given in Tables 9.8 and 9.9 (data for the first handling of each individual were used). For each bird, factors fell into one of two classes: survivors and non-survivors, adults and juveniles, below mean mass or equal to and greater than mean mass. Mass had the expected significant effect on the size-adjusted masses of both sexes, but there was no relationship between overwinter survival and size-adjusted masses.

In males, USVOL, USI1 and USI3 were all significantly greater in those birds that survived the winter; USI2 just failed to reach the 5% significance level (Table 9.8). With the exception of USVOL, these relationships were not confounded by age or mass class differences. Although mass did have an independent effect on USVOL, the absolute volume of pectoralis tissue, there was no significant interaction between mass and overwinter survival. Similarly, mass had the expected significant effect on USVOLA in females but in this case, and all other pectoralis muscle condition indices, autumn condition was a very poor predictor of overwinter survival (Table 9.9).

These analyses were repeated using biometrics and ultrasound data from the last handlings of multiple caught birds together with the single data points for the remaining birds. For both sexes, the effect of mass on SIZE1-SIZE3 remained. However, in males all significant relationships between pectoralis muscle indices and overwinter survival were lost though mass continued to exert a significant effect on USVOL ($F = 8.17$, $p<0.01$). The results were virtually unchanged in females, with mass remaining the only significant

Table 9.8. Three-way analysis of variance for autumn condition indices in male Dippers with overwinter survival class, age and mass as factors.

Dependent variable	Factors main effects	F	P	Degrees of freedom (explained, residual)
SIZE1	OWS	0.10	n.s.	1, 37
	Age	0.15	n.s.	1, 37
	Mass	55.41	<0.001	1, 37
SIZE2	OWS	0.05	n.s.	1, 37
	Age	0.12	n.s.	1, 37
	Mass	37.63	<0.001	1, 37
SIZE3	OWS	0.12	n.s.	1, 37
	Age	2.85	n.s.	1, 37
	Mass	42.90	<0.001	1, 37
USVOL	OWS	4.36	<0.05	1, 37
	Age	0.06	n.s.	1, 37
	Mass	6.84	<0.05	1, 37
USI1	OWS	4.29	<0.05	1, 37
	Age	4.02	=0.052	1, 37
	Mass	0.97	n.s.	1, 37
USI2	OWS	4.05	=0.051	1, 37
	Age	2.79	n.s.	1, 37
	Mass	3.96	=0.054	1, 37
USI3	OWS	5.04	<0.05	1, 37
	Age	2.09	n.s.	1, 37
	Mass	1.79	n.s.	1, 37

Notes:

1. No significant 2-way interactions between factors (overwinter survival x age, overwinter survival x mass, age x mass) were observed.
2. No significant 3-way interactions were observed.
3. The following abbreviations used in the above table: OWS = overwinter survival; n.s. = not significant.

Table 9.9. Three-way analysis of variance for autumn condition indices in female Dippers with overwinter survival class, age and mass as factors.

Dependent variable	Factors main effects	F	P	Degrees of freedom (explained, residual)
SIZE1	OWS	0.18	n.s.	1, 37
	Age	<0.01	n.s.	1, 37
	Mass	35.75	<0.001	1, 37
SIZE2	OWS	2.86	n.s.	1, 37
	Age	1.31	n.s.	1, 37
	Mass	11.00	<0.01	1, 37
SIZE3	OWS	0.58	n.s.	1, 37
	Age	1.56	n.s.	1, 37
	Mass	31.12	<0.001	1, 37
USVOLA	OWS	0.15	n.s.	1, 37
	Age	0.38	n.s.	1, 37
	Mass	12.68	=0.001	1, 37
USI1A	OWS	0.36	n.s.	1, 37
	Age	0.48	n.s.	1, 37
	Mass	0.11	n.s.	1, 37
USI2A	OWS	<0.01	n.s.	1, 37
	Age	0.52	n.s.	1, 37
	Mass	2.02	n.s.	1, 37
USI3A	OWS	0.64	n.s.	1, 37
	Age	0.49	n.s.	1, 37
	Mass	0.46	n.s.	1, 37

Notes:

1. No significant 2-way interactions between factors were observed.
2. No significant 3-way interactions between factors were observed.
3. The following abbreviations used in the above table: OWS = overwinter survival; n.s. = not significant.

factor affecting USVOLA ($F = 9.06$, $p<0.01$) though a significant three-way interaction between overwinter survival, age and mass appeared to explain the variation in SIZE3 ($F = 4.74$, $p<0.05$).

9.3.8. Autumn Condition and Breeding Success

Variation in breeding success of recruits could not be explained by any of the autumn derived condition indices (three-way ANOVAs, Tables 9.10 and 9.11). There was a significant interaction, however, between breeding success and mass for two of the pectoralis muscle condition indices of both males and females. These relationships are difficult to explain as there were no significant differences between mass and any pectoralis condition indices or size-adjusted masses of successful and unsuccessful breeders (t-tests).

9.4. DISCUSSION

9.4.1. The Ultrasound Technique

The ultrasonic flaw detector used in this study weighs approximately 5.1kg and measures 95 x 240 x 300mm. It is perhaps one of the first truly field portable instruments to be used in the precise assessment of pectoralis protein mass/volume in small birds. Application of the technique requires the retention of a bird for 15-20 minutes above that needed for routine ringing and processing operations. Most of the extra time is taken up by feather drying: use of a small battery-powered hot-air dryer could reduce handling time considerably. Dippers are somewhat exceptional among passerine birds in having an extensive covering of small downy feathers for insulation during diving and swimming and feather wetting was necessary for a bird to be processed by a single person. However, the body feathers of most other terrestrial passerines can be blown aside without undue wetting, although the need for a moist skin contact will remain. Also, as there were no significant differences in muscle thickness between left and right sides of the keel then processing time may be reduced further in future

Table 9.10. Three-way analysis of variance for autumn condition indices in male Dippers with breeding success (of overwinter survivors), age and mass as factors.

Dependent variable	Factors main effects	F	P	2-way inter-actions	F	P	D.o.F (expl., res.)
SIZE1	BS	0.04	n.s.	BS x age	0.34	n.s.	1, 15
	Age	0.65	n.s.	BS x mass	0.26	n.s.	1, 15
	Mass	35.85	<0.001	age x mass	0.07	n.s.	1, 15
SIZE2	BS	0.02	n.s.	BS x age	0.49	n.s.	1, 15
	Age	0.03	n.s.	BS x mass	0.27	n.s.	1, 15
	Mass	41.36	<0.001	age x mass	1.99	n.s.	1, 15
SIZE3	BS	0.11	n.s.	BS x age	1.09	n.s.	1, 15
	Age	1.81	n.s.	BS x mass	0.01	n.s.	1, 15
	Mass	37.25	<0.001	age x mass	0.03	n.s.	1, 15
USVOL	BS	0.65	n.s.	BS x age	1.63	n.s.	1, 15
	Age	1.27	n.s.	BS x mass	2.39	n.s.	1, 15
	Mass	7.82	<0.05	age x mass	<0.01	n.s.	1, 15
USI1	BS	0.10	n.s.	BS x age	0.30	n.s.	1, 15
	Age	0.57	n.s.	BS x mass	4.69	<0.05	1, 15
	Mass	2.74	n.s.	age x mass	0.58	n.s.	1, 15
USI2	BS	0.38	n.s.	BS x age	0.36	n.s.	1, 15
	Age	0.02	n.s.	BS x mass	3.42	n.s.	1, 15
	Mass	6.61	<0.05	age x mass	0.49	n.s.	1, 15
USI3	BS	0.20	n.s.	BS x age	0.83	n.s.	1, 15
	Age	0.02	n.s.	BS x mass	4.56	<0.05	1, 15
	Mass	3.45	n.s.	age x mass	0.18	n.s.	1, 15

Notes:

1. 3-way interactions were suppressed in this analysis.
2. The following abbreviations used in the above table:

D.o.F. = Degrees of Freedom
expl. = explained
res. = residual
BS = breeding success
n.s. = not significant

Table 9.11. Three-way analysis of variance for autumn condition indices in female Dippers with breeding success (of overwinter survivors), age and mass as factors.

Dependent variable	Factors main effects	F	P	2-way interactions	F	P	D.o.F (expl., res.)
SIZE1	BS	0.21	n.s.	BS x age	0.25	n.s.	1, 13
	Age	0.09	n.s.	BS x mass	0.10	n.s.	1, 13
	Mass	11.59	<0.01	age x mass	0.31	n.s.	1, 13
SIZE2	BS	0.21	n.s.	BS x age	0.03	n.s.	1, 13
	Age	0.79	n.s.	BS x mass	<0.01	n.s.	1, 13
	Mass	2.88	n.s.	age x mass	0.79	n.s.	1, 13
SIZE3	BS	0.01	n.s.	BS x age	0.07	n.s.	1, 13
	Age	0.39	n.s.	BS x mass	0.01	n.s.	1, 13
	Mass	12.49	<0.01	age x mass	0.15	n.s.	1, 13
USVOLA	BS	2.04	n.s.	BS x age	2.23	n.s.	1, 13
	Age	3.23	n.s.	BS x mass	11.18	<0.01	1, 13
	Mass	16.05	=0.001	age x mass	0.42	n.s.	1, 13
USI1A	BS	0.02	n.s.	BS x age	0.02	n.s.	1, 13
	Age	1.36	n.s.	BS x mass	0.90	n.s.	1, 13
	Mass	0.07	n.s.	age x mass	0.23	n.s.	1, 13
USI2A	BS	1.06	n.s.	BS x age	1.00	n.s.	1, 13
	Age	1.76	n.s.	BS x mass	4.70	<0.05	1, 13
	Mass	0.60	n.s.	age x mass	0.81	n.s.	1, 13
USI3A	BS	0.03	n.s.	BS x age	<0.01	n.s.	1, 13
	Age	1.84	n.s.	BS x mass	1.61	n.s.	1, 13
	Mass	2.04	n.s.	age x mass	0.13	n.s.	1, 13

Notes:

1. No significant 3-way interactions between factors were observed.

2. The following abbreviations used in the above table:

D.o.F. = Degrees of Freedom
expl. = explained
res. = residual
BS = breeding success
n.s. = not significant

studies by measuring a single body side of the breast only.

