The effect of altitude on the breeding ecology of the dipper (*Cinclus cinclus*)

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degree of MSc Ecology (by research)

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Declaration

I declare that this thesis is my own work, except where acknowledged, and has not been submitted elsewhere in the same form for the fulfilment of a higher-level degree.

Richard Wilkinson

May 2019

Dedications

In thanks for the lives of:

Jean Thornley
1926 - 2018

Martin John Bickerdyke BSc, MSc, PGCE
1961 - 2018

Thesis abstract

In many migratory populations, only some individuals migrate each year whereas others are resident; this is known as partial migration. Empirical studies of the causes and consequences of altitudinal partial migration are few, and the costs and benefits of the different life-history strategies involved require further study. In this thesis, I investigate the effect of altitude and other factors on the timing of breeding, reproductive success and parental care in a partially migrant species; the dipper (*Cinclus cinclus*), a specialised riparian passerine that is thought to be declining in the UK. Most dipper populations comprise partial migrants that move to higher altitudes to breed and sedentary residents at lower elevations, but little is known about the effects of elevational gradients on the life-history traits and reproductive success of these birds. Here, I used mixed effect models to analyse field data from a long-term study population and: (1) examine the effects of altitude, female age and size on lay date, nestling mass, fledging success, number of fledglings and annual productivity; and (2) investigate the effect of altitude and prey availability on parental provisioning rate. Compared to residents, migrant dippers bred later and were less likely to have a second brood, possibly influenced by the time taken to migrate and establish breeding territories but were equally likely to fledge young, perhaps because of lower risk of flooding and predation. Altitude had no effect on nestling mass, number of fledglings or annual productivity. Provisioning rates decreased with increasing altitude despite no apparent difference in prey availability and this suggests increased time travelling to foraging sites possibly compensated by reduced handling costs and increased prey loads. Altitudinal migration is likely to be a tactic driven by competition for lowland nest sites. Annual productivity of subordinate migrants was unaffected by migration and this is likely to be because single broods are offset by fewer nests lost to flooding and predation, and compensatory provisioning strategies match those of residents. Together, these results provide insights into the impact of elevation on breeding ecology in birds and suggest that there are adaptive benefits to both altitudinal migration and residency. Age may not affect timing of breeding but older females are more likely to produce heavier nestlings, fledge broods, and have a higher number of fledglings. This may be explained by previous breeding experience and more investment in parental care. However, a decline in productivity with age suggests senescence. Further research is needed to determine the underlying causes of migration and residency, and to establish whether the net fitness benefits of the two behaviours are similar.

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Without the work of members of the Ring Ouzel Study Group, namely, Peter Ullrich's survey of the ring ouzels of Ennerdale (and our numerous phone conversations), Dave Shackleton of RSPB Hawsewater, and Dr Innes Sim of the RSPB, the possibility of a research project on avian ecology wouldn't have suggested itself – thank you all for planting a seed. Innes was generous with his time and suggested potential areas of study – apologies again that it turned out to be dippers! Andy Harrod and Stacey Lofthouse in the PGR office were not only good and sympathetic listeners but always had sound practical solutions to problems and worked on my behalf to resolve them – my deepest thanks to you both.

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There were days during the study that will remain etched in my mind forever, like being hidden on a stream bank waiting for dippers returning to feed chicks, a redstart singing above me and a pair of otters gently gliding and rolling in the water so close, it felt I could almost touch them. There were long days in the high fells, returning at dusk after finding remote nests, and wild camps with owls calling at night and being awoken at dawn by cuckoos and willow warblers. It would not have been possible for me to return to study and to have been rewarded by such experiences during this research, or, to have met so many special people without the assistance provided by my late mother, Margaret Ann Wilkinson - thank you for your belief in me, and I know you would have been pleased that I spent my time, energy and your generosity so wisely.

Final thanks again to Stuart for allowing me the opportunity to take the red pill!

Richard Wilkinson

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Reports that say that something hasn't happened are always interesting to me, because as we know, there are known knowns; there are things we know we know. We also know there are known unknowns; that is to say we know there are some things we do not know. But there are also unknown unknowns - the ones we don't know we don't know.

Donald Rumsfeld US Secretary of Defense

This is your last chance. After this, there is no turning back. You take the blue pill, the story ends; you wake up in your bed and believe whatever you want to believe. You take the *red* pill, you stay in Wonderland, and I show you how deep the rabbit hole goes. Remember, all I'm offering is the truth. Nothing more.

Morpheus to Neo in *The Matrix*

A man’s got to know his limitations.

Clint Eastwood as Inspector Harry Callahan
in *Magnum Force*

Do not go gentle into that good night,
Old age should burn and rave at close of day;
Rage, rage against the dying of the light.

Dylan Thomas from
Do not go gentle into that good night

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Abbreviations referred to in the text

°	Degrees
‘	Minutes
″	Seconds
~	Separates the response and explanatory variables in an R formula
:	Interaction between explanatory variables in an R model formula
“+”	Presence of a categorical variable in an R model formula
(1|X)	Random term fitted to account for repeated measures of a variable X
ΔAICc	Difference between a models mean AICc value and that of the best fitting model
%	Percentage
<	Less than
>	Greater than
AED	Analysing ecological data
AIC	Akaike Information Criterion
AICc	AIC corrected for small sample size
Al^{3+}	Aluminium ion
AMTs	Alternative migratory tactics
ARTs	Alternative reproductive tactics
asl	Above sea level
ASPT	Average Score Per Taxon
BMWP	Biological Monitoring Working Party
BTO	British Trust for Ornithology
cm	Centimetre
c.	Approximately
df	degrees of freedom
ED	Extra low dispersion (glass)
EA	Environment Agency
EPT	Ephemeroptera, Plecoptera and Trichoptera (and separately as E, P and T)
FBA	Freshwater Biological Association
g	Gram
GLMM	Generalised linear mixed-effect model
ICUN	International Union for Conservation of Nature
JNCC	Joint Nature Conservation Committee
km	Kilometre
LMM	Linear mixed-effect model
loglik	Log-likelihood, used for a model fitted by maximum likelihood
m	Metres
Met Office	Meteorological Office
mm	Millimetres
n	Sample size
NAO	North Atlantic Oscillation
NCA	National Character Area
°C	Degrees Celsius
OS	Ordnance Survey
PCB	Polychlorinated biphenyl
pH	pH acidic / basic solution
Q-Q	Quantile-quantile
RPW	Richard Paul Wilkinson
R^2	Measure of how close data are to the fitted regression line
R^2c	Values associated with fixed effects plus random effects in models
R^2m	Values associated with fixed effects in models
SD	Standard deviation
SE	Standard error
SSSI	Site of Special Scientific Interest
STAR	Scientific, Technical and Assessment and Reporting
UK	United Kingdom
VIFs	Variance Inflation Factors

Species / taxonomic group referred to in the text

Alpine water pipit	*Anthus spinoletta*
American dipper	*Cinclus mexicanus*
American mink	*Neovison vison*
Arctic tern	*Sterna paradisaea*
Bluethroat	*Luscinia svecica*
Bracken	*Pteridium aquilinum*
Brown dipper	*Cinclus pallasii*
Brown rat	*Rattus rattus*
Caddisfly	Trichoptera
Carrion crow	*Corvus corone*
Cattle	*Bos taurus*
Common sandpiper	*Actitis hypoleucos*
Corvids	Birds of the crow (Corvidae) family
Crustaceans	An invertebrate group within the arthropods
Dippers	Family Cinclidae with a single genus, *Cinclus*
Diptera	Order of winged insects known as flies
Domestic / feral cat	*Felix cattus*
Elk	*Cervus canadensis*
European robin	*Erithacus rubecula*
Feather lice	Mallophaga
Fish	Class Osteichthyes (bony fish)
Fleas	Siphonaptera
Fox	*Vulpes vulpes*
Freshwater shrimp	*Gammarus pulex*
Gammarid	Familes of *Gammarus* type freshwater crustaceans
Geese	Waterfowl species in the family Anatidae.
Grey heron	*Ardea cinerea*
Grey wagtail	*Motacilla cinerea*
Heather	*Calluna vulgaris*
Kingfisher	*Alcedo atthis*
Marine turtles	Families within the Chelonioidea
Mayfly	Ephemeroptera
Meadow pipit	*Anthus pratensis*
Miller's thumb or bullhead	*Cottus perifretum*
Mites	Acari
Molluscs	An invertebrate group including river limpets
Moorhen	*Gallinula chloropus*
Moose	*Alces alces*
Mustelids	Carnivorous mammals e.g. otters, weasels and mink of the family Mustelidae
Otter	*Lutra lutra*
Passerines	Perching birds of the order Passeriformes
Pony	*Equus ferus caballus*
Simuliidae	A Dipteran fly group known as simulids or blackflies
Stonefly	Plecoptera
River limpet	*Ancylus sp.*
Rufous-throated dipper	*Cinclus schulzi*
Salmon / trout	Salmonids
Sheep / lamb	*Ovis aries*
Snow bunting	*Plectrophenax nivalis*
Tree swallow	*Tachycineta bicolor*
Twite	*Linaria flavirostris*
Ungulates	Mammals with hooves
White-capped dipper	*Cinclus leucocephalus*
White-clawed crayfish	*Austropotamobius pallipes*
White-throated dipper	*Cinclus cinclus* (and races *C. c. aquaticus, C. c. cinclus, C. c. gularis, C. c. hibernicus*)

Chapter 1

General introduction

1.1 Life-histories

Natural selection has shaped life-histories through the effects of spatio-temporally variable environmental conditions acting upon the genes, morphology, physiology and behaviour of individuals within a population (Partridge and Harvey 1988; Partridge *et al.* 1991; Shefferson 2010). This process has shaped traits including the timing and pattern of life-stage development, mode of reproduction, number and size of offspring, levels of parental care and longevity (Stearns 1989; Roff 1993; Walsh and Lynch 2018). Investing time or energy into one trait often elicits corresponding decreases in others, making trade-offs necessary (Agrawal *et al.* 2010; Garland 2014). The most significant life-history trade-offs occur between reproduction and survival, and between current and future reproduction (Stearns 1989; Roff and Fairbairn 2007).

Phenotypic and genotypic variation within populations bestows individuals with different capacities to make reproductive and survival trade-offs (Stearns 1989). Individual trade-offs made in reproductive effort in one year will affect the probability of survival to the next breeding season whilst intergenerational trade-offs affect the probability that offspring will survive to the next year (Stearns 1989, 1992). In varying environmental conditions, the outcomes of these trade-offs are complex and difficult to predict (Gustafsson and Sutherland 1988; Stearns 1989; Daan *et al.* 1996; Brommer *et al.* 2000). Annually repeating seasonal conditions select traits expressed in diverse life-history strategies for phenologically timed events such as matching food availability with breeding, and temperature with migration or hibernation (Shefferson 2010). Intraspecific competition for finite resources during the breeding season will lead to reduced fitness in subordinate individuals as investment efforts become allocated to obtaining resources elsewhere, impacting the reproduction-survival trade-off (Stearns 1989).

Organisms can trade reduced fitness under typical conditions in exchange for increased overall fitness under unpredictable hostile circumstances (Olofsson *et al.* 2009). This 'bet-hedging' reduces short-term fitness in favour of maximising survival and reproductive success over the longer term (Shefferson 2010). Variants include conservative, 'play it safe' low risk strategies; diversified, investing in simultaneous multiple strategies; and 'adaptive coin flipping', whereby alternative phenotypes are adopted seemingly at random for unknown future conditions (Cooper and Kaplan 1982; Philippi and Seger 1989; Olofsson *et al.* 2009). Alternatively, organisms may exhibit adaptive plasticity in which environmental cues provide predictive value for a phenotypic response from individual genotypes (Cooper and Kaplan 1982; Fusco and Minelli 2010; Rago *et al.* 2019). Environmental uncertainty can influence life-histories by the trade-off and bet-hedging decisions that individuals make to preserve fitness (Lips 2001; Wilbur and Rudolf 2006; Haaland *et al.* 2019). However, what is less well-known is how ecological constraints acting alone or in combination influence this decision-making (Hatchwell and Komdeur 2000; Ricklefs and Wikelski 2002).