Application of this technique did not influence the probability of a bird surviving over the winter. Approximately three quarters of the autumn population of Dippers in the study area was handled in this way and the nesting density the ensuing spring was almost identical to that recorded during the preceding three years. The overwinter survival of 48% (Table 9.2) is probably a minimal estimate as some birds may have been involved in relatively long-distance altitudinal migration to upland nesting sites in parts of the adjacent hill country which was not thoroughly checked for breeding birds in 1988. A small minority of birds, no more than two or three, may have remained within the study area and escaped detection on minor side burns.

9.4.2. Variation in Autumn Condition and Overwinter Survival

In this study, pectoralis muscle thicknesses derived from ultrasound measurements were used to generate four condition indices that reflect true variation in the mass or volume of tissue present in the birds concerned. This tissue is primarily protein (see compositional data in Chapter 8) and thus, those birds with large pectoralis muscles for their skeletal size probably have greater potential reserves for use in activities other than flight. Kendall *et al.* (1973) have demonstrated the presence of a labile protein reserve in the sarcoplasm of pectoralis muscles of Red-Billed Queleas *Quelea quelea*. The mass of this tissue fluctuated independently of food availability and they concluded that this protein reserve was available as a source of amino acids. The relative condition of pectoralis muscles in the Dipper has been shown to vary independently of body mass (Table 9.3) in birds caught on several occasions. To some extent, in both sexes, a decline in potential pectoralis protein reserve was observed during the course of the autumn.

In males, this only became apparent during the latter part of the capture period (Figure 9.2). This trend was also apparent in the analyses of Dipper carcasses presented in Chapter 8. Increased lipid storage probably countered this inferred loss of pectoralis mass/volume and hence no significant seasonal trend in body mass was detected.

"Condition indices" based on size-adjusted body mass have been commonly used in many avian ecology studies (e.g. Slagsvold 1982, Summers *et al.* 1987). The findings presented here suggest that these are likely to be poor predictors of overwinter survival in small birds, particularly when the relative dynamics and importance of lipid stores and protein reserves are unknown. Lehikoinen (1986a) was unable to find convincing evidence for enhanced overwinter survival of "fatter" Great Tits *Parus major* and concluded that other factors were more important. This finding is inconsistent with findings presented by Fretwell (1968), who showed that in Field Sparrows *Spizella pusilla*, fatter birds were more likely to survive.

This study has demonstrated that autumn condition is more important for overwinter survival in male than female Dippers. The precise reasons for this are unknown though Bryant & Tatner (1988) have shown that the highest daily energy expenditure and hence requirement for males, outside the brood-rearing period, was in midwinter. These higher running costs may need to be backed up with an insurance policy in the form of greater protein reserves held in the skeletal muscles, notably the pectoralis in Dippers. Marcström and Kenward (1981) have also shown a differential role for autumn condition between the sexes in the Goshawk *Accipiter gentilis*. This species shows reversed size dimorphism and winter survival was enhanced in females with higher early autumn body masses. No such relationship was detected in the smaller males. The results of Haramis *et al.* (1986)

also suggest that autumn condition is more important to males than females in the Canvasback *Aythya valisineria*. In this case, males with higher body mass were more likely to survive overwinter and also had increased annual survival probabilities. Sample sizes for females were smaller but survival tended to be less dependent on body mass.

9.4.3. Body Condition and Breeding Success

Autumn body condition in Dippers failed to influence breeding success the following spring. Successful breeders did not have significantly greater pectoralis protein mass/volume in late autumn. Data from carcass analyses presented in Chapter 8 showed that males appeared to build up their potential pectoralis protein reserves in early spring as the breeding season approached. An ultrasound derived condition index based on the March capture of an individual would perhaps be a better predictor of breeding prospects for a Dipper, or its likelihood of defending a high-quality nesting territory or gaining and keeping a mate.

Body condition in spring has been shown to be of crucial importance in determining breeding success in several Arctic-nesting species of goose. Svalbard nesting Barnacle Goose *Branta leucopsis* females in better spring condition, as judged by abdominal profiles (Owen 1980, 1981), were more likely to return to the wintering grounds the following autumn with families. A similar finding was reported by Ebbinge *et al.* (1982) for Dutch wintering Dark-bellied Brent Geese *Branta bernicla bernicla*, though the "condition index" was based solely on the body mass of females about to migrate to their breeding grounds. In neither, of these studies, were differences in male body condition described or related to breeding success.

CHAPTER TEN

GENERAL DISCUSSION & CONCLUSIONS

10.1. THE SIGNIFICANCE OF BODY SIZE

Dippers are moderately sexually dimorphic, with females about 10% smaller than males in most body size measures. The functional significance of this has rarely been discussed in the extensive Dipper literature (Spitznagel 1985, but see Schmid & Spitznagel 1985). Both natural and sexual selection can act on phenotypic characters such as body size measures that show variation between individuals in a population. Natural selection usually acts on components of fitness that pertain to survival and reproductive success whereas sexual selection occurs in response to mate choice and intrasexual competition (usually between males) and is ultimately related to mating success. Natural and sexual selection can act on characters in the same or opposite directions, where any resulting trade-off generally gives rise to some stability in, for example, body size measures of each sex (Schluter & Smith 1986).

Most authors consider the Dipper to be territorial throughout the year and mainly monogamous: thus, frequent agonistic encounters are likely and such competition between males for territories may give rise to selection for larger body size measures in this sex. In the absence of a need to defend a territory, the smaller size of females may be better for survival in this species as their daily energy expenditure is lower as a result (Bryant & Tatner 1988). Size differences between sexes in the Dipper could also result in some niche partitioning (prey size, habitat) and this in turn may allow males and females to coexist in closer proximity during the non-breeding season than might be expected from their territorial and aggressive behaviour. Potential Dipper pairs indeed consort to some extent during the autumn and winter (D. Bryant pers. comm., own observations). Alatalo *et al.* (1986) and Slagsvold (1986) have both shown that female Pied Flycatchers *Ficedula hypoleuca* choose territory quality rather than male characteristics but the cues used by female Dippers have not been established.

Evidence of natural selection acting on juvenile Dipper body size characters in relation to fitness components such as overwinter survival, home range (=autumn territory) ownership and future breeding success obtained from this study is summarised in Table 10.1. The direction of selection in females varied between years, though overall consistency was evident in only a few characters. There was a tendency for larger females, in terms of wing and tarsus lengths, to establish autumn home ranges and to survive overwinter; and females of low mass in autumn to breed successfully. Very few trends were apparent in the male cohorts, higher autumn masses tended to be associated with successful breeders the following spring. Murphy (1986) has shown that small female Eastern Kingbirds *Tyrannus tyrannus* breed earliest, irrespective of clutch size; also, Dunn (1976) demonstrated that smaller species of tits (Paridae) breed earlier within the same temperate wood level. Perhaps small, early breeding female Dippers acquire higher quality mates and thus nest sites and territories. Davies *et al.* (1988) found that small Lesser Snow Geese *Chen c. caerulescens* recruited to the breeding population at an earlier age and possibly lived longer than larger birds, with no diminution in viability. Despite heritability of body size traits, they failed to detect any reduction in adult body size over five generations. As for Dippers, there was little evidence for persistent directional selection. In this study population of Dippers body size within each sex is optional for the prevailing, broadly stable climatic conditions. Alternatively, size may be held between narrow limits by natural selection, but for much of the time is not subject to detectable selection.

Table 10.1. Relative importance of body size measures in the component processes of recruitment (all years combined, 1985–88).

Autumn biometrics	Juveniles				Adults
	Establish autumn home range	Overwinter survival	Breed successfully	Birds in spring population	Birds in spring population
FEMALES:					
Body mass	0	0	0	0	0
Wing length	++	++	--	--	--
Tarsus length	0	++	-	0	0
Bill length	0	0	0	++	++
Bill depth	0	0	0	0	++
SIZE1	--	0	0	0	0
SIZE3	0	0	-	0	0
MALES:					
Body mass	+	0	0	0	0
SIZE1	+	0	0	0	0
SIZE3	+	0	0	0	0

Note:

++ = character bigger, $p<0.05$
\+ = character bigger, $0.10>p>0.05$
-- = character smaller, $p<0.05$
\- = character smaller, $0.10>p>0.05$
o = no relationship.