Sæther *et al.* (1996) suggest that species with iteroparous life-history strategies can be broadly categorised as: 'high-reproductive species' that mature early, have high fecundity but low survival rates; 'survivor species' that are late maturing, have low fecundity, and high survival rates; and 'bet-hedging' species that mature late, have high fecundity but low survival rates. A population distributed allopatrically or clinally within a relatively small geographic area but subject to differing ecological conditions may show variation between conspecifics / individuals in the strategy adopted that could influence fecundity and survival rates and could contain simultaneous variants of Sæther's categories. Breeding pairs attempting to maximise fitness under different environmental conditions could have different life-history strategies and fecundity-reproduction outcomes mediated by optimal trade-offs (Stearns 1989; Polačik *et al.* 2014). In some species, intraspecific competition drives individuals to adopt discontinuous behaviours and different life-history traits to maximise reproductive success; these are known as alternative reproductive tactics (ARTs).

ARTs are variant patterns of behaviour within a population that aim to maximise fitness though different investment decisions in response to trade-offs in reproduction and optimal life-history (Brockmann 2001; Taborsky *et al.* 2008; Taborsky and Brockmann 2010). These tactics may be fixed for life by genes or by developmental process, or, be plastic responses, with tactics being switched dependent on current circumstances; they may be driven by disruptive selection, negative frequency dependence, density dependence, interactions between genetic expression and developmental processes, and environmental influences (Taborsky and Brockmann 2010). ARTs likely evolve because of fitness being gained by pursuing different reproductive paths in order to achieve fertilisation. In particular, competition for resources during the breeding season may promote alternative reproductive tactics and lead to partitioning of resources or segregation of individuals within a population. Analogous to ARTs are alternative migratory tactics (AMTs) of partially migrating populations in which fitness is attained by either remaining as a resident, or, becoming a migrant (Chapman *et al.* 2011a, 2011b; Sahashi and Morita 2018).

1.2 Migration

Migration is the seasonal movement of animals from one location to another and can occur across many scales of time and distance, and by migratory behaviour as diverse as the taxa that undertake it (Dingle 2014). The extremes of migration range from vertical movements of tens to a few hundred metres in deep lakes and oceans by crustaceans (Cisewski *et al.* 2010; Brierley 2014), to the 90,000km transpolar flights between northern breeding grounds and Antarctic wintering areas made by Arctic terns (*Sterna paradisaea*; Fijn *et al.* 2013). Other examples of long distance migrations include those undertaken by marine turtles, ungulates, fish, geese and passerine bird species (Hughes *et al.* 1998; Fox *et al.* 2003 ; Luschi *et al.* 2003; Thirgood *et al.*

2004; Block *et al.* 2005; Stutchbury *et al.* 2009). Migration is believed to reduce intraspecific competition for limited and declining resources and allows access to alternative and potentially plentiful supplies; it allows seasonal climatic extremes to be avoided, lowers risk of predation, disease and parasitism, and, under some circumstances, maximises fitness by increasing survival and reproduction (Griswold *et al.* 2010; McKinnon *et al.* 2010; Altizer *et al.* 2011; Skov *et al.* 2013; Avgar *et al.* 2014; Eggeman *et al.* 2016; Shaw and Binning 2016).

Seasonal migration is a response to changing ecological conditions resulting from environmental periodicity and seasonality (Berthold 2001). It is a yearly repeated return movement between distinctly different geographic breeding and non-breeding or wintering grounds, with each having asynchronously advantageous ecological conditions (Dingle and Drake 2007; Newton 2008; Faaborg *et al.* 2010; Rappole 2013). Long-distance migration is not without risks that increase rates of mortality (Sillett and Holmes 2002) and influence life-history characteristics (Roff 1991), for example energetic costs, variabilities in climate and weather, and vulnerability to predation and disease (Newton 2008). However, despite these costs, migration can confer benefits such as increased survival in less harsh overwintering locations, and early arrival and access to higher quality breeding sites have implications for fitness (Alves *et al.* 2013).

It is important to study migration to understand how it can affect population dynamics particularly during periods of changing environmental conditions such as climate change. Migration can affect intra-annual population size, which may have consequences for localised populations in seasonally distinct habitats that may affect survival, carry-over effects upon reproduction, and experiential effects on life-history strategies that could influence demography and population dynamics (Reid *et al.* 2018a).

1.2.1 Partial migration

In populations of migrant species, individuals may vary in their migratory tendency or in the timing or distance of movement (Newton 2008). In many cases, populations comprise both sedentary individuals, which typically remain resident in one habitat, and individuals that migrate between breeding and non-breeding sites, usually in different habitats (Dingle 1996) (Chapman *et al.* 2011a, 2011b; Reid *et al.* 2018a). This is known as partial migration, and is widespread amongst invertebrate and vertebrate taxa (Slager and Malcolm 2015; Reid *et al.* 2018a), but particularly well documented in temperate and tropical bird species (Jahn *et al.* 2010; Boyle 2011, 2017; Barçante 2017; Hsiung 2018). If migratory and sedentary strategies have a fixed genetic dimorphism, each having equal fitness (Lundberg 1987, 1988), any difference in breeding success between strategies must be balanced by survival differences (Cox 1985). Persistence of such a dimorphism could occur if fluctuations in the most successful resident-migrant genetic strategy produce corresponding fluctuations in the direction of selection (Lundberg 1987, 1988). Alternatively, resident-migrant strategies may be condition dependent and vary with environmental circumstances or individual characteristics e.g. sex, age, body condition or dominance status (Ketterson and Nolan 1983; Lundberg 1987, 1988). Thus, individual strategies can vary over time and offspring may differ from their parents. In strategy-switching species, residents generally have higher breeding success than migrants (Adriaensen and Dhondt 1990; Warkentin *et al.* 1990), and migrants are more likely to switch strategies than residents (Adriaensen and Dhondt 1990). Residents may be more competitive individuals forcing subordinates to migrate and manage with unfavourable conditions (Lundberg 1987, 1988; Adriaensen and Dhondt 1990).

1.2.2 Altitudinal migration

One form of partial migration is altitudinal migration, in which migratory individuals make return movements between breeding and non-breeding or wintering sites along elevational gradients in response to seasonal environmental changes (Cade and Hoffman 1993; Dingle and Drake 2007; Norbu *et al.* 2013). These changes include factors that affect habitat quality such as climate, resource availability and levels of predation risk. These migrations are typically short-distance facultative movements, and residents and migrants usually occupy at least one seasonal habitat together (Chapman *et al.* 2011b; Boyle 2017; Reid *et al.* 2018a). Altitudinal migration is known to occur in a wide variety of taxa (Berthold 2001; Hsiung *et al*. 2018; Reid *et al.* 2018a), yet relatively little is known about the factors that influence variation in altitudinal migratory behaviour but these may include differences in an individual's social rank and condition (Barçante *et al.* 2017; Hsiung *et al.* 2018).

Altitudinal migration is variable across a diverse range of species, life-history strategies, habitat and geographical regions and, where all possible combinations of residents and migrants can occur either together or separated during breeding and non-breeding seasons, and at either high or low elevations (Rabenold and Rabenold 1985; Stiles 1988; Laymon 1989; Burgess and Mlingwa 2000; Solórzano *et al.* 2000; Hobson *et al.* 2003; Dingle 2004; Powell and Bjork 2004; Middleton *et al.* 2006; Hess *et al.* 2012; Boyle and Martin 2015; Boyle 2017; Hsiung *et al.* 2018).

Altitudinal migration by birds is found in montane environments on all continents except Antarctica (Barçante *et al.* 2017; Boyle 2017; Hsiung *et al.* 2018). It occurs over scales of a few hundred metres in distance and elevation to hundreds of kilometres and thousands of metres of altitude (Berthold 2001), and has important implications for seasonal population distribution and structure (Blake and Loiselle 2000; Fraser *et al.* 2008, 2010). Ecological conditions such as temperature, precipitation and wind velocity are typically more variable as elevation increases in temperate regions, and alongside any altitudinal gradient in season length that could be driven by temperature or moisture, together, could produce limiting conditions for migrants (Körner 2007). Steep elevational gradients accomplished over short distances, especially in temperate regions, are usually accompanied by changes in seasonality and phenology, unpredictable and episodically extreme weather conditions and generally becoming colder, windier, and with greater precipitation and persistence of deeper snow layers, shorter breeding seasons and unpredictable food supplies (Brinck 1974; Newton 1998; Nour *et al.* 1998; Tremblay *et al.* 2003, 2005; Körner 2007). Any of these conditions can act to limit survival and completion of reproductive cycles, but decreasing temperature has the most acute effects upon life-history strategies (Convey 1997; Sandercock *et al.* 2005; Blix 2016). Transitions in challenging physiographic and ecological conditions require species to have specialised morphology, behaviour and life-history strategies to survive and breed there (Badyaev and Ghalambor 2001; Potapov 2004; Bears *et al.* 2009; Martin 2014; Laiolo and Obeso 2017; Riesch *et al.* 2018). Climate change could influence altitudinal migration as changing temperatures and weather-related events along elevational gradients may constrain ecological conditions that influence montane phenology including food availability, and which may lead to range shifts and affect population dynamics (Flousek 2015).

In comparison to long-distance latitudinal migrants, similar fitness benefits may be obtained as energetic costs of altitudinal migration are much reduced, but ecological conditions can change quickly over short distances of elevational gradients (Körner 2007). Benefits gained may include reduced risk of predation, disease and parasitism, benefits from advanced or delayed phenology to favourable weather, avoiding hostile climate (and capitalising on increased food abundance), and habitat gains including access to territories, nests and foraging sites, and mate acquisition (Cox 1985; Loiselle and Blake 1991; Solórzano *et al.* 2000; Boyle 2008; Barçante *et al.* 2017; Hsiung *et al.* 2018). However, in temperate upland regions ecological conditions tend to become less favourable with increasing elevation with a greater likelihood of adverse weather, lower quality habitat conditions including food availability and shortened breeding seasons and it is speculated that subordinate individuals occupy these marginal and poorer quality breeding sites (Barçante *et al.* 2017).

Studies of the life-history strategies of phylogenetically paired races of passerines at different elevations suggest that selection pressures acting at higher altitudes on migrants may cause a trade-off between fecundity and parental care, and differences in breeding success may be due in part to variation in nestling investment (Badyaev and Ghalambor 2001). By reducing clutch size and having fewer offspring this could enable greater investment in offspring quality and survival through more parenting effort, and, smaller broods may promote adult survival and therefore the potential for future reproduction. When compared to lowland birds, those at higher altitudes tended to breed later, have single broods, have variable lengths of incubation but longer nestling periods, and have shorter breeding seasons (Badyaev 1997; Badyaev and Ghalambor 2001; Lu 2005; Lu *et al.* 2009, 2010; Li and Lu 2012a, 2012b). Some studies also report that high altitude breeding birds with small clutch sizes had larger eggs and suggests that at higher elevation, with poor climate and reduced food supply, the strategy is to invest in nestlings pre-hatch and increase egg size in a smaller clutch to improve breeding success (Lu 2005 and references therein; Li and Lu 2012a, 2012b; Lu *et al.* 2010). This shift to greater parental care at higher altitudes may be in response to poor food supply, predation, limitations of time and unpredictably changing adverse conditions, and result in reduced population-level productivity (Martin 1995; Badyaev and Ghalambor 2001; Bears *et al.* 2008; 2009; Lu *et al*. 2009; Hille and Cooper 2015; Balasubramaniam and Rotenberry 2016). Differences in fecundity and parental care across elevational gradients may be genetically determined or the result of phenotypic adaptive responses to varying ecological conditions along an elevation continuum (Badyaev and Ghalambor 2001). However, most studies have involved geographically separated populations, or even pairs of related species or races (Badyaev and Ghalambor 2001), which may limit the value of any comparisons between the selection pressures and fitness consequences of migration and residency.