Body size has impinged on many aspects in this study of juvenile recruitment. Dominance status in adult Dippers may be influenced largely by plumage badges and status signalling but in juveniles body size appears to hold greater significance. Presumably, larger birds are better in competitive situations and gain access to key autumn resources such as roosts and home ranges with good feeding riffles. Rivers rarely provide continuous, high quality Dipper habitat and thus smaller individuals, including subordinates, can usually find niches by utilising more dispersed resources and flying further to roosts and breeding on hill burns. Dippers residing on deeper stretches of the River Devon lacking riffles often forage mostly by diving from tree root perches and may take a higher proportion of fish in their diets (personal observations). The relative costs and benefits of maintaining a high quality, lowland home range, as opposed to the more flexible behavioural repertoire shown by probable subordinates requires investigation in terms of lifetime fitness or longevity. This inter-relationship of social dominance, habitat quality and geographical dispersal of the species closely fits the models of Gauthreaux (1978) in which all resources in a heterogeneous environment are utilised. The regular seasonal movements of Dippers between upland and lowland (presumed to be high quality) areas probably enables subordinate individuals to monitor home range/territory occupancy and compete for vacancies created by the death of dominant birds.

Outwith the breeding season, the presence of rigid territoriality was difficult to demonstrate in the western Ochils/River Devon study area. At one extreme, some birds were clearly territorial year-round whereas others were more akin to the "floaters" of Smith (1978) and Arcese (1987). Floaters may include both true subordinates continually excluded from areas and middle ranking birds prospecting for vacancies. Under such circumstances, territoriality in Dippers resembles the space-related dominance of Kaufmann (1983). For example, juvenile females comprise the smallest and lowest ranking of the age and sex cohorts in the Dipper. The present study has demonstrated that these small birds often predominate in the autumn/winter and breeding subpopulations residing in upland areas. This could result from both the higher tendency for upland reared females to recruit to upland sites (whereas males competed for lowland home ranges) and also from the competitive exclusion of small birds from lowland stretches of river.

10.2. THE SIGNIFICANCE OF PLUMAGE VARIABILITY

The adaptive significance of plumage variation in passerines is still widely debated. Many authors have investigated relationships between plumage colour, brightness, type or tail ornament length and dominance (Rohwer 1975, Watt *et al.* 1984, Möller 1987a), mating and breeding success (Ralph & Pearson 1971, Andersson 1982, Rõskaft & Järvi 1983, Knapton *et al.* 1984, Möller 1988, 1989) or habitat and territory quality (Knapton & Falls 1982, Studd & Robertson 1985a). Plumage variation is often consistent between age and sex classes and thus may parallel mass or body size differences. Consequently, it is difficult to unravel the independent significance of plumage over age or experience and the interpretations of many results is therefore equivocal. The importance of restricting consideration to within age and sex groups is only now coming to the fore (Whitfield 1987, Jackson *et al.* 1988). The consequences of plumage variability for lifetime reproductive success has yet to be investigated.

Plumage characteristics may be under either weak or strong selective forces. The former may produce near random variability of little obvious fitness benefit though may indicate individual identity, whereas the latter implies that the plumage "signal" communicates important information to potential competitors, mates or perhaps predators.

This study has identified consistent differences between sex and age classes in one of the more striking plumage characteristics of the Dipper – the chestnut or rufous colouring on the breast and belly. Male Dippers are brighter than females while within sexes, juveniles are less bright than adults. The differences between age classes is not the result of selection against (mortality) relatively dull individuals during their first year; juveniles acquire a brighter plumage during their first full moult in their second summer. This entails an increase in the area of chestnut feathering on the breast/belly, sometimes accompanied by a slight tonal deepening in the colour.

Dominance rankings of age and sex classes parallel these inter-class plumage differences, with adult males dominant and juvenile females subordinate. Within age and sex classes, plumage correlated with dominance ranking in adults but not juveniles. Body size was more important in determining dominance status in juvenile classes. There was some evidence for directional selection in plumage characters during the course of this study. The mean autumn plumage scores of juveniles increased between 1985 and 1987, whereas adult females tended to become duller and there was no trend in adult males.

Three hypotheses concerning functional aspects of within- and between-class plumage variability are presently receiving close scrutiny. The central tenet of the status signalling hypothesis (SSH) (Rohwer 1977) is that plumage asymmetry between two or more birds can be used to predict the outcome of agonistic contests. Data from this study are in broad agreement with the SSH, particularly if birds from different age and/or sex classes are grouped, but within classes the predictive value of plumage is much reduced except in adult males. I propose that juveniles in their first autumn and winter are inexperienced in assessing subtle plumage differences and necessarily engage in physical interactions to resolve contests. Through increasing experience in agonistic encounters, juveniles eventually learn to associate big badges with big birds and this allows small birds to avoid contests which they are unlikely to win.

The individual recognition hypothesis (IRH) (Collias 1943) could have an equal role in advertising social status: birds either residing in a relatively stable flock, or coming into contact with relatively few conspecifics, may be able to identify one another by means of distinctive plumage markings. Given prior interactions between such birds, then associations between fighting ability and identity could arise. Although this hypothesis cannot be ruled out in the Dipper, I have no supportive evidence, and the nature of the plumage variability itself does not offer obvious opportunities for unique patterning as has been postulated for the Turnstone *Arenaria interpres* (Ferns 1979, Whitfield 1986, 1988).

The delayed plumage maturation hypothesis (DPMH) (Rohwer *et al.* 1980) was offered to explain why some passerine species bear duller plumage during their first winter and breeding season. DPMH was initially described for North American species showing strong dichromatism between sexes, in which first-year males in particular retain female-like plumage until after their first breeding attempt. Explanations for this phenomenon vary from crypsis and predator avoidance in winter to deception of conspecifics in the breeding season. Female-like young males probably arouse less antagonism from adult males in the vicinity of their breeding territories and thus may allow the former to establish nesting territories themselves. On this view, juvenile male Dippers could be mimicking adult females for much of their first year in order to prevent escalation of agonistic encounters during the non-breeding season and to allow exploration of potential breeding habitat in the spring. Although direct evidence for the Dipper is lacking, indeed some juvenile males are brighter than adults, the hypothesis should not be dismissed.

Finally, Balat (1961) proposed a fourth explanation for plumage variability with particular reference to his Dipper population in Czechoslovakia. He considered that birds residing in narrow canyons (cooler, humid and presumably with less light penetration) during the summer usually moulted into relatively duller coloured breast and belly feathering. My evidence does not support such a hypothesis as juveniles inevitably became brighter in their second year, irrespective of habitat and microclimate, and there was no significant change in adult plumage scores between years. Also, habitat heterogeneity in central Scotland is considerable and the ranging behaviour of many individuals between open and shaded parts of the river system and upland and lowland areas during the year prevented a particular plumage type from conferring any sustained selective advantage.

Clearly, much remains to be discovered about the significance of plumage variability in avian populations, especially with respect to the comparative lifetime fitness of different plumage morphs. The Dipper is a suitable species on which to base such investigations as controlled laboratory assessments of dominance status in relation to plumage and body size variation can be integrated with field assessments of behaviour in the same individuals over periods of several years.

10.3.DISPERSAL

Much recent discussion on juvenile dispersal has dealt with the proximate and ultimate causes and the likely function of dispersal behaviour (Greenwood 1979, Fleischer *et al.* 1984, Lombards 1987, Nilsson 1989). This behaviour in turn has repercussions for the demography of a species and is closely linked to the evolution of mating systems (Greenwood 1980, 1983, Clutton-Brock 1989). Most hypotheses attribute sex or age differences in dispersal to inbreeding avoidance, competition for mates, competition for resources or combinations of the three (Moore & Ali 1984, Packer 1985, Dobson & Jones 1985, Liberg & von Schantz 1985). During the course of this study, approximately 200 breeding attempts were monitored, yet inbreeding was recorded on only two occasions. In both instances, sons bred with their mothers at their natal site; for one it was his first breeding attempt while the other was a two year old. These males may well have initially established themselves close by, after a short dispersive movement, but later replaced their fathers after death or by competitively replacing them. Such a low incidence of inbreeding suggests that virtually all juveniles make some dispersive movement at some time after fledging. Juvenile Dippers rarely show overt signs of pairing behaviour before mid winter (personal observations) and, as most dispersal movements occur during the three months after fledging, competition for resources (food, roost, territory) remains as the factor most likely to influence the distance moved. Access to resources is probably mediated through a dominance hierarchy and this in turn may in part induce dispersal amongst subordinates.

The post-fledging behaviour of Dippers in this study is outlined below. Detailed confirmatory evidence is often lacking, so the outline should more properly be considered a model of juvenile dispersal in Dippers. Fledged young remain dependent on their parents for two to four weeks, often roosting in riverside bushes and trees close to the nest site. Parents probably stop provisioning at approximately two weeks, but do not actively exclude offspring from their territory. During the ensuing two weeks, fledglings either remain within their natal territory or may make a rapid movement to a new daytime range and roost site. Those that move may remain at their first chosen site and attempt to establish themselves or on subsequent days make further rapid moves, presumably until a satisfactory site is located. There is no evidence that intraspecific aggression at this stage influences greatly the likelihood of settlement, though the effect of the presence of conspecifics (i.e. earlier arrived fledglings/juveniles and resident adults) is unknown. Such movement to the primary site of settlement is termed "Phase 1" of autumn dispersal, and occurs at a time when adults are generally rather secretive during their summer moult and are tolerant of unrelated fledglings. Most first brood young have fledged by early to mid June and thus the period with greatest flux is the second half of June and first half of July. In late July and August, fledglings start moulting out their juvenile plumage and interactions develop sufficiently for local hierarchies to appear. Towards the end of the period, the adults also emerge from moult and they begin to reestablish their territories and home ranges. This marks the onset of "Phase 2" of autumn dispersal. Higher ranking juveniles are able to compete with adults for territories, and in rare cases may oust them, and thus remain in their primary locale. Low ranking birds probably move to poorer quality areas, where they experience less intense competition, and attempt to settle. Some juveniles may fail to get established and such excluded birds may die or be more susceptible to predation.