The main investment of parental care is in provisioning offspring and is largely dependent on the quality of the habitat to provide sufficient and high quality food at low foraging costs, and access to food under changing weather conditions (Nour *et al.* 1998; Tremblay *et al.* 2003, 2005; Stauss *et al.* 2005; Mägi *et al.* 2009; Öberg *et al.* 2015; Leroux *et al.* 2018). This is modulated by seasonal extremes of weather conditions, abundance of predators, disturbance and level of experience, expertise and age of individuals. Results from the studies of total and gender provisioning rates at different altitudes have produced conflicting results (Badyaev 1993, 1994 and referenced by Badyaev 1997; Badyaev and Ghalambor 2001; Johnson *et al.* 2007; Zeng and Lu 2009; Lee *et al.* 2011, 2016) and can have fitness consequences for adults and offspring (Gowaty 1983; Lyon *et al.* 1987; Lee *et al.* 2011).

Within-species studies of the effects of partial altitudinal migration in birds are limited but differences in the breeding outcomes, provisioning rate and the quality of offspring for resident and altitudinal migrant American dippers (*Cinclus americanus*), have been shown (Morrissey 2004; Mackas *et al.* 2010; Green *et al.* 2015). However, little is known of what drives altitudinal migration in dippers and further research is needed to identify what influences breeding success and parental care along elevational gradients. This may be important to understand how changing environmental conditions such as the effects of climate change may alter them and, in turn, have fitness and conservation consequences for both residents and altitudinal migrants (Sekercioglu *et al.* 2008; Sorte and Jetz 2010; Elsen and Tingley 2015).

1.3 The study species: the dipper (*Cinclus cinclus*)

1.3.1 Introduction

The Cinclidae or dippers are a family of aquatic songbirds of the Passeriformes, comprising five species and a number of races within a single genus, *Cinclus*, and occurring on all continents except Australasia (Figure 1.1; Omerod and Tyler 2005). The ecology of dippers is characterised by their shared morphological likeness, distribution almost exclusively along shallow, fast-flowing waters, and uniqueness as the only swimming passerine predators of aquatic invertebrates and small fish (Ormerod and Tyler 2005).

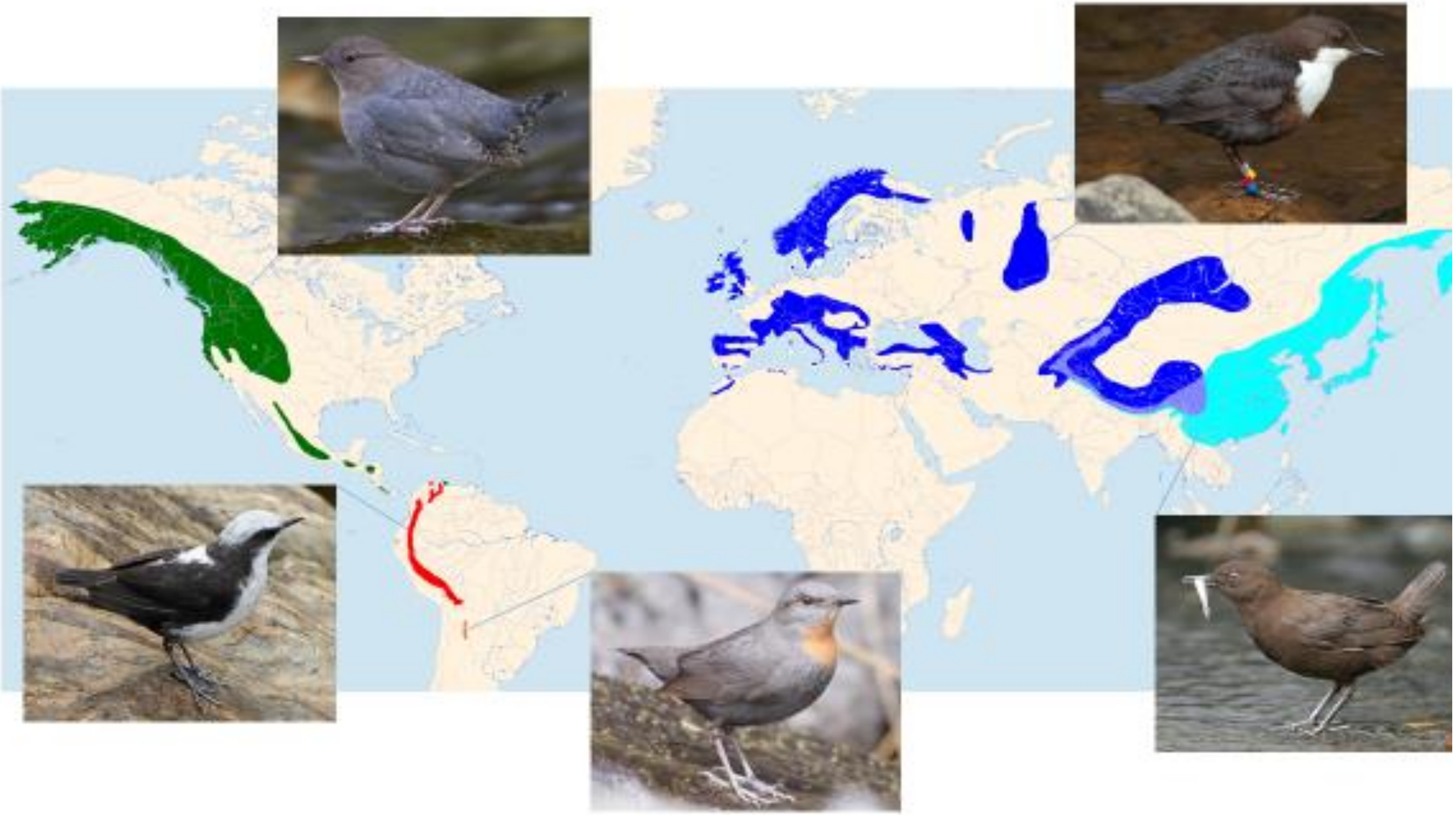

Figure 1.1. The distribution of the five species of dippers in the family Cinclidae, clockwise from top right: White-throated dipper *Cinclus cinclus*; Brown dipper *Cinclus pallasii*; Rufous-throated dipper *Cinclus schulzi*; White-capped dipper *Cinclus leucocephalus*; and American dipper *Cinclus mexicanus*. (Wikiwand at: http://www.wikiwand.com/en/Dipper).

The white-throated dipper *Cinclus cinclus* (hereafter dipper) is found throughout Europe, North Africa, the Middle East, and Western and Central Asia, from sea level to 5000m. There are two British races, *C. c. hibernicus* found in western Scotland, the Inner Hebrides and Ireland, and *C. c. gularis* in the remainder of Scotland, Wales, and northern, western and central England (Figure 1.2); the latter is the race studied here (Figure 1.3; Cramp 1988). Dippers in the UK are mostly found on upland rivers and streams of circumneutral and weakly acidic pH capable of supporting invertebrate and fish prey species (Tyler and Ormerod 1994).

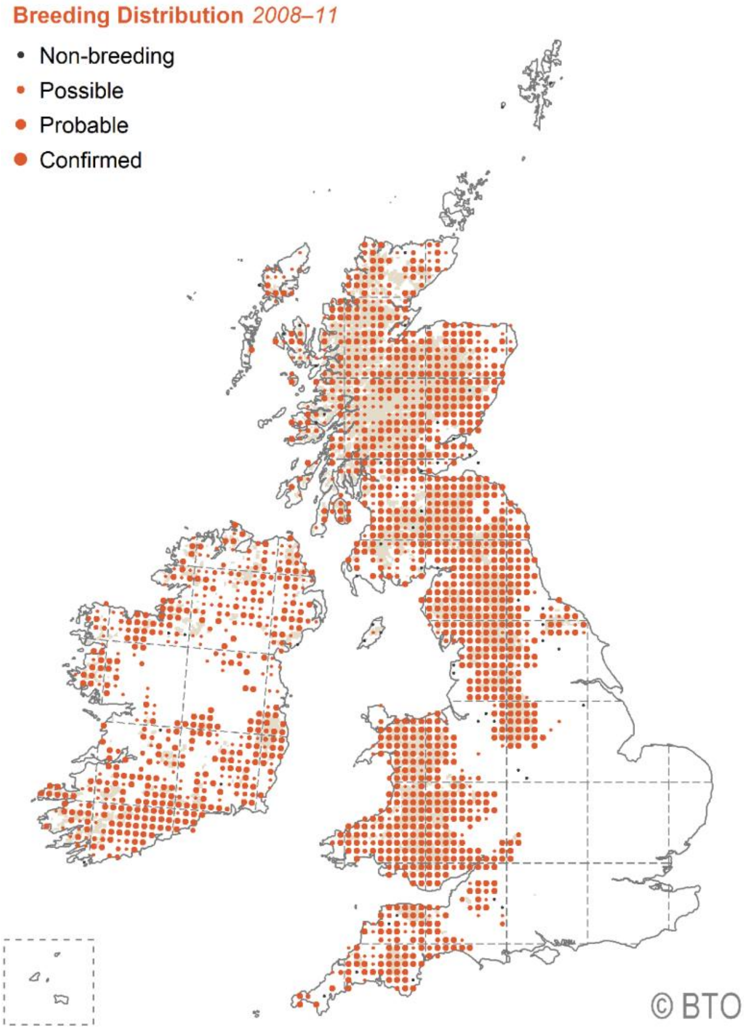

Figure 1.2. Dipper breeding distribution in the British Isles 2008-11.
(© British Trust for Ornithology, BTO).
(*BTO map store* at: https://app.bto.org/mapstore/StoreServlet?id=339).

Figure 1.3. Adult dipper with stonefly prey. (Photograph by Andrew Mawby).

Dippers are yearlong UK residents but Scandinavian birds *C. c. cinclus* can migrate long distances for the winter (Lundberg *et al.* 1981; Tyler and Ormerod 1994; Johansson *et al.* 2017), and also interbreed with Carpathian birds *C. c. aquaticus* in northern Poland suggesting considerable movements (Sikora 1994; Sikora and Neubauer 2008). Local movement in the UK occurs over a range of a few hundred metres to several kilometres when pairs breeding at higher altitudes on tributary streams descend post-breeding to over-wintering lowland altitudes or during periods of severe weather (Tyler and Ormerod 1994).

1.3.2 Morphology and adaptations

Dippers are round-bellied, thrush-sized birds measuring 16-20cm in length with short and often cocked tails. Both sexes have dark brown upperparts, a white throat and breast bib, chestnut-brown below to the mid-abdomen and flanks, then darker brown to the vent, with brown eyes, a black bill and dark brown legs (Figure 1.3). However, males and females differ in size and weight; males typically weigh 65-75g and have wing lengths exceeding 92mm, whereas females weigh 55-60g and are shorter winged (Tyler and Ormerod 1994).