The model outlined above combines dispersal, dominance and territoriality as a unified dynamic process which only approaches resolution in September or October. This model can provide both proximate and ultimate justification for most of the points on sex differences in dispersal distance outlined in Chapter 6. Females were shown to move farther than males eventually (i.e. after Phase 2), though initially (i.e.after Phase 1) they are often close to their natal site, with apparent dispersal distances similar to those of males. Juvenile females, the smallest and lowest ranking age/sex class, also commonly end up wintering at the lowest densities and probably in the poorest quality areas, such as small upland burns. However this apparent disadvantage may confer some benefits in that such birds would not undergo a spring altitudinal migration and could prospect potential nest sites during the non-breeding season. They are later joined by lower ranking males that are likely to have failed to establish lowland breeding territories.

The least understood component of this model is the factor that stimulates the initial break from the natal territory. Other authors have noted this phenomenon in small birds (Goodbody 1952, Weise & Meyer 1979) and supposed it is a preprogrammed dispersal mechanism (Howard 1960). Several studies have shown that siblings tend to disperse approximately similar distances Keppie 1980, Newton & Marquiss 1983, this study), but the consistency of dominance status within members of a brood, and its relationship to this preprogrammed mechanism, is unknown at this stage.

Dispersal distance *per se* may not always be the most relevant measure on which to evaluate an individual's competitive performance. Arcese (1989) has suggested that the time interval between fledging and settlement is a better measure with more biological significance. Patterns emerging from detailed studies of the post-fledging/settlement period lend support to this idea. Nilsson (1989) has shown that male Marsh Tits *Parus montanus* tried to become established as soon as possible after independence. Individuals from early nests dispersed less and were better at establishing themselves, whereas later birds were less successful, primarily because of negative effects related to the density of established birds. Nilsson (1989) also considered that males did not select sites on the basis of habitat quality and that, once established, dispersal distances did not affect survival or eventual breeding performance. Nuthatches *Sitta europaea* of both sexes likewise attempt to settle soon after independence (Matthysen 1987). In this case, there is competition for better quality territories and this suggests that earliest fledged birds will be more successful. However, Nuthatches are unusual in that they settle as territorial pairs (usually by the end of June) and this may partly explain why there is no difference in dispersal distance between the sexes (Matthysen & Schmidt 1987). Marsh Tits do show a sexual difference in dispersal distance; Nilsson (1989) attributes the greater distance moved by females to a searching strategy for suitable (presumably higher quality) sites. Larger females, especially from early nests, moved farther and had higher lifetime reproductive success. Earlier work on this species (Nilsson & Smith 1985) indicated the possible importance of dominance from an early age: early dispersers from family parties were larger individuals that were likely to become dominants. Small siblings remained in the safety of their natal territory for longer, while improving foraging skills, but at the same time the likelihood of rapid settlement was reduced. Eden (1987a, 1987b) has recorded the reverse pattern in Magpies *Pica pica*. The dominant fledglings remain in the natal territory and subordinates disperse to join a flock. Those in the flock had reduced overwinter survival probabilities compared to the philopatric individuals but, within the flock, the earliest to arrive were most dominant and presumably had better breeding and survival prospects.

In these studies and others (Arcese & Smith 1985, Nilsson & Smith 1988), relative age is clearly of key significance for settlement, dominance and the survival prospects for recently independent birds. Yet fledging age is solely dependent on how early in the season parents begin breeding. This will partly be determined by the seasonality of resources (Perrins 1970, Bryant 1975). Many intriguing questions remain on the relative importance of individual quality versus habitat quality, or chance factors, in determining laying date relative to that caused by within and between year variations in food supply and other resources.

10.4. BODY COMPOSITION, CONDITION & SURVIVAL

The study of seasonal variation in avian body composition and condition, as well as that occurring between individuals, has generated a plethora of vague terms and definitions. Frequently, "condition" is cited in a study when body mass was the only variable measured (Crick & Fry 1986, Meijer *et al.* 1988). Also, confusion is caused by the inconsistent use of terms such as "lipid index" (LiI). Most authors (Dunn 1975, O'Connor 1977, Bryant & Gardiner 1978, Johnston *et al.* 1985, this study) define lipid index as lipid mass/lean dry mass whereas Evans & Smith (1975), Pienkowski *et al.* (1979) and Davidson (1984) misleadingly refer to LiI as lipid mass/whole-body (= wet or live) mass, a ratio more usually termed "percentage lipid". There is obviously a need for some uniformity of treatment, or at least presentation of all data to enable comparison of the different indices.

The importance of lipid storage and utilisation in the annual cycle of many species is well known (Blem 1976, White & West 1977, Carey *et al.* 1978, Summers & Waltner 1978) and lipid content can usually be estimated for live birds from body mass and body size measures with some precision (Bailey 1979, Wishart 1979, Iverson & Vohs 1982, Davidson 1983, Piersma 1984). Other proven techniques include visual fat scoring (Fry *et al.* 1970, Owen 1981, Bryant & Westerterp 1983, Jones 1987) and the use of ultrasound-based techniques has shown some potential (Baldassarre *et al.* 1980) but has not been tested thoroughly in the field. However, measurement of the protein content/component of live birds has proved less practicable and has rarely been attempted (but see Davidson 1979 and Sibly *et al.* 1987), probably because variation is not so marked as in lipid. This situation has arisen despite the supposed importance of some muscles as potential reserves for use during breeding (Kendall *et al.* 1973, Jones & Ward 1976, Houston *et al.* 1983) or moult (Ward 1969, Baggott 1975).

This study has demonstrated that assessment of pectoralis muscle thickness in the field is feasible using ultrasound devices because such measurements are strongly correlated with the mass and volume of muscle tissue present. Sears (1988) has already successfully used this technique on Mute Swans *Cygnus olor* and further studies on a wider range of species should be encouraged. This is, however, the first study to demonstrate the fitness consequences of muscle mass variation measured in this way.

To be of value, condition indices should be size-adjusted indicators of lipid stores or protein reserves that give some demonstrable benefit in terms of survival probability (Table 10.2) or enhanced reproductive success to the individuals concerned. This study has shown that pectoralis muscle volume, a presumed correlate of the labile protein reserve, declined in both male and female Dippers through the course of the autumn. The autumn condition index was a predictor of overwinter survival for male but not for female Dippers. The predictive value of the muscle index was especially valuable because the decline in the protein reserve was apparently matched by increased lipid deposition resulting in relatively constant body mass through the course of the winter. During the spring, constancy of mass in males masked the build-up of pectoralis protein reserves at the expense of lipid stores. The spring body composition of female Dippers is unknown, although some females may gain as much as 10g during laying and incubation (Bryant & Tatner 1988, personal observations). Krementz & Ankney (1988) showed no variation in mass of female House Sparrows *Passer domesticus* during this period whereas female Starlings *Sturnus vulgaris* studied by Ricklefs and Hussell (1984)

Table 10.2. Summary of studies investigating relationships between condition and overwinter survival.

Species	Sex/age class	Condition factor measured	When assessed	Overwinter survival benefit	Reference
Canvasback	A, M A, F J, M, F	Standardised body mass	Dec-Mar	++ o +	Haramis *et al.* (1986)
Field Sparrow	n.d.	Fat score	Dec-Jan	++	Fretwell 1968
Goshawk	M F	Body mass	Aug-Mar Oct-Jan	o ++	Marcström & Kenward (1981)
Dipper	M F	Pectoralis muscle thickness	Oct-Nov	++ o	This study
Great Tit	A, M J, M A, F J, F	Fat score	Nov-Dec	o o o o	Lehikoinen (1986a)

Note:

Abbreviations:

A, J, M, F = Adult, juvenile, male, female respectively.
++ = strong positive relationship between condition and survival.
+ = weak positive relationship between condition and survival.
o = no detectable realtionship between condition and survival.
n.d. = not differentiated.

showed comparable mass changes to Dippers. Thus, it seems unwise to speculate on whether this mass increase is the result of increased lipid stores or build up of protein reserves or primarily represents development of the reproductive organs.

Dippers in the present study in central Scotland are unusual amongst temperate resident passerines, in showing no mass increase in mid-winter (= "winter-fattening"). However, Dippers wintering at 60°N in Finland did show signs of fattening in December and January, detectable as mass changes (Lehikoinen & Hakala 1988) but not to the extent recorded in Yellowhammers *Emberiza citrinella* (Evans 1969) and Bullfinch *Pyrrhula pyrrhula* (Newton 1969).

Some unknown advantage (possibly aerodynamic or hydrodynamic) may accrue to Dippers (in the present study for central Scotland) in maintaining a constant mass throughout autumn and winter. Alternatively, and more likely, this may be the result of a balance between the maintenance of pectoralis condition, which may enhance long-term prospects, and the deposition of more easily mobilised lipid necessary for short-term, and overnight survival. During adverse winter conditions, when replenishment of lipid on a daily basis may prove inadequate, those Dippers with greater potential protein reserves could supplement their daily energy budgets by mobilisation of such reserves. Smaller Dippers (i.e.females) have lower daily energy expenditures (Bryant *et al.* 1985, Bryant & Tatner 1988) and in absolute terms their food requirements will therefore be less, resulting in less dependence on nutrient stores and reserves.

Marsh (1984) has shown that muscle fibre hypertrophy was not responsible for the increase in pectoralis muscle mass recorded during pre-migratory fattening in Gray Catbirds *Dumetella carolinensis*. He also argued that the increase in pectoralis tissue was in response to increased load (overall body mass) and "exercise" usage, and concluded that maintenance of a protein reserve for mobilisation in times of increased demand was unlikely. During the annual cycle, daily energy expenditure and apparent foraging rate of male Dippers was at its highest in spring (Bryant & Tatner 1988). This implies a high level of activity which in turn may induce the second increase in pectoralis protein volume/mass, as observed in this study during March and April. Such potential "reserves" may not be primarily intended for improvement of fecundity but instead, generate the power to facilitate high levels of activity (including territorial contests) in spring.

10.5. POPULATION REGULATION

Dipper populations in the British Isles have been monitored by the British Trust for Ornithology's Waterways Bird Survey since 1974. Annual indices of the breeding population were exceptionally stable between 1974 and 1983 (Carter 1989). Since that date, the index has risen slightly, but the year to year stability of the index over the 15 year period remains notable compared to the often dramatic fluctuations shown by most other riparian species. Williams *et al.* (1988) monitored numbers of riparian species in the Blackwater catchment of Northern Ireland before and after an extensive drainage scheme which involved dredging and canalisation of the rivers. Again, Dipper numbers remained constant, despite this major alteration to their habitat, whereas five other riparian species declined considerably.

Virtually all demographic parameters monitored in this study showed an exceptional constancy (Figure 10.1): the proportion of juveniles and the sex ratio in the mid to late autumn (45-50%); the number of breeding attempts; clutch size; the number of young fledged per breeding attempt and the number of known origin (ringed as nestlings) recruits. Klomp (1980) has argued that such stability indicates density-dependence is involved

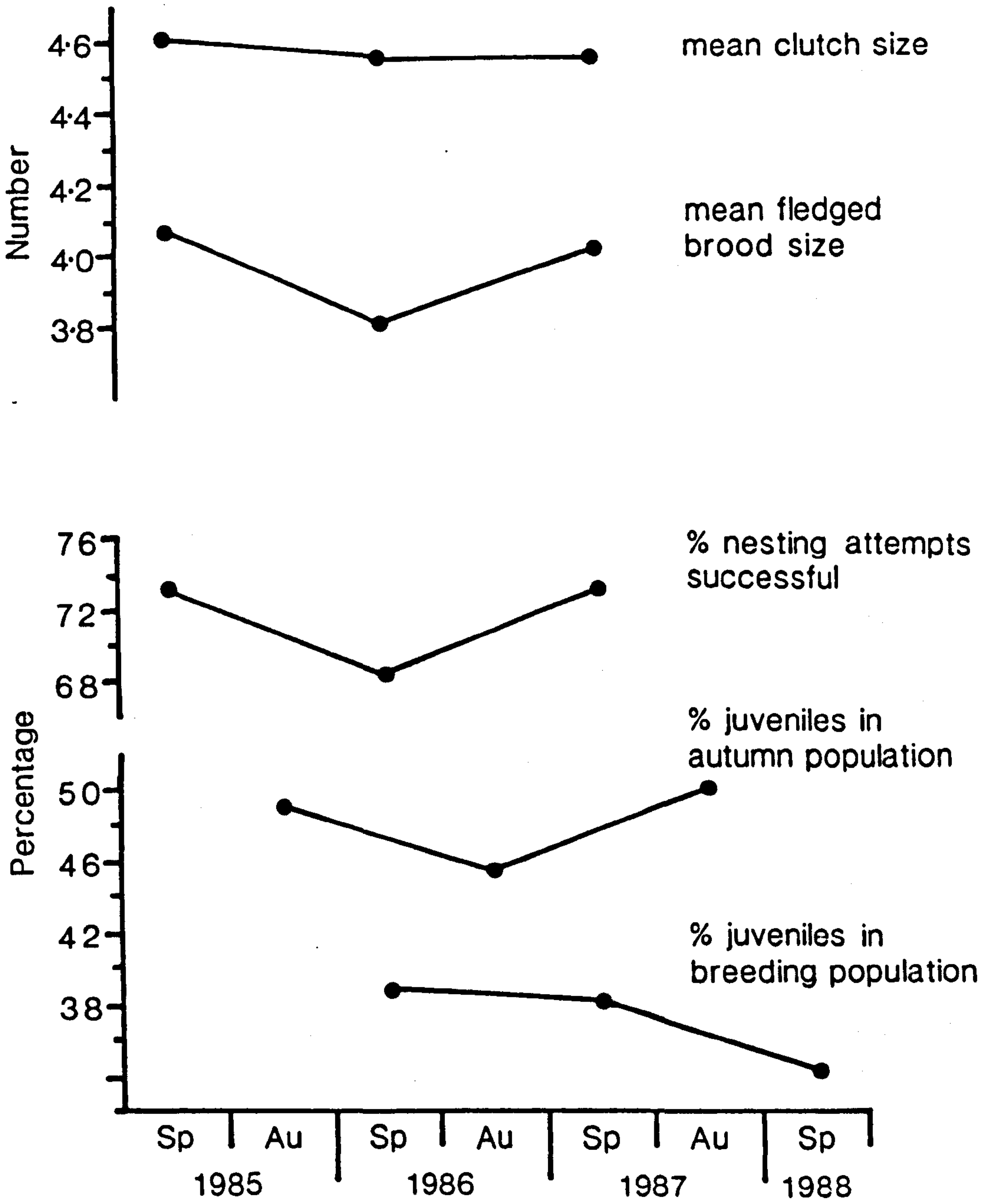


Fig. 10.1 Demographic parameters from a Dipper population in Central Scotland, 1985-1988.

in the regulatory process. Even so, the constancy of climatic conditions during the study gave little opportunity for observing any marked effects of weather on population size or breeding success.

At this stage, it is useful to identify the factors underlying this overall stability. Potential limiting factors in Dippers (i.e. those resources individuals compete for and defend) include space – territory or home range – roosts, food and nest sites. The relative importance of these was not demonstrated directly and further, may change between seasons or may differ between age or sex classes. In the course of the study, none of these resources was known to have changed significantly, although food availability was not monitored.

Changes in the timing and degree of mortality and emigration/immigration presumably caused Dipper numbers to be matched to available resources. Two periods of high juvenile losses were identified: the initial post-independence period (centred around "Phase 1" of autumn dispersal) and later during October and November. Predation of inexperienced fledglings was thought to be important in the former, yet this was unlikely to be perfectly density-dependent. The agent of late autumn losses was not apparent, but probably involved "territorial" intolerance and exclusion of subordinates to fringe habitats where they were vulnerable to predators and food inaccessibility during spates.

Many studies have demonstrated the importance of territoriality with the approach of breeding in population regulation (Brown 1969, Klomp 1980, Patterson 1980, Drent 1983, Tinbergen *et al.* 1987), with density-dependent mortality and emigration one of the factors involved. However, in some instances passerine breeding territories are compressible (e.g. Nuthatch, Nilsson 1987) where, in those seasons following an autumn with a good beech mast crop, breeding densities are higher and territory size reduced. This situation does not pertain in the Dipper, as the number of breeding territories on a given stretch of river is almost constant and thus recruitment of juveniles is probably mainly controlled by vacancies arising due to adult mortality (see also Newton & Marquiss 1986). The seasonal distribution of adult Dipper mortality was not determined in this study, but it is presumably spread throughout the year and vacancies are filled by the highest ranking individuals from the local "pool" of juveniles. Furthermore, some adult deaths or displacements may be induced by competition from dominant juveniles in early autumn.

Breeding territories seem to be the principal limiting resource in Dipper populations. The nest box experiments showed that Dippers could be encouraged to nest in areas with no "natural" nest sites but existing territories were not compressed in areas with sufficient natural sites. Ormerod *et al.* (1985a, 1985b) have shown strong correlations between larval invertebrate abundance and the density of breeding Dippers. Presumably breeding territory size and thus spring population density is governed by the food resource base needed to provision an incubating female and brood successfully.

10.6. CONCLUSIONS

The research work presented in this thesis has focussed on movements, dominance, body condition and biometrics of Dippers and on assessing their importance in relation to overwinter survival and, for juveniles, recruitment to the breeding population. The interplay between these factors and the variation in presumed heritable or parentally controlled traits such as body size, plumage variation, innate dispersal tendency and natal habitat, have been investigated during a three year period characterised by generally benign weather conditions. There was little evidence for consistent directional selection on such traits and some prolonged or dramatic perturbation (meteorological or habitat change) would be necessary to assess properly their adaptive significance.

Three new techniques were introduced and their potential evaluated in the study of recruitment dynamics in resident passerines. Firstly, the ultrasonic flaw detector was used to measure variation in pectoralis muscle thickness in a sample of autumn caught birds. Condition indices derived from such measurements were able to identify overwinter survivors in the samples of males but not in females. However, this result does not exclude the possible importance of body condition in females at other stages in the annual cycle, such as during the pre-breeding period (February - March) or soon after independence in their first summer/early autumn (July - September). Future work should be directed towards a biannual assessment of condition at these times to investigate its effect on breeding success and on entry to the overwintering population. The interpretation of spring condition indices would require a small sample of female Dippers to be taken for carcass analysis.

Secondly, a technique was developed for assessing dominance relations of free-living birds under controlled laboratory conditions. The "test arena" and experimental protocol used result in minimal interference with a wild bird's normal daily routine. Although only samples of 4-6 birds can be handled at a time using this technique, the results obtained from birds used on several occasions with different, randomly collected opponents yielded consistent measures of dominance. The general pattern of dominance observed here was typical of many other passerine species, with males dominant over females and, within age classes, adults dominant over juveniles. Plumage brightness, in Dippers best described by the relative size of the rufous/chestnut plumage on the breast and belly, was the most reliable indicator of status in adults, whereas body size was more important in juveniles. Further work using the dominance test arena will establish the consistency of these correlates of dominance and will allow the significance of social status to be investigated more thoroughly without bringing all individuals into the laboratory.