Dippers have short broad wings and highly developed wing muscles producing rapid wing beats and a fast low 'whirring' flight along watercourses, and sometimes higher during display or when pushed to territory boundaries, and over land connecting nest and feeding sites. In water, their small size and hydrodynamic shape and 'swimming' wing movements are adapted for foraging and diving in fast flows. A large waterproofing oil producing preen gland protects feathers reducing inefficiencies of drag and additional water mass, and insulating outer feathers and down. Large feet and toes grip substrates and paddle for surface swimming. A short and slender bill is adapted to catch mobile or sedentary prey attached to or located under submerged substrates or aerial surfaces.

Diving is assisted by closure of a nasal flap; solid bones to reduce buoyancy; eye lens curvature to enable accommodation in both water and air; and a protective nictitating membrane, which moves across to clean the eye surface (Goodge 1960; Katzir and Howland 2003). Sustained diving is achieved by a lower heart rate and a lower metabolic oxygen consumption, and higher haemoglobin concentration and oxygen storage capacity (Murrish 1970).

Dippers communicate by a sharp 'zit' call often made during flight and a slow subdued warbling song heard throughout the year (Magoolagan 2017; Magoolagan *et al.* 2019). In noisy turbulent flowing water, rapid frequent blinking of fine white feathered eyelids sometimes accompanied by body-bobbing and tail-wagging may be visual communication during courtship and territorial defence or an anti-predator response (Ormerod and Tyler 2005).

1.3.3 Habitat

During breeding, dippers occur on clear, shallow, fast-flowing rocky rivers and tributary streams in upland areas, and at other times on lakes, larger slower rivers and coastal shorelines. Resident dippers establish and vigorously defend linear territories throughout the year, nesting close to flowing water. Territories of year-round resident dippers in lowland valleys are often surrounded by pastureland, on shallow, fast-flowing rivers with gentle gradients, few cascades and waterfalls, sometimes steeply banked supporting well-developed bankside vegetation with mature broad-leaved trees (Figure 1.4). Some dippers breed on tributary side-streams at higher elevations where the gradient is often steeper with very fast water flow between high rocky-sided gullies, with frequent cascades and waterfalls, and in bank-side tree and vegetation-free grazed upland areas (Figure 1.4).

Figure 1.4. Typical dipper habitat. Above, upland sites; below, lowland sites. (Photographs by Richard Wilkinson).

Surface water riffles created by turbulent shallow water flow over just-submerged rocks aerate water required by oxygen sensitive macroinvertebrates. Riffle substrates hold more of nearly all prey taxa compared to pools (Logan and Brooker 1983; Brown and Brussock 1991), and microhabitat selection and partitioning by benthic taxa reflect adaptations to current speed, competition, food and predator avoidance (Ormerod 1988; Brooks *et al.* 2005; Pastuchová *et al.* 2008).

1.3.4 Predators and parasites

Predators of dipper eggs and nestlings include corvids, mustelids such as American mink (*Neovison vison*) and otter (*Lutra lutra*), domestic and feral cats (*Felix cattus*); juvenile and adult dippers are taken by various raptor species but also by mammals, especially on the nest or at roost sites (Tyler and Ormerod 1994). Shaw (1978) states that brown rats (*Rattus rattus*) cause 60% nest failures and, in Ireland, as much as 75% (Perry 1986). Dippers harbour ectoparasitic mites (Acari), feather lice (Mallophaga) and fleas (Siphonaptera) (Fain and Macfarlane 1991; Tyler and Ormerod 1994), and while brood infestation may not affect fledging success it can prohibit second brooding in the same nest (RPW personal observation).

1.3.5 Breeding ecology

Nest locations and nests

Dippers nest by running water in natural sites including cliff faces and ledges, waterfalls, large boulders, holes in banks, hollow trees, branches and exposed roots (Tyler and Ormerod 1994). Nests can also be located on bridge supports and ledges, holes in walls and pipes, and nest boxes (examples Figure 1.5) (Tyler and Ormerod 1994). Dippers will reuse the same nest in successive years and may use alternative nests when double brooding, but this is extremely rare unless they change partner. Old nests may be relined each year or new nests built nearby or on top of previous nests. Nests are large dome shapes up to about 25cm in diameter with a low downward facing entrance hole (Figures 1.5 and 4.1). Construction of completely new nests takes up to 28 days by both parents; a thick outer shell of moss surrounds an inner base forming a grassy cup smoothly lined with leaves (Shaw 1978; Tyler and Ormerod 1994).

Figure 1.5. Dipper nests and locations. Clockwise from top left: upland locations, in the vegetation between the two lower waterfalls and on the rock wall of a gulley; lowland locations, on a conglomerate cliff and beneath a packhorse bridge. (Photographs by Richard Wilkinson).

Breeding

Dippers are monogamous breeders although polygyny with unpaired females does occur (Øigarden and Linløkken 2010). Surviving pairs usually remain together in subsequent years but ‘divorce’ and new pairings occur. Pairs defend breeding and winter territories with song and pursuit of trespassing birds. Breeding in the UK commences from February onwards as temperatures rise, rainfall decreases and the risk of winter flooding recedes, and before the main aquatic macroinvertebrate prey items emerge as adults. Male courtship song and display behaviours occur from January through to second brooding in June (Tyler and Ormerod 1994).

Eggs and nestlings

Eggs are white, smooth and glossy, sub-elliptically shaped (Figure 1.6), with a typical length of 26 mm and breadth of 18.5 mm and weighing 4-5 g (Tyler and Ormerod 1994). Clutch sizes range from 2-6 but are mostly 4 and 5 eggs, with eggs usually laid one per day and incubation, entirely by the female, commencing after laying of the final egg and lasting for 16-18 days (Shaw 1978). Altricial nestlings are brooded by the female and initially fed mostly by the male with female feeds increasing with nestling age until brooding ceases at 5-7 days (eggs, nestlings and juvenile dippers in Figure 1.6). Nestlings are fed in rotation at the nest entrance, noisily begging and showing a wide, bright orange-yellow gape. Adults remove faecal sacs until they defecate out the nest from about day 9. Brood survival rates depend upon weather events, flooding, predation, brood size and food availability affected by territory quality (Tyler and Ormerod 1994) and consequently provisioning rates can vary throughout the nestling phase. At about 14 days old – and still not fully developed – young dippers have an escape response to predators and can jump explosively from the nest into the water, diving and swimming away then hiding under banks and amongst tree roots. Fledging occurs after about 22 days and both parents continue to feed juveniles for up to two weeks as they remain hidden, developing foraging skills and becoming increasingly independent, completing post-juvenile moult after 4-6 weeks and then dispersing from the natal territory (Tyler and Ormerod 1994).

Figure 1.6. Clockwise from top left: deserted dipper egg; recently hatched day 0 nestlings; *c.*day 12 nestling; juvenile dipper. (Photographs by Richard Wilkinson).

Second brooding

Second brooding occurs after early spring first broods in good quality habitat and at low altitude (Tyler and Ormerod 1994), with the nest cup being removed and relined. It is likely that sufficient time before summer moult from July onwards and continuing high prey biomass are required to embark on a further brood.

1.3.6 Diet and foraging ecology

Dippers are found in greatest numbers where rivers and streams have abundant large invertebrate communities (Ormerod 1985a) and biomass and species composition is important for breeding and double brooding (Da Prato and Langslow 1976). Dippers prey almost exclusively upon aquatic invertebrates by diving below surface riffles to stony substrates and into deep water, shallow wading between rocks, in bankside surfaces and vegetation, and taking aerial insects or feeding on flooded grass (Tyler and Ormerod 1994; S. P. Sharp personal communication). Strong currents, high flow rates, turbidity and energetic inefficiencies of foraging during severe spate restrict diving and wading (Da Prato 1981; Bryant *et al.* 1985), and flood-induced reductions in benthos are linked to decline in brown dippers (*Cinclus pallasii*) (Chiu *et al.* 2008). Drought and low flow conditions expose marginal foraging habitat (Royan *et al.* 2013) but water level variability can affect riverine species and trophic relationships detrimentally (Edwards *et al.* 2012; Ledger *et al.* 2012; Royan *et al.* 2014). Foraging activity is diurnal and constrained by trade-offs with time spent in courtship, defence, parenting and self-maintenance (Da Prato 1981; Tyler and Ormerod 1994; Yoerg 1994, 1998; Taylor and Halloran 2001). Foraging time is higher on acidic streams compared to prey abundant circumneutral streams, and increases to meet energy costs during winter and provisioning nestlings in the breeding season before declining during moult (Tyler and Ormerod 1994). Energy budgets based on body size, daily activities, annual life stage activity, hydrological and environmental conditions and prey requirements suggest dippers are effective predators making substantial demands upon a territory (Brey *et al.* 1988; Bryant and Tatner 1988; Ormerod and Tyler 1991; Jenkins and Ormerod 1996; D'Amico and Hémery 2007).

Prey

The principal invertebrate prey taxa of dippers are nymphs of the orders Ephemeroptera, and Plecoptera (hereafter mayfly or E, and stonefly or P), and larvae of the order Trichoptera (hereafter caddisfly or T), collectively hereafter EPT (Tyler and Ormerod 1994). Additional prey include Diptera larvae, molluscs such as river limpets (*Ancylus* sp.*)*, freshwater crustaceans e.g. Gammarids (family types like freshwater shrimp, *Gammarus pulex*), and beetles. EPT pass through a number of aquatic instars increasing in biomass before emerging as aerial forms, often in mass hatches thought to be cued by environmental factors including light intensity and water temperature (Brittain 1982; Watanabe *et al.* 1999).

Stream acidity adversely affects the presence of dippers and their reproductive success as a consequence of reduced prey abundance, particularly of mayfly and caddisfly but less so for stonefly (Ormerod *et al.* 1986a; Vickery 1991; Tyler and Ormerod 1992; Ormerod and Tyler 1993). Under acidic conditions, calcium (mostly as bicarbonate) acts as a buffer of free H^+ and heavy metal ions lowering dissolved calcium levels insufficient to support mollusc shells and *Gammarus pulex* (Patterson and Morrison 1993). Molluscs, crustaceans, fish and other calciphilic taxa play an important role in contributing to female body calcium reserves prior to egg formation (Graveland and Van Gijzen 1994). Ormerod *et al.* (1988) found calcium content in stonefly and caddisfly increased with increasing stream pH, especially above pH 6, and an absence of *Gammarus pulex* below pH 6.5. Acidic waters impoverished of molluscs, gammarids and fish could place female dippers in calcium deficit (Ormerod and Tyler 1986; Turnpenny *et al.* 1987; Ormerod *et al.* 1988; 1991). Clutch sizes, brood sizes, and number of chicks fledged are positively correlated with water pH and calcium (Ormerod *et al.* 1987; Vickery 1992; Tyler and Ormerod 1994; Øigarden and Linløkken 2010).

Nestling diet

Adult and nestling dippers have similar diets of mayflies, stoneflies and caddisflies but as nestlings grow, their diet changes to include more caddisfly (Tyler and Ormerod 1994). Ormerod (1985a) found small mayfly prey in younger nestlings' diet, then larger caddisflies up to day 15 after hatching contributing more with increasing nestling age (Tyler and Ormerod 1994). The diet of adult dippers and nestling dippers in spring varies across Europe and probably reflects localised food availability (Tyler and Ormerod 1994). Small gape size restricts prey size for recent hatchlings and highly sclerotised exoskeletons are hard to digest. On acidic streams, small stonefly nymphs are selected in the absence of mayflies by nestlings and adults, and prey size selection is important to optimise feeding and delivery efficiency to nestlings as energy requirements increase with increasing age (Tyler and Ormerod 1994).