Thirdly, many studies in population and behavioural ecology have used density manipulations to answer pertinent questions. Almost invariably, however, these have involved removal experiments. Here, I have demonstrated that introductions are feasible and that, in some cases, the introduced individuals can be followed through all component processes between independence and recruitment to the breeding population. Introductions have the advantage over removals in studies of recruitment in that they simultaneously standardise timing of arrival at a site, habitat quality and the density of resident conspecifics.

A combination of proven approaches, such as the doubly-labelled water ($D_2{}^{18}O$) technique for measurement of energy expenditure and radio-tracking of movements used alongside assessment of body condition and dominance, could provide a powerful suite of techniques for unravelling the details of recruitment processes in avian populations. In particular, use of ultrasound condition assessment, dominance testing in an arena, $D_2{}^{18}O$ and radio-tracking during autumn introductions of Dippers, could demonstrate the pattern, energetic cost and key factors in home range establishment, and the extent to which it is influenced by condition and status, and also illuminate the fate of those juveniles which neither establish a home range nor recruit the following year.

CHAPTER ELEVEN

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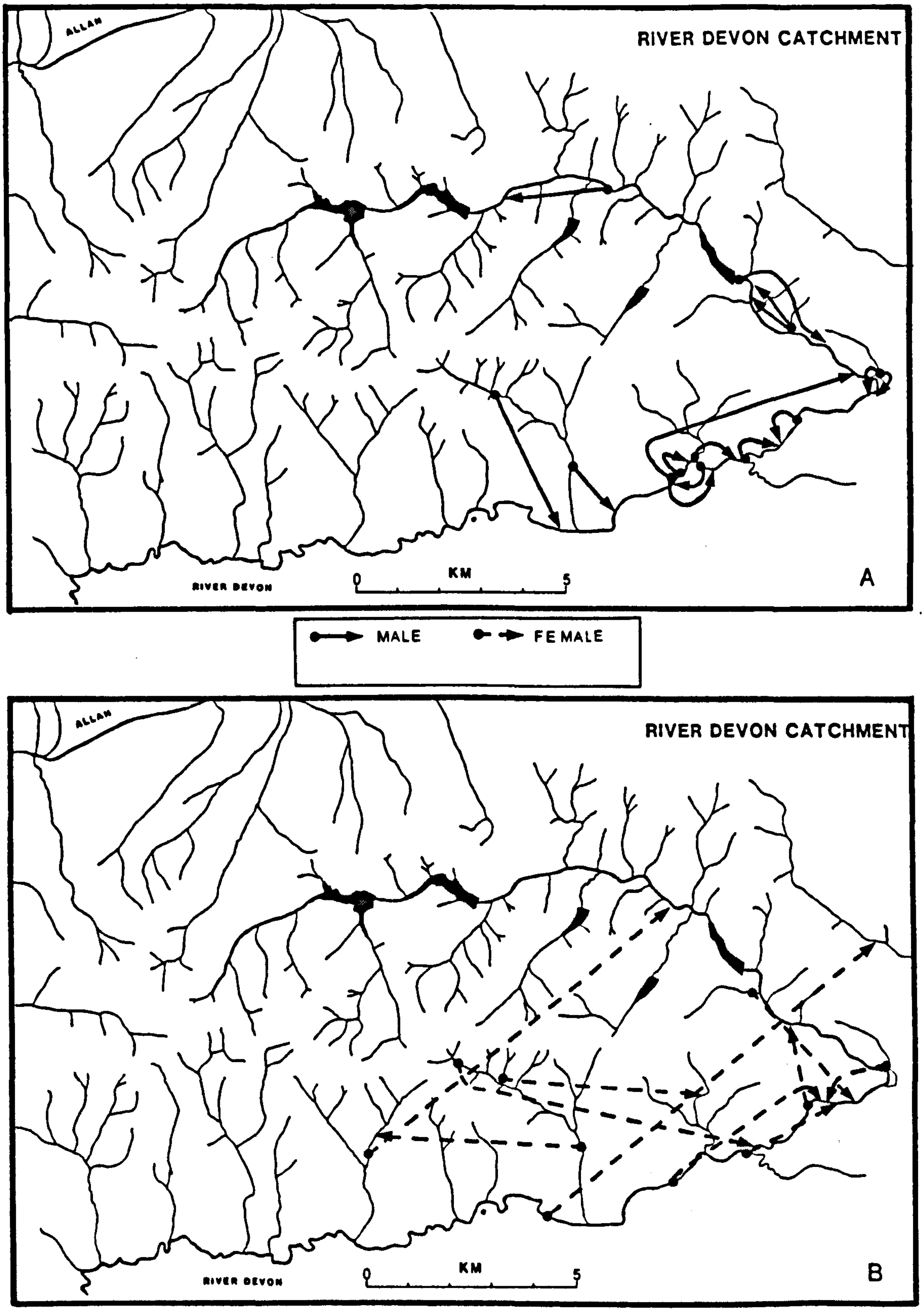
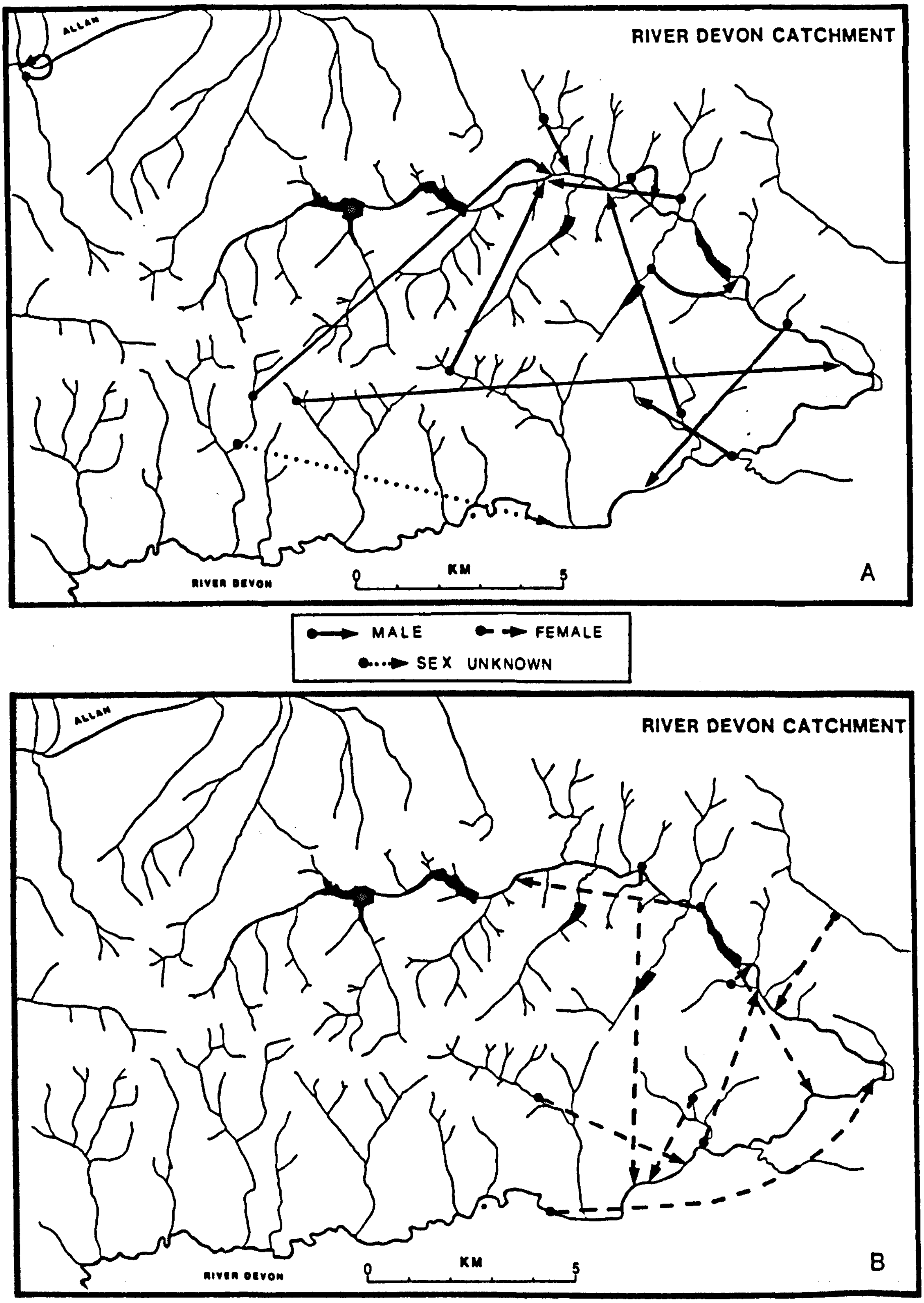
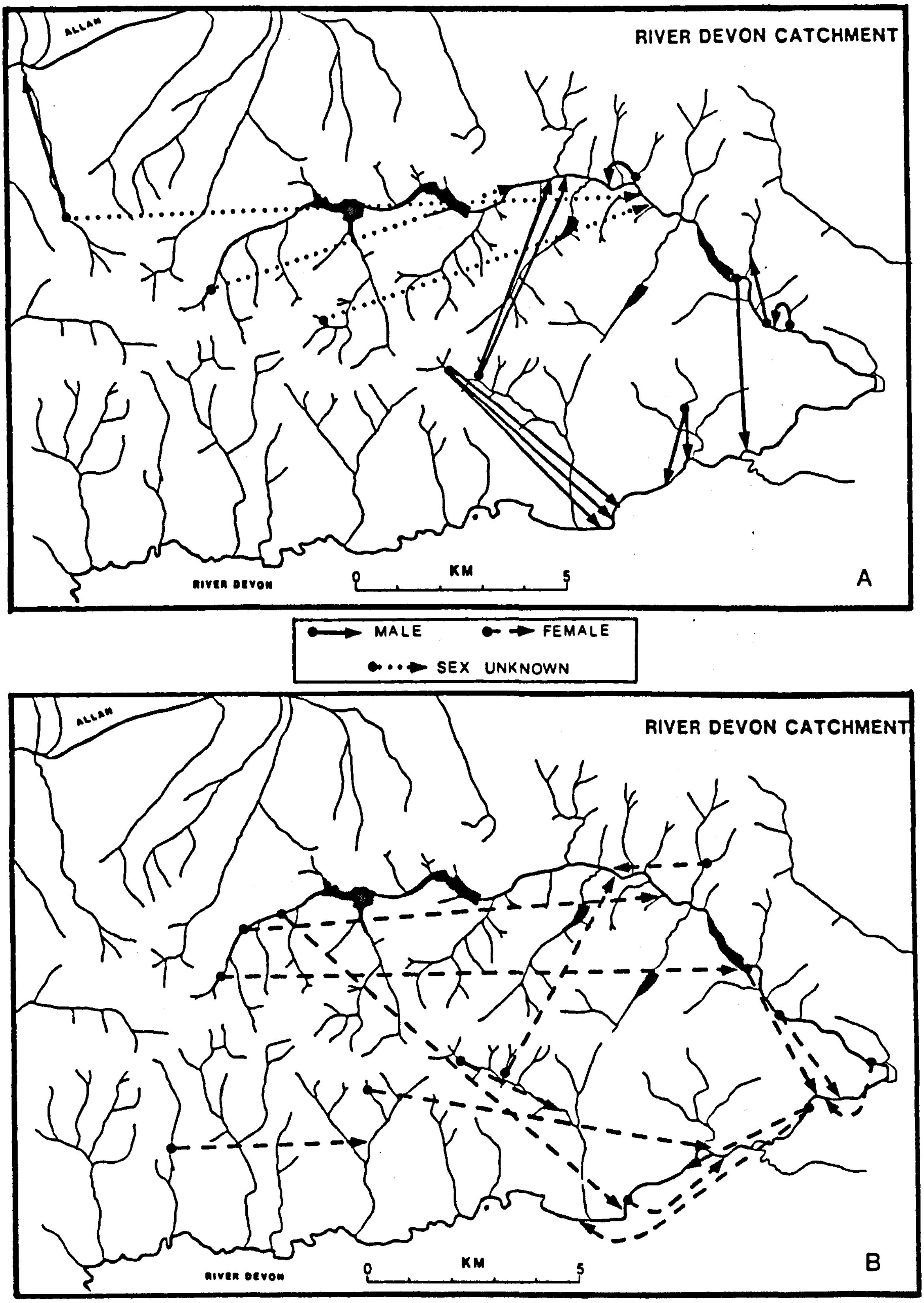