Adult diet

Adults mostly take mayflies and caddisflies during the breeding season, and also stoneflies but these may be less favourable due to sclerotisation making them less nutritious or being energetically costly to forage (Tyler and Ormerod 1994). During moult, EPT comprise over 60% of prey items, Diptera (mostly Simuliidae) over a third, and fish contributing varying amounts with birds probably feeding opportunistically according to local food availability (Ormerod and Tyler 1986; Smith and Ormerod 1986; Tyler and Ormerod 1994). Winter diets show the greatest variation between areas but reflect greater opportunistic feeding, with simulids, mayflies and caddisflies predominating but with few stoneflies except on acidic streams (Tyler and Ormerod 1994). Coarse and game fish species and their eggs are taken, notably bullhead (Cottidae; Tomlinson and Perrow 2000) and the fry of Salmonids (Ormerod and Tyler 1991). Fish may make up over 25% of the dietary mass during the breeding season and over 60% in the winter and whilst fish occurs infrequently as a prey item, it provides a substantial energy and nutrient source especially of calcium if molluscs or crustaceans are limited (Ormerod and Tyler 1986; Tyler and Ormerod 1994; Øigarden and Linlokken 2010).

1.3.7 Dippers and altitude

As gradient increases in upland areas, the amount of shallow water foraging riffles may be important alongside depth, bank structure and boulders for dippers (Tyler and Ormerod 1994). However, some higher altitude territories may only be occupied when the population is high (Tyler and Ormerod 1994). Higher elevations are considered to be more constraining (Körner 2007), and if habitat quality declines with altitude, competition for higher quality territories could force subordinate individuals to migrate.

Dipper populations are sometimes partially migratory. In some upland areas of the UK with relatively low hills and few tributary streams, they are largely confined to major rivers e.g. the limestone dales of the Peak District and the River Derwent (Shooter 1970). However, in hill regions where valley rivers are fed by significant upland draining streams, some populations contain short-distance partially migratory birds. These populations are comprised of yearlong sedentary residents and migrants that overwinter together on valley rivers at low altitudes, and individuals that migrate along an altitudinal gradient to breed. These partially migratory populations present different life-history strategies that appear to persist. A study of dippers in the river Devon catchment in Scotland found no significant difference in the number of eggs laid or the number of young fledged between sedentary residents and altitudinal migrants (Logie 1998). This contrasts with studies of American dippers in North America, where migrants were less productive than residents and were considered to be subordinate individuals unable to compete for lowland nest sites (Morrissey 2004; Gillis *et al.* 2008; Mackas *et al.* 2010).

1.3.8 Status

Threats to UK freshwater habitats arise from agricultural and industrial-urban sources, abstraction and flow regulation, disturbance and continued acidic deposition, chemical contamination and climate change (Dudgeon *et al.* 2006; JNCC 2018; Reid *et al.* 2018b). The use of organisms and particularly birds as proxies for the health of ecosystems is well established (Landres *et al.* 1988; Chambers 2008; Parmar *et al.* 2016; Egwumah *et al.* 2017; Mekonen 2017), and dippers in the UK are widely accepted as an ideal sentinel species indicating water quality as they are mostly resident, easily monitored, potentially long lived and prey on benthic macroinvertebrate prey and small fish. This makes them sensitive to perturbations in the food chain and reflect subtle changes in environmental status over spatial, temporal and trophic scales (Caro and O'Doherty 1999; Sorace *et al.* 2002; Tabor and Aguirre 2004). American dipper numbers were found to reflect prey abundance and assist in indices of biotic integrity of stream bioassessment (Feck and Hall 2004). As an ‘umbrella species’ requiring a large habitat area to sustain populations, dippers often signal the presence of less habitat demanding sympatric species (Simberloff 1998; Carignan and Villard 2002), and reflect habitat conditions, species richness and wider biodiversity of riparian communities.

Being resident in well-defined territories and having specific diets, mainly of invertebrates, dippers can reflect the status of pollution sensitive EPT (Feck and Hall 1994). Surface water acidification reduces pH, lowers calcium carbonate solubility and mobilises aluminium ions. These factors can reduce prey availability by limiting exoskeleton and shell formation, and can impact upon dippers by affecting egg formation and shell thickness, and nestling growth and development (Ormerod *et al.* 1985a, 1985b, 1988, 1989, 1991; Scheuhammer 1987; Buckton *et al.* 1988; Tyler and Ormerod 1994; Logie *et al.* 1996; Logie 1998; Øigarden and Linlokken 2010). Chemical contaminants of water from industrial and agricultural run-off and air borne deposition such as pesticides and heavy metal residues have been linked to bioaccumulation in predators, including dippers (Mason *et al.* 1986; Ormerod and Tyler 1990; Mason and Macdonald 1993; Tyler and Ormerod 1994; Nybø *et al.* 1996; Ormerod *et al.* 2000; Fowler 2011). Harmful effects recorded include mortality, sub-lethal stress, decreased fertility, incomplete egg formation and thinning eggshells, and reduced quality of incubation and parenting (Tyler and Ormerod 1994; Fry 1995).

Dipper population changes

Dippers in the UK have advanced lay dates since the 1960s (Figure 1.7: Woodward *et al.* 2018), and similar trends have been observed for other UK bird species (Crick and Sparks 1999). Asynchrony of timing between early shooting plants on breeding grounds and later arriving migrant birds may have fitness consequences for populations unable to pace-match phenologies, and also seen in resident species and over short spatial scales and could have implications for population declines (Visser and Both 2005; Visser *et al.* 2006, 2012; Saino *et al.* 2011; Cole *et al.* 2015; Mayor *et al.* 2017).

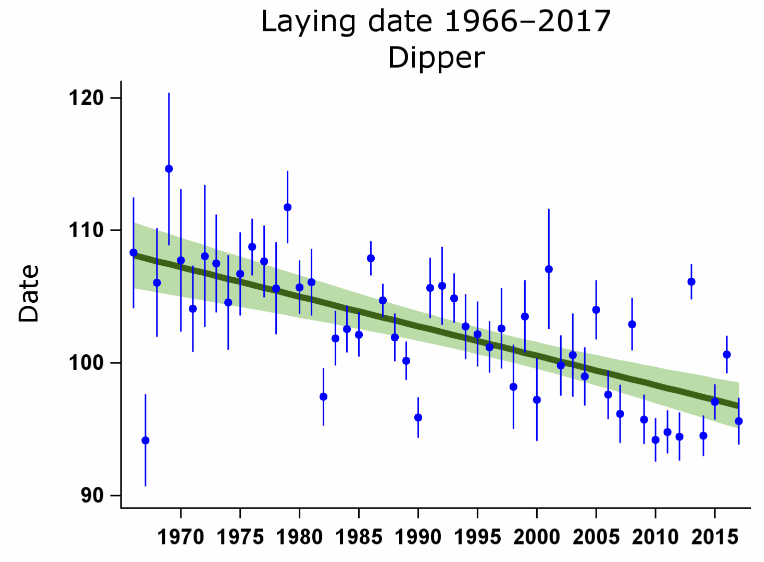

Figure 1.7. Mean laying date of UK dippers in Julian days (April 1st = day 91; data from the BTO nest record scheme). Blue bars represent standard error, shaded area 95% confidence limits and the line shows the long term trend. (© British Trust for Ornithology, BTO). (*BTO/JNCC BirdTrends Report* at: https://app.bto.org/birdtrends/species.jsp?year=2018&s=dippe).

Dipper populations have recently fluctuated but the long-term trend across England and the UK has been one of decline over a number of decades (Figures 1.8a and 1.8b: Woodward *et al.* 2018).

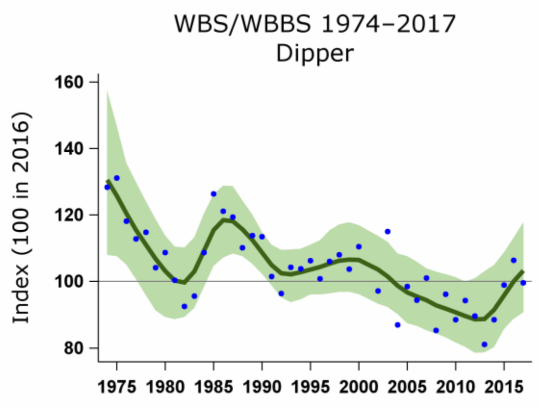

Figure 1.8a Waterways Bird Survey / Waterways Breeding Bird Survey UK 1974-2017.
Smoothed population index, relative to an arbitrary 100 in the year given, with 85% confidence limits shaded. (© British Trust for Ornithology, BTO).
(*BTO/JNCC BirdTrends Report* at: https://app.bto.org/birdtrends/species.jsp?year=2018&s=dippe).

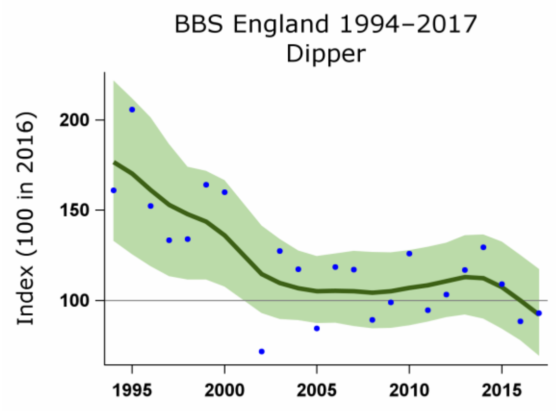

Figure 1.8b. Breeding Bird Survey England 1994 -2017.
Smoothed population index, relative to an arbitrary 100 in the year given, with 85% confidence limits shaded. (© British Trust for Ornithology, BTO).
(*BTO/JNCC BirdTrends Report* at: https://app.bto.org/birdtrends/species.jsp?year=2018&s=dippe).

However, the change in breeding dipper populations varies across the British Isles and within regions (Figure 1.9a: Sharrock 1976; Gibbons *et al.* 1993; Balmer *et al*. 2013) (Figure 1.9b: Gibbons *et al.* 1993; Balmer *et al*. 2013). The causes for the decline in this and other riverine species, including grey wagtail and common sandpiper (Balmer *et al.* 2013), are not fully understood but may be a consequence of slow biological recovery of rivers from chemical degradation exacerbated by climate change and other challenges to rivers and streams.

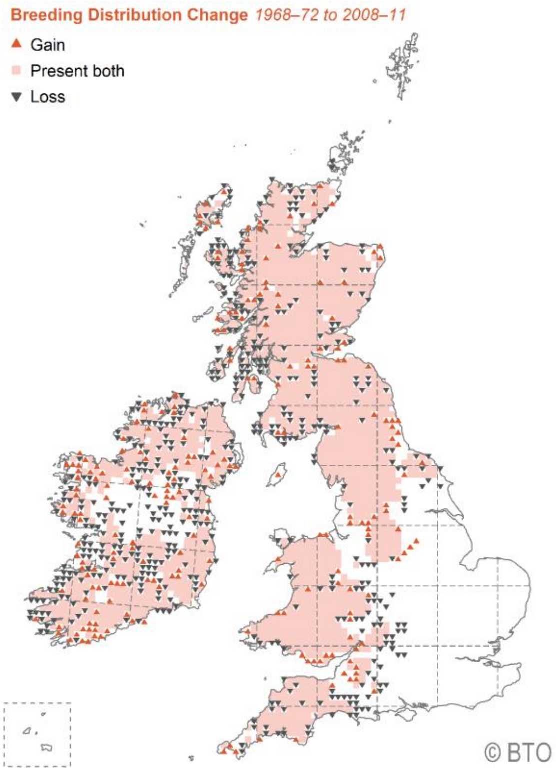

Figure 1.9a. Composite breeding distribution change in dippers across the British Isles 1968-72 to 2008-11. (© British Trust for Ornithology, BTO). (*BTO map store* at: https://app.bto.org/mapstore/StoreServlet?id=339).