Appendix Fig. 1 Dispersal of juvenile male (A) and female (B) Dippers between natal sites and autumn home ranges, 1985.



Appendix Fig.2 Dispersal of juvenile male (A) and female (B) Dippers between natal sites and autumn home ranges, 1986.



Appendix Fig. 3 Dispersal of juvenile male (A) and female (B) Dippers between natal sites and autumn home ranges, 1987.

Table A. Short term sightings of resident and introduced birds, river section 05, September - October 1986.

			September (——— Date After Release ———) October															
			17	24	26	27	29	1	3	5	7	8	8	9	10	13	15	17
Days after second release												0	0.5	1	2	5	7	9
Days after first release			-9	-2	0	1	3	5	7	9	11	12	12.5	13	14	17	19	21
Ring	Age	Sex																
44898	A	M	++	++	--	++	++	++	XX	XX	++	--	XX	++	++	XX	++	XX
84815	A	M	XX	++	--	XX	++	XX	++	++	++	--	XX	++	++	XX	++	XX
84904	A	M	++	++	--	++	++	++	++	++	++	--	++	++	++	++	++	++
84907	A	M	++	++	--	XX	++	XX	++	++	++	--	++	++	XX	XX	XX	++
93501	A	M	++	++	--	++	++	++	++	++	++	--	++	++	XX	++	++	XX
05076	A	F	++	XX	--	++	XX	XX	XX	XX	XX	--	XX	XX	XX	XX	XX	XX
05157	A	F	XX	++	--	XX	XX	++	XX	XX	++	--	++	++	++	++	XX	++
84821	A	F	XX	++	--	++	++	++	++	++	++	--	++	++	++	XX	++	XX
84905	A	F	XX	++	--	++	++	XX	++	++	XX	--	++	++	++	++	++	++
84908	A	F	XX	++	--	XX	++	++	++	++	++	--	XX	++	++	++	XX	++
84909	A	F	++	XX	--	XX	++	++	++	++	XX	--	++	++	XX	++	XX	XX
93503	A	F	..	++	--	++	++	++	++	++	++	--	++	++	++	++	++	++
93504	A	F	++	++	--	++	++	XX	XX	++	XX	--	++	XX	XX	XX	XX	XX
21984	J	M	XX	XX	--	++	XX	++	XX	XX	XX	--	XX	XX	XX	XX	XX	XX
21813	J	F	XX	++	--	++	XX	++	++	++	++	--	++	++	XX	++	XX	XX
84846	J	F	XX	XX	--	XX	XX	XX	XX	++	XX	--	XX	XX	XX	XX	XX	XX
84861	J	F	XX	XX	--	XX	XX	XX	XX	XX	XX	--	XX	XX	XX	++	XX	XX
84866	J	F	..	++	--	++	XX	++	++	XX	XX	--	++	++	++	++	++	++
93502	J	F	..	++	--	++	XX	++	++	++	++	--	++	++	++	++	++	++
93505	J	F	..	++	--	XX	XX	XX	XX	++	XX	--	XX	XX	XX	XX	XX	XX
93506	J	F	..	++	--	++	XX	XX	++	XX	++	--	XX	++	++	++	++	++
UNR01	J	?	XX	XX	--	++	++	XX	++	XX	XX	--	XX	++	XX	XX	XX	XX
UNR02	J	?	XX	XX	--	XX	XX	XX	++	++	XX	--	XX	++	++	XX	XX	XX
UNR03	J	?	XX	XX	--	XX	XX	XX	++	XX	XX	--	++	XX	XX	XX	XX	++
05047	J	M	Note 1		++R	?	XX	XX	XX	XX	XX	--	++	XX	XX	XX	XX	XX
05048	J	M	Note 1		++R	++	++	++	++	XX	XX	--	XX	XX	XX	XX	XX	XX
05049	J	M	Note 1		++R	++	XX	XX	XX	XX	XX	--	XX	XX	XX	XX	XX	XX
05050	J	M	Note 1		++R	++	++	XX	++	XX	XX	--	XX	XX	XX	XX	XX	XX
05260	J	M	Note 1		++R	++	++	++	XX	XX	XX	--	++	XX	XX	XX	XX	XX
05258	J	M	Note 2									++R	XX	XX	XX	XX	XX	XX
05261	J	M	Note 2									++R	++	XX	XX	XX	XX	XX
05268	J	F	Note 2									++R	++	++	XX	++	XX	XX
05269	J	M	Note 2									++R	XX	XX	XX	XX	XX	XX
05270	J	F	Note 2									++R	++	++	++	XX	XX	XX

Notes:

1. This represents Release 1.
2. This represents Release 2.
3. Abbreviations used are:

A	adult
J	juvenile
M	male
F	female
++	sighted in study area
xx	not located
??	probably present
?	sex unknown
--	no census
R	released
..	not yet ringed

Table B. Short term sightings of resident and introduced birds, river section 02 (mid), December 1986.

			Date after release: Dec →					
			5	6	8	9	10	12
Days after release			-3	-2	0	1	2	4
Ring	Age	Sex						
05097	A	M	++	++	--	xx	xx	++
44848	A	M	++	++	--	++	xx	++
44896	A	M	xx	++	--	++	++	xx
84815	A	M	xx	(++)	--	++	xx	xx
84901	A	M	++	xx	--	++	++	++
84904	A	M	xx	(++)	--	xx	xx	++
84912	A	M	xx	xx	--	xx	xx	++
05152	A	F	++	++	--	++	++	xx
29278	A	F	xx	++	--	xx	xx	++
84809	A	F	xx	++	--	xx	++	++
84817	A	F	++	xx	--	++	++	xx
84821	A	F	++	++	--	xx	++	xx
05261	J	M	xx	xx	--	++	++	xx
84859	J	M	xx	++	--	xx	xx	xx
84867	J	M	xx	xx	--	xx	++	xx
84868	J	M	++	++	--	++	++	++
21940	J	F	xx	++	--	++	xx	xx
84847	J	F	++	xx	--	xx	xx	xx
84860	J	F	xx	xx	--	++	xx	xx
UNR01	J	?	++	xx	--	++	++	xx
05277	A	F	Note 1		++R	xx	xx	xx
05278	A	M	Note 1		++R	xx	xx	xx
05279	J	M	Note 1		++R	++	++	xx
05280	A	M	Note 1		++R	xx	xx	xx
05281	J	F	Note 1		++R	++	xx	xx
55170	A	M	Note 1		++R	xx	xx	xx

Note 1: This represents Release (3).