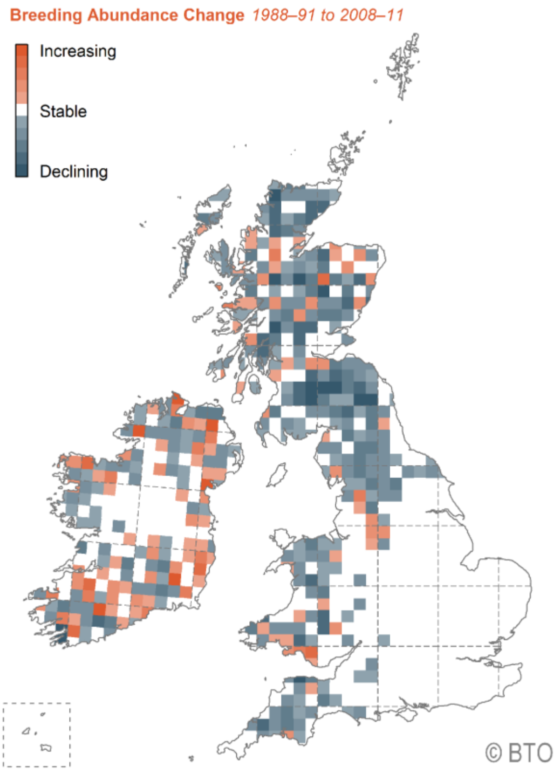

Figure 1.9b. Relative breeding abundance change in dippers across the British Isles 1988-91 to 2008-11. (© British Trust for Ornithology, BTO). (*BTO map store* at: https://app.bto.org/mapstore/StoreServlet?id=339).

1.4 Aims

Dippers present an ideal model system to investigate the impact of altitude and partial migration on breeding ecology. Studies have been carried out on resident and migrant American dippers (Morrissey 2004; Gillis *et al.* 2008; Mackas *et al.* 2010; Green *et al*. 2015), and in white-throated dippers (Logie 1998), but no study has investigated the effect of an altitudinal gradient to determine if reproductive success or measures of parental care of residents versus migrants in a dipper species was similar. In this study, I investigated the effects of altitude on (1) reproductive success and (2) parental care in a partial altitudinal migrant dipper population in the River Lune catchment, UK.

1.5 General methods

1.5.1 The study area

Fieldwork was undertaken in the River Lune catchment of the Howgills and Yorkshire Dales National Character Areas (NCAs) near to the town of Sedbergh, Cumbria, UK (54°19'25.0"N 2°31'41.5"W; Figure 1.10). These western dales and uplands of the Howgills and Baugh Fell of the Yorkshire Dales National Park contain nationally important carboniferous geological features designated as Sites of Special Scientific Interest (SSSIs) (Kimber 1987; Natural England 2013; 2014). Self (2010) provides a narrative of the physical character, natural history, historical and cultural contexts of the whole study area and wider landscape.

The Howgills are a range of high, exposed dome shaped hills up to 676m high with rounded ridges dissected by deep, steep-sided valleys, up to 10km long with an underlying geology of Silurian and Ordovician sandstone, gritstone, siltstone and mudstone. Much of the upper Howgills are grazed by sheep (*Ovies aries*), cattle (*Bos Taurus*) and fell ponies (*Equus ferus caballus*) and comprise peat soils with poorly drained acid grassland and some blanket bog;

bracken and a few patches of heather; and sparse tree cover except in steep-sided becks (Natural England 2014). The loam soiled lower slopes are characterised by hedgerows with trees and dry-stone walls enclosing damp flower-rich hay meadows and pasture, leading down into the river valley bottoms which consist of underlying red conglomerate of pebbles cemented with weathered granite (Natural England 2014).

Figure 1.10. The location of the study site within the UK 🟪 .
(Digimap University of Edinburgh at: https://digimap.edina.ac.uk/).

In the western Yorkshire Dales, approximately 5km south-east of Sedbergh, carboniferous limestone underlies the lower river valley of Dentdale where the river Dee flows over tiered steps of eroded limestone. Enclosed and often damp riverine pastures and flower meadows, together with improved agricultural land, provide pasture for sheep and cattle grazing and hay meadows. Trees line the riverbanks and hedge boundaries with pockets of small woodlands occupying steep-sided tributary streams. Near to the south-east end of the study site lies Combe Scar SSSI, supporting plant communities including nationally important species with base-rich and base-poor soils formed by the complex of rocks of the Upper Silurian Coniston Grits, Lower Silurian Coniston Flags and volcanic Ordovician rocks, brought together by the Dent Fault (Kimber 1987; Natural England 2018).

The upland area of Baugh Fell lies to the east of the Howgills, rising to a height of 678m and having a bedrock of millstone grit and sandstone on the summit plateau and limestone on the lower slopes (Self 2010). Grazed by sheep, the unenclosed and poorly drained fell consists of acid grassland and rushes with deep gills. It has gently west-facing slopes down to the river Rawthey and steeper southerly slopes above the river Clough. The River Lune rises in Newbiggin, Cumbria, flowing westwards initially and then southwards towards the Lune estuary and into Morecombe Bay. Near Sedbergh, the rivers Clough, Dee and Rawthey flow into the Lune, and the surrounding uplands drain radially into a network of streams, gills or becks and their tributaries, which then discharge into the rivers. The dipper territories located along these four rivers and their associated waterways are the subject of this study. The topography of the study area is shown in Figures 1.11-13 and in the Appendix Figures 2-5.

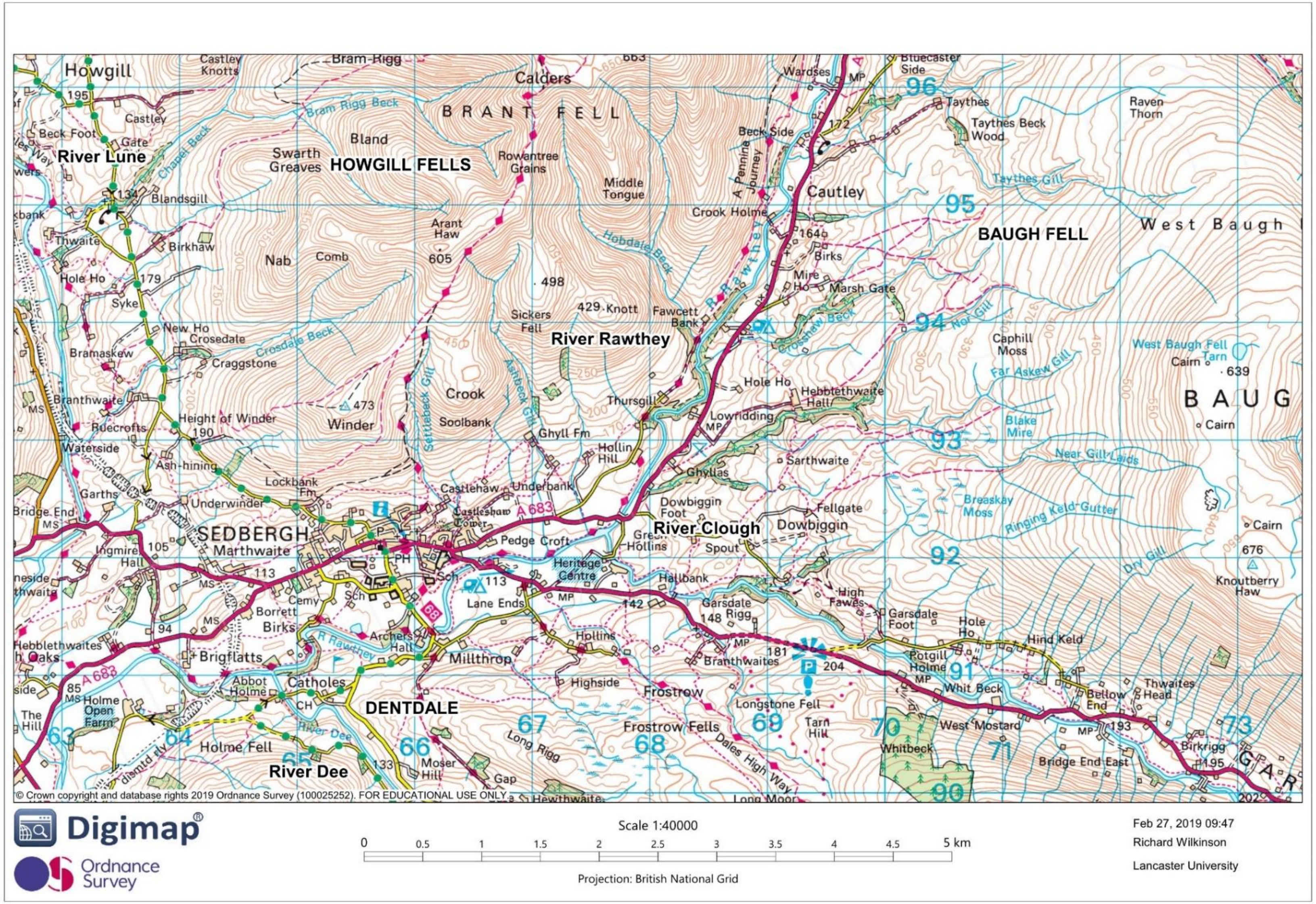

Figure 1.11. A map of the study area. (Digimap University of Edinburgh at: https://digimap.edina.ac.uk/).

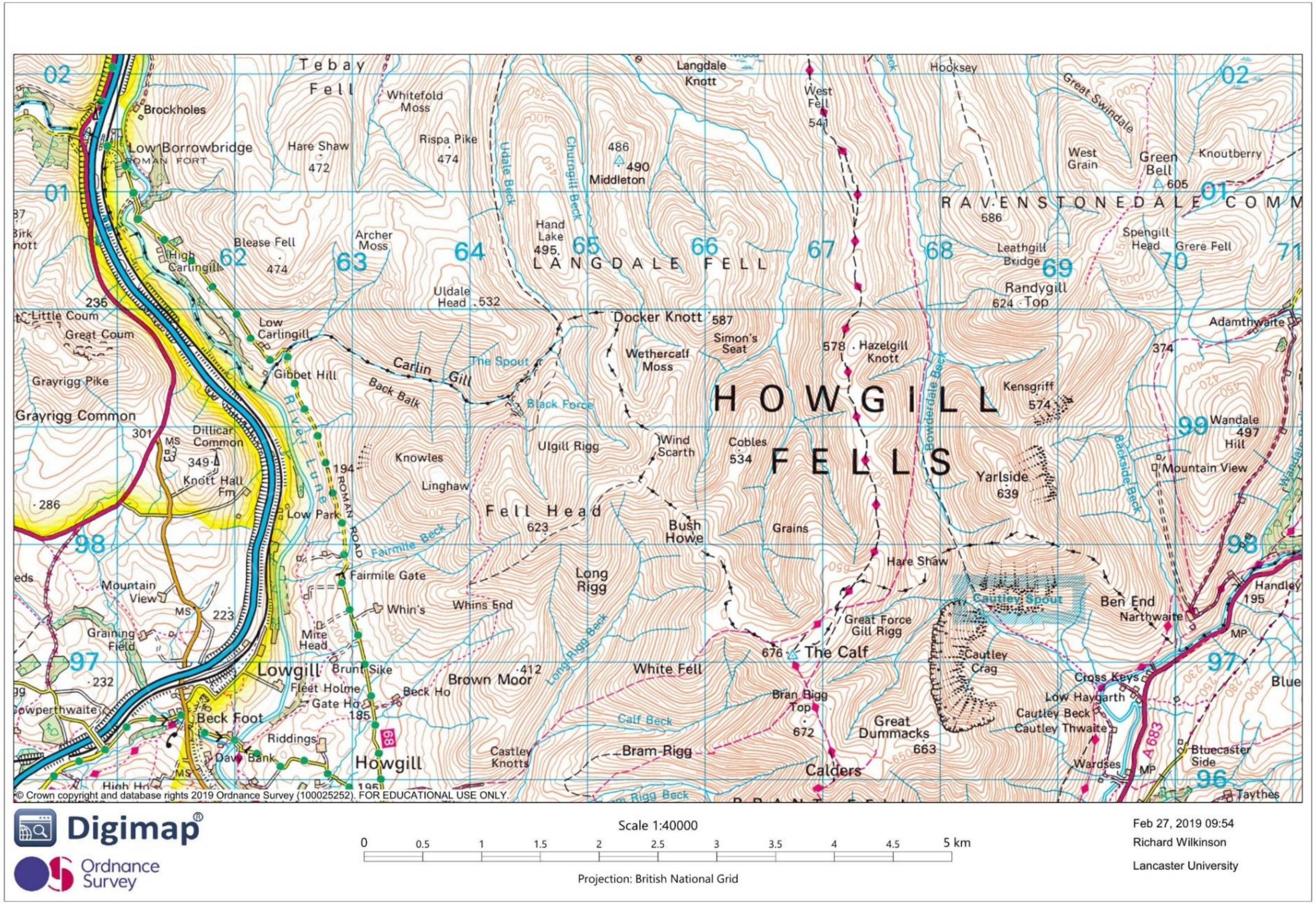

Figure 1.12. A map of the study area immediately north of Figure 1.11. (Digimap University of Edinburgh at: https://digimap.edina.ac.uk/).

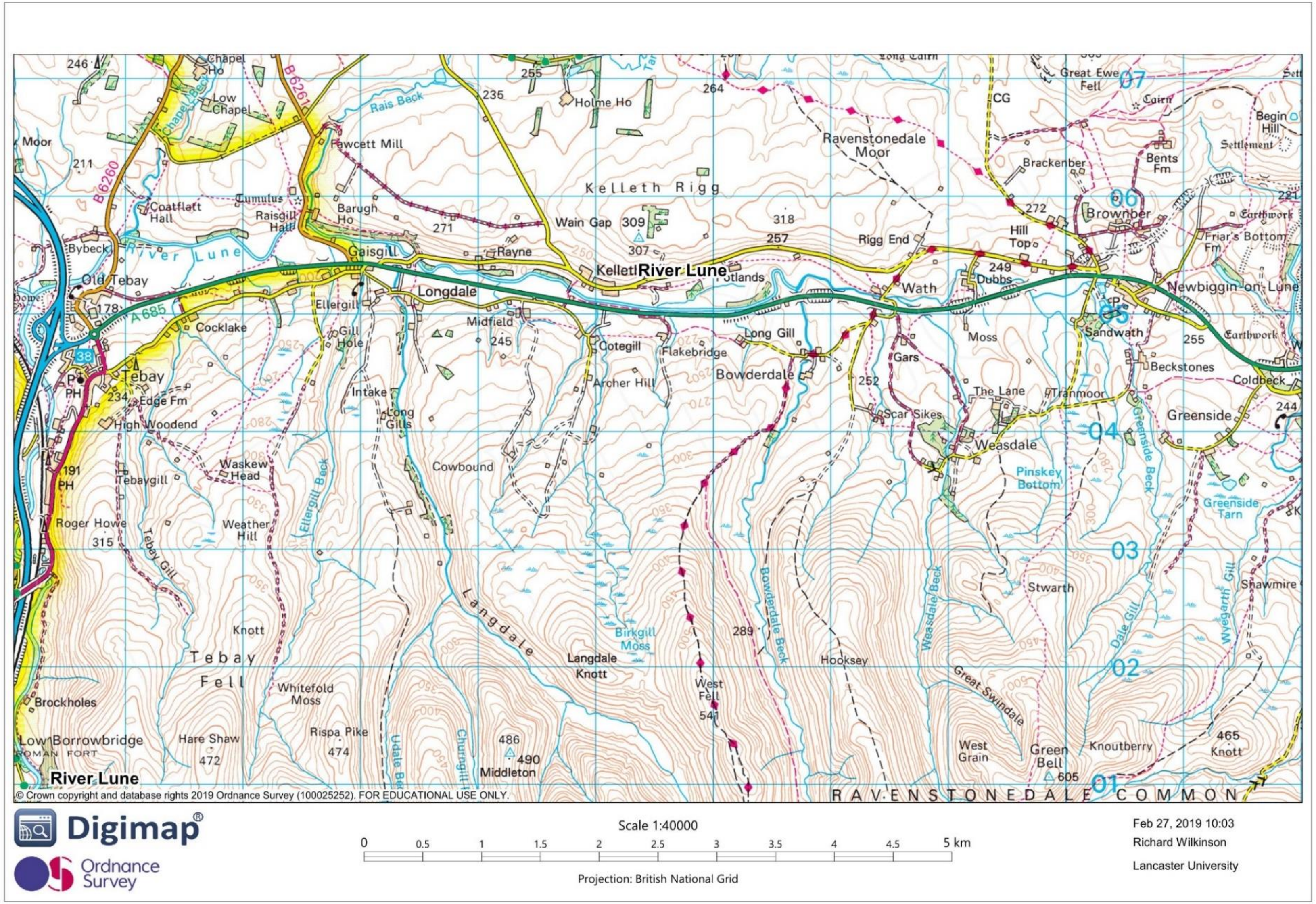

Figure 1.13. A map of the study area immediately north of Figure 1.12. (Digimap University of Edinburgh at: https://digimap.edina.ac.uk/).

In this study, upland nesting dippers were defined as those breeding at an altitude of at least 200m above sea level (asl). At this elevation, the landscape is steeply sloped with unenclosed and grazed pastureland with little or no tree cover. Rivers or streams tend to be narrow, shallow and fast flowing with small cascades and waterfalls, sometimes within steep-sided gullies (Figure 1.4). Dippers nesting in these areas generally undertake seasonal movement to lower altitudes during autumn and winter, followed by late winter and early spring return to the uplands to breed (Crowther 2018; S. P. Sharp unpublished data). Lowland breeding dippers were defined as nesting below an altitude of 200m asl; here, rivers or streams are often lined with dense, mature bankside trees on gently sloping ground with enclosed grazing pastures (Figure 1.4). In contrast to upland waters, lowland rivers and streams are usually wider (>3m), deeper and with slower flow rates, occasionally containing deep pools, big rapids or waterfalls. Lowland breeding dippers remain at these lower altitudes throughout the year, in many cases defending the same territory during and outside the breeding season (Crowther *et al.* 2018).

1.5.2 Historical monitoring of dippers in the study area

Robson (1956) refers to dipper surveys along the River Lune in 1939 and 1953. Cleasby (1999) describes the 1939 British Trust for Ornithology (BTO) census of the main rivers of the Lune, Clough, Dee and Rawthey and their associated tributary streams made by Kenneth Martin; this recorded the number of pairs, descriptions of breeding habitats and nest sites. The census of 1953 by C. Moody is lost but contributes to that year's BTO ringing report. Cleasby (1999) also chronicles further dipper surveys: Michael Jackson in 1962 and David Bishop in 1963 collected detailed breeding data, and reference is made to further surveys in 1964 and 1965. In total, records were collected for nine breeding seasons between 1958 and 1966.

In 1958, Peter Mawby, a pupil at Sedbergh School at that time, began studying the breeding population of dippers along the 50km of rivers and streams in the Lune catchment within about 5km of Sedbergh (P. J. Mawby personal communication). Mawby, assisted by his brother

Andrew and members of the Sedbergh School Ornithological Society, undertook annual monitoring of this area until 1966, recording lay dates, productivity and other aspects of breeding behaviour (Mawby 1961). For ten breeding seasons between 2003 and 2012, Peter Mawby resumed his monitoring in the same study area, this time colour ringing nestlings with a yearly cohort combination.

In 2013, Stuart Sharp of Lancaster University established an individually marked population within Peter Mawby's study area (see below for details of ringing); working together, they thereby began a long-term study of individual life-histories, behaviour and population ecology which is still running (e.g Magoolagan 2017; Crowther *et al.* 2018; Magoolagan *et al.* 2019). All surviving birds from previous years were retrapped in 2013 and given individual colour ring combinations. In order to increase sample sizes, the area was extended in 2014 to include all territories within a 7km radius of Sedbergh; this area forms the study site for much of the research described here. However, to increase the sample of upland nests in 2017, a number of additional territories were added from parts of the catchment just outside of the core site (for more details of the 2017 sites, see Chapter 3; for maps of all territory locations, see Appendix Figures 1-5).

1.5.3 Ringing and biometric data

All adults, juveniles and pulli in the study site are individually marked with a standard metal BTO ring and a unique combination of three plastic colour rings (two rings per leg, all fitted below the tarsal joint). In nearly all cases, the plastic rings retain their colours across successive seasons and it is extremely rare for rings to be lost; when necessary, birds are retrapped to confirm or replace the colour rings (approximately one bird per year). Colour ringing enables reliable field observations to be made without the need for recapture, for example including territory ownership and breeding behaviours. Each year, any unringed adult or juvenile birds, which have moved into the study site, are trapped and ringed (under BTO licence), mostly using mist nets placed across the waterways or other flight paths. Incubating females are also caught by placing a landing net over the nest (male dippers play no role in incubation); this method is only used after the first seven days of incubation in order to minimise the risk of nest desertion.

For fully-grown birds (juveniles and adults), wing length (maximum chord to the nearest mm, measured with a wing rule) is recorded. Most adult birds can be aged as being either in their first calendar year or older according to the presence or absence of unmoulted primary coverts, respectively (Demongin 2016). A small proportion of birds are unclassified if the age of the primary coverts cannot be judged reliably. All fully-grown birds can be sexed according to their wing length with little overlap between genders (Demongin 2016), for many birds, this can be confirmed from observations of breeding activities (e.g. incubation) and in no cases has there been a discrepancy using this method.

Nestlings were ringed on day 7 of the nestling period (day 0 = the day of hatching) in 2013 but on day 9 thereafter (and this enables confirmation of juvenile identity and fledging when close to empty nests); and body mass is also measured at this time. Wherever possible, birds, which recruit into the breeding population, are retrapped when fully grown in a subsequent year in order to collect the full set of biometric data.

1.5.4 Nest monitoring

Intensive nest monitoring of rivers and streams was carried out in the core study site and adjacent upland habitat between February and July in each year from 2013 to 2017 to identify birds as either territory holding or as ‘floating’. Individuals were defined as floaters if they were unpaired and failed to display territorial behaviour (and were often observed in different and sometimes widely separated locations). Almost all nests which reach the egg stage (or further) are found and can be monitored through to fledging or failure; occasionally, it is clear from a pair’s behaviour that they have an active nest and the female is laying or incubating, but the nest fails before it can be found and the pair are then seen building again (1-2 nests per year).

Nests are found by systematically surveying all stretches of river or stream to establish territory occupancy and ownership (i.e. the pair's identity), and checking traditional nest-sites in February and March; periodic checks of any vacant stretches are made later in the season to ensure that pairs which move into the study site to breed relatively late are not missed. Dippers involved in territory occupation and defence, song, courtship display and mating, nest-site prospecting, carrying obvious nest material (moss in the early stages of construction, grass and leaves as nest cup lining in the latter stages of completion) or apparent nest guarding, are carefully observed. Each pair is then observed at least once per week until the nest is found, usually by following birds carrying nest material or females returning to the nest to lay or incubate. For long stretches of river or traditional territories in which no birds or nest were found, repeat visits were made to ensure that an overlooked breeding pair was extremely unlikely (Morrissey 2004). Using these established methods, very few (if any) nests are missed in either lowland rivers or upland streams. Each nest location was recorded with a Garmin eTrex H GPS (Garmin Ltd, Switzerland), from which altitude could be measured and cross-checked with OS (Ordnance Survey) survey data to the nearest 10m.