Note 2: Abbreviations:

A	adult
J	juvenile
M	male
F	female
++	sighted in study area
xx	not located
--	no census
R	released
(++)	sighted just downstream of study area.

Table C. Short-term sightings of resident and introduced birds, river section 05, July-September 1987.

			July (—— Date After Release ——) September																				
			20	21	22	22	23	24	25	26	27	30	2	19	20	21	22	23	25	27	29	15	26
Days after second release															0	1	2	3	5	7	9	26	37
Days after first release			-2	-1	0	0.5	1	2	3	4	5	8	11	28	29	30	31	32	34	36	38	55	66
Ring	Age	Sex																					
05261	A	M	++	++	--	xx	++	++	++	xx	++	++	++	xx	--	++	xx	++	++	xx	xx	xx	xx
44898	A	M	xx	xx	--	++	++	xx	xx	xx	xx	xx	++	xx	--	xx	xx	xx	xx	xx	xx	xx	xx
84815	A	M	xx	++	--	xx	xx	xx	xx	xx	xx	xx	xx	xx	--	++	++	++	++	++	++	xx	++
84901	A	M	++	xx	--	xx	++	++	++	++	xx	xx	++	xx	--	xx	xx	++	++	xx	++	xx	xx
84904	A	M	++	xx	--	++	xx	++	++	xx	++	++	++	++	--	++	++	++	++	++	++	++	xx
05157	A	F	xx	xx	--	xx	xx	xx	++	xx	xx	++	++	xx	--	++	++	++	++	++	++	++	xx
05282	A	F	xx	++	--	xx	xx	++	xx	xx	xx	xx	xx	++	--	xx	++	++	++	++	++	xx	xx
21813	A	F	++	xx	--	++	++	++	++	++	++	++	++	xx	--	++	++	++	++	xx	++	++	xx
84909	A	F	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	xx	++	--	++	xx	++	xx	xx	++	xx	xx
84975	A	F	++	++	--	xx	xx	xx	xx	xx	++	xx	++	++	--	xx	++	xx	xx	xx	xx	xx	xx
93502	A	F	xx	++	--	xx	++	++	++	xx	xx	xx	xx	xx	--	xx	xx	xx	xx	xx	++	++	xx
93503	A	F	xx	++	--	++	++	++	xx	++	xx	++	++	xx	--	++	++	++	++	xx	++	xx	xx
05298	J	M	xx	++^{4}	--	xx	xx	xx	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	xx
93669	J UNR02	M	xx	++	--	++^{3}	xx	++^{3}	xx	xx	xx	++^{4}	xx	++^{5}	--	xx	++^{5}	xx	++	xx	++	xx	xx
84872	J	F	++^{2}	++	--	++^{2}	++	++	xx	xx	++^{4}	++^{4}	++^{4}	xx	--	xx	++^{5}	++^{5}	xx	xx	++	++	xx
84875	J	F	++^{4}	xx	--	xx	++^{4}	++^{4}	++^{4}	++	xx	++^{4}	++^{4}	++^{5}	--	xx	++^{5}	++	xx	xx	++	++	++
84893	J	F	xx	++^{1}	--	++^{1}	xx	xx	xx	++^{2}	xx	xx	xx	xx	--	xx	++^{5}	xx	++^{5}	xx	xx	xx	xx
84895	J	F	++^{1}	++^{2}	--	xx	xx	++^{2}	++^{2}	++	++	++	xx	++^{5}	--	xx	++^{5}	++^{5}	xx	xx	xx	xx	xx
93551	J	F	xx	++^{4}	--	xx	xx	xx	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	xx
93663	J	F	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	++^{5}	xx	xx	++^{5}	++
05238	J	?	++^{2}	xx	--	++^{2}	++^{2}	++	xx	++^{3}	xx	++^{3}	xx	++^{5}	--	xx	xx	xx	xx	xx	xx	xx	xx
84885	J	?	xx	xx	--	xx	++^{2}	xx	xx	++^{3}	++^{3}	++^{3}	++^{4}	xx	--	++^{5}	++^{5}	xx	xx	xx	++	xx	xx
93654	J	?	++^{0}	xx	--	xx	xx	xx	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	xx
UNR01	J	?	++	xx	++	xx	++^{2}	++^{2}	xx	++^{2}	++^{2}	xx	xx	xx	--	++^{5}	xx	xx	xx	xx	xx	xx	xx
05227	J	F	Release 4		++R3	++	++	xx	xx	xx	++^{4}	++	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	xx
93536	J	M	Release 4		++R2	++^{2}	++	xx	xx	++	xx	xx	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	xx
93656	J	M	Release 4		++R4	xx	++	++	xx	xx	xx	++^{5}	++^{5}	++^{5}	--	++	xx	xx	xx	xx	xx	xx	xx
93657	J	M	Release 4		++R4	xx	++	xx	++^{4}	xx	++	xx	++^{5}	++^{5}	--	xx	++^{5}	++	++	++	++	xx	xx
93658	J	F	Release 4		++R0	++	xx	xx	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	xx
93647	J	M												Release 5	++R2	xx	xx	xx	xx	xx	xx	xx	xx
93665	J	F												Release 5	++R1	++^{1}	xx	xx	xx	xx	xx	xx	xx
93666	J	M												Release 5	++R5	xx	xx	++^{5}	xx	++^{5}	xx	xx	xx
93667	J	M												Release 5	++R5	++^{5}	xx	xx	xx	xx	xx	xx	xx
93668	J	F												Release 5	++R2	xx	++^{2}	xx	++^{2}	++^{2}	++^{2}	++^{4}	++^{5}

Abbreviations:

A = adult;J = juvenile;M = male;f = female;
? = sex unknown;++ = sighted in the study area;
xx = not located;-- = no census;R = released,
0, 1, 2, 3, 4 & 5 = post-juvenile moult stages.

Table D. Short-term sightings of resident and introduced birds, river section 02 (upper), September - October 1987.

			September (—— Date After Release ——) October														
			1	3	4	4	5	6	7	11	18	28	1	1	2	3	5
Days after second release													0	0.5	1	2	4
Days after first release			-3	-1	0	0.5	1	2	3	7	14	24	27	27.5	28	29	31
Ring	Age	Sex															
05269	A	M	xx	++	--	++	(++)	xx	++	++	xx	++	--	xx	++	++	++
84804	A	M	++	xx	--	xx	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx
84851	A	M	xx	++	--	++	xx	++	++	++	xx	++	--	++	++	++	++
05080	A	F	++	++	--	xx	xx	++	xx	++	xx	++	--	++	++	++	++
05152	A	F	xx	xx	--	xx	xx	++	xx	xx	xx	++	--	++	++	++	++
84803	A	F	xx	xx	--	++	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx
84809	A	F	++	++	--	xx	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx
84852	A	F	++	++	--	++	++	++	++	xx	++	++	--	++	++	++	xx
51201	J	M	++	xx	--	xx	xx	xx	xx	xx	xx	xx	--	++	xx	xx	xx
84874	J	M	xx	++^{5}	--	xx	++	xx	xx	++	++	xx	--	xx	xx	xx	xx
84882	J	M	++	++^{5}	--	++	xx	++	xx	xx	xx	++	--	xx	xx	xx	xx
84900	J	M	++	++^{5}	--	xx	xx	++	++	++	++	xx	--	xx	++	xx	xx
93652	J	M	xx	xx	--	xx	xx	xx	xx	xx	xx	xx	--	++	xx	++	++
93667	J	M	xx	xx	--	xx	(++)	xx	xx	xx	xx	xx	--	xx	xx	xx	xx
93674	J (/UMR05)	M	xx	xx	--	xx	xx	++^{5}	xx	xx	++	xx	--	xx	xx	xx	xx
51202	J (/UMR06)	F	xx	xx	--	xx	xx	xx	xx	xx	++	++	--	++	++	xx	++
93627	J	F	++	++^{5}	--	xx	++	++	++	xx	++	++	--	xx	xx	xx	++
93673	J (/UMR03)	F	++^{2}	xx	--	xx	++^{2}	++^{2}	xx	xx	++^{4}	xx	--	xx	++	xx	xx
93675	J (/UMR04)	F	xx	++^{5}	--	++	xx	++^{5}	++	xx	++	xx	--	xx	++	xx	++
UMR07	J	?	xx	xx	--	xx	xx	xx	xx	xx	xx	++	--	xx	xx	xx	xx
28467	A	F	Release		++R	++	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx
93661	J	F	(6)		++R5	++	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx
93670	J	F			++R5	++	xx	++	xx	xx	xx	xx	--	xx	xx	xx	xx
93671	J	M			++R4	++	xx	xx	xx	xx	xx	xx	--	xx	xx	xx	xx
93672	J	F			++R5	xx	++	xx	xx	xx	xx	xx	--	xx	xx	xx	xx
93534	J	M										Release	++R5	xx	xx	xx	xx
93678	A	F										(7)	++R	++	xx	xx	xx
93679	J	M											++R5	xx	xx	xx	xx
93680	J	F											++R5	++	xx	++	xx
93681	J	M											++R5	xx	xx	xx	xx

Abbreviations:
A = adult;J = juvenile;M = male;f = female;
? = sex unknown;++ = sighted in the study area;
xx = not located;-- = no census;R = released,
0, 1, 2, 3, 4 & 5 = post-juvenile moult stages.