Once found, nests were visited approximately once per week until construction had progressed to a grassy cup which the birds had started to line with leaves (Tyler and Ormerod 1994). A breeding attempt was recorded as one that progressed to at least the egg stage (and nests found during the laying period have cold, unincubated eggs). From this point, visits were made every 2-3 days to determine lay date (i.e. the date on which the first egg of the clutch was laid). Dippers very rarely have clutches smaller than three eggs and, typically for small passerines, lay one egg per day until the clutch is complete and commence incubation once the final egg has been laid (Perrins and McCleery 1989; Tyler and Ormerod 1994). Lay date can therefore be back-calculated once an incomplete clutch of cold eggs has been found in the nest. Checking nests for eggs was carried out after noon to reduce the possibility of disturbing the female during egg laying and the risk of desertion. The nest was then revisited after one to two weeks to measure clutch size and thereby establish the start of incubation (taken as the day on which the final egg is laid; Tyler and Ormerod 1994). Daily checks resume after 14 days of incubation to establish the date of hatching (known as 'hatch date' hereafter; the minimum duration recorded in the study site, S. P. Sharp unpublished data) and based on a typical incubation period of 16-18 days (Tyler and Ormerod 1994). If a nest is not found until the incubation stage, then visits are made as regularly as possible to record hatch date. If any hatch date was missed it was determined by ageing nestlings from their appearance up to three days old (and lay date can be back-calculated this way, assuming an incubation period of 16 days which is the mean for the study site, S. P. Sharp unpublished data), after which ageing becomes less reliable. If the chicks are judged to be older than three days when the nest is first visited, then lay date, clutch size and hatch date are left undetermined. Nestlings were ringed when nine days old (if possible) by which point they are no longer brooded by the female; standardised biometrics could then be taken including nestling mass, measured with an electronic balance (to the nearest 0.1g). Finally, daily visits were made once the nestlings were 20 days old in order to establish the timing of fledging (typically at age 21-22 days; Tyler and Ormerod 1994) and the number of fledglings; fledged nests were inspected for dead chicks to ensure that brood reduction had not occurred since ringing, although this is rare (S. P. Sharp unpublished data). A small number of nests (1-2 per year) are built in inaccessible sites and unless information can be obtained e.g. using endoscopes for nests in rock cavities, approximate dates for each of the major breeding stages are estimated from the behaviour of the pair; these data, together with chick measurements for broods of unknown age, are excluded from all analyses unless otherwise stated. If inaccessible nests are successful, the chicks are caught by hand or in mist nets soon after fledging for ringing and measuring. Nests that fledge before the end of May were visited approximately five days after fledging, and return visits were made to check for evidence of second brooding (e.g. re-lining of the nest); this continued for up to another 14 days, after which point second broods are very rare. Where behaviour suggested a second brood attempt was initiated, daily lay checks were carried out. For any failed nest during the breeding season, the territory is visited at least weekly until the pair show no further indication of breeding activity after repeat visits or until they cannot be located.

1.5.5 Biological assessment of water quality

Water quality was assessed by using biotic indices. Initially, by totalling Biological Monitoring Working Party (BMWP) scores of 1-10 assigned to invertebrate families based on their sensitivity to pollution (low oxygen levels) with 10 indicative of little pollution and then divided by the number of scoring taxa to give the Average Score Per Taxon (ASPT). ASPT is the preferred scoring of water quality being less sensitive to sampling effort, and a high ASPT with a value of >6.00 indicates excellent water quality with large numbers of high scoring sensitive taxa (Armitage *et al.* 1983; Hawkes 1998; River Habitat Survey 2019). All territories over the entire elevational range were in excess of ASPT 6.30 and are in line with figures obtained by Magoolagan (2017), being indicative of high water quality having high BMWP scoring pollution sensitive taxa present, namely EPT, which are the main dipper prey items. In addition, Environmental Agency (EA) measures of water quality recorded in the catchment and study area in 2016 report overall hydromorphology as classed as ‘good’, physico-chemical conditions and pH ‘high’ (a positive quality), ecological conditions ‘good’, invertebrates ‘good’ and mostly ‘high’, and with no hazardous chemical inputs (Environment Agency 2016). Field and laboratory measurements of water pH taken from rivers and streams throughout the study site have all recorded values >pH 7.0 (S. P. Sharp unpublished data). These findings suggest that water quality *per se* does not appear to be a constraining factor for riverine communities in the Sedbergh upper River Lune catchment area.

Chapter 2

Altitude and its effect upon breeding success in dippers (*Cinclus cinclus*)

2.1 Abstract

In some populations, breeding territories may be limited and this can lead to a partial migration in which some individuals migrate whilst others remain resident. Partial migration can occur along altitudinal gradients but the fitness consequences of this are poorly known, especially in the UK's upland species, many of which are in decline. This study examined long-term field data from a population of a partial altitudinal migrant and specialist riverine bird, the dipper (*Cinclus cinclus*). Most dipper populations consist of migratory individuals that breed at higher altitudes and overwinter with residents at lower elevations, but the effects of altitude on their life-history traits and breeding success have rarely been studied. Here, I used mixed effect models to investigate whether altitude predicts lay date, nestling mass, fledging success, the number of fledglings and annual productivity, while controlling for female age, at nest sites across an altitudinal range of 90m-520m monitored from 2013-2017. Dippers at higher altitudes tended to breed later, possibly because of the time taken to migrate and establish breeding territories, and also have a marginally higher fledging success, perhaps due to a lower risk of flooding and predation. However, altitude had no effect upon nestling mass or the number of fledglings and was unlikely to have any effect on annual productivity. Later breeding females (particularly migrants) that do not have a second brood are likely to be less productive than those breeding early. Age may not affect timing of breeding but prior parenting experience may explain the production of a greater number of fledglings by older females, although productivity later declines with age presumably due to senescence. Older females are more likely to fledge broods and produce heavier nestlings, which suggests higher parental investment with smaller broods. Altitudinal migration is likely to be an alternative migratory tactic resulting from competition for lowland nest sites, with migrants having to forgo second broods but possibly benefitting from a lower risk of flooding and predation. The results of this study suggest that altitudinal migration and residency may each provide adaptive benefits for dippers. Further research should investigate what drives altitudinal migratory tendency and the long-term fitness consequence for dippers.

2.2 Introduction

Competition for resources in territorial species can force individuals to breed in sub-optimal habitats or conditions, often with negative fitness consequences (Clutton-Brock 1988; Newton 1998; Johnson 2007). In some species, individuals adopt different life-history traits to mitigate these effects or aim to maximise breeding success by means of alternative reproductive tactics (ARTs), making differential investment decisions in response to trade-offs in reproduction and survival (Gross 1996; Oliveira *et al.* 2008; Taborsky and Brockmann 2010). While some ARTs may be fixed for life, for example by genetic or developmental mechanisms, others are plastic and may be switched according to current conditions, including population density and competition (reviewed in Taborsky and Brockmann 2010). Comparable to ARTs are alternative migratory tactics (AMTs) of partially migrating populations (Chapman *et al.* 2011a, 2011b; Sahashi and Morita 2018). Many of the life-history traits that aim to maximise fitness are discontinuous but flexible behaviours, such as nomadism versus site tenacity (e.g. Andersson 1980) or migration versus residency (e.g. Dodson *et al.* 2013).

Variation within a population in whether or not individuals migrate is known as partial migration. This is a widespread phenomenon in migratory animals from various taxa, but the causes and consequences of partial migration are not fully understood (Chapman *et al.* 2011a; 2011b; Reid *et al.* 2018a). In most altitudinal migrants, for example, populations comprise sedentary residents and individuals that make short, seasonal, return movements between breeding and nonbreeding or wintering sites along an elevational gradient (Boyle *et al.* 2016; Barçante *et al.* 2017; Hsiung *et al.* 2018). Suggested drivers for these movements include temporal variation in the availability of food (e.g. Hebblewhite *et al.* 2008; Blake *et al.* 2013), breeding sites (e.g. Ketterson and Nolan 1976; McGuire and Boyle 2013), roost sites (e.g. Russo 2002; Encarnação *et al.* 2005), avoidance of predators (e.g. Hebblewhite and Merrill 2007; Boyle 2008), and extreme climatic conditions (e.g. Igota *et al.* 2004; Liu *et al.* 2015), but there is considerable variation in the responses made to these drivers within and between species (Hsiung *et al.* 2018). Furthermore, residents and migrants differ in their breeding success or survival in some species but not others; in elk (*Cervus canadensis*), for example, migrants have better foraging opportunities but lower survival resulting from higher predation (Hebblewhite and Merrill 2011), whereas partial migration has no effect on survival rates in moose (*Alces alces*), yet breeding success and net fitness are higher in migrants (Rolandsen *et al.* 2017). Further research is needed to better understand this variation, especially in a time of rapid environmental change when species breeding at high altitudes are among the first to be affected (Russo 2002; Thackeray *et al.* 2010; Dodson *et al.* 2013; Flousek *et al.* 2015; Gibson-Reinemer *et al.* 2015; Báez *et al.* 2016; Scridel *et al.* 2018).

Altitudinal migration is particularly well-documented in birds; in the UK, examples include snow bunting (*Plectrophenax nivalis*; Smith 1994), twite (*Linaria flavirostris*; Haworth and Thompson 1990) and meadow pipit (*Anthus pratensis*; Rose 1982). Many studies have compared the breeding success of migrants and residents (Badyaev 1997; Boyle *et al*. 2016; Barçante *et al.* 2017), and individuals breeding at higher altitudes tend to have smaller clutches, are less likely to have multiple broods, devote more to parental care or produce fewer and heavier fledglings (e.g. Badyaev 1997; Badyaev and Ghalambor 2001; Bears *et al.* 2009; Lu *et al.* 2009). The variation in these traits as altitude increases suggests a trade-off between fecundity and parental care; greater investment in parental care may compensate for the production of fewer offspring by increasing offspring quality and survival, or by increasing adult survival and therefore the potential for future reproduction (Badyaev and Ghalambor 2001; Bears *et al.* 2009; Hille and Cooper 2015; Balasubramaniam and Rotenberry 2016). However, studies involving geographically distinct populations, or pairs of related species or races (Badyaev and Ghalambor 2001), may have limited value for any comparisons between the selection pressures and fitness consequences for alternative migratory tactics.

Here, I investigate how the timing of reproduction and breeding success vary across an elevational gradient in a population of dippers (*Cinclus cinclus*), an altitudinal migrant. Dippers are monogamous passerines found on shallow, fast flowing rivers and streams in the uplands of Europe, North Africa and Western Asia, feeding mostly on freshwater macroinvertebrates but sometimes small fish (Tyler and Ormerod 1994). Although listed as 'Least Concern' by the IUCN, populations are in decline across Europe and this species is 'amber-listed' in the *UK Birds of Conservation Concern*, with a breeding population decrease of 27% over 25 years (Eaton *et al.* 2015). These declines are poorly understood, although known threats to dippers include xenobiotic pollutants that affect water quality and prey species, alteration of flow rates and water courses from water impoundment, abstraction, hydro-electric and irrigation schemes, and habitat degradation (Ormerod and Tyler 2005). Climate change is also thought to be a contributory factor (Sæther *et al.* 2000; Nilsson *et al.* 2011a; Royan *et al.* 2013, 2014, 2015), making studies of altitudinal migration in this species especially important.

In the UK, dippers breeding at high elevations (on tributary streams) typically migrate to lower altitudes where they winter in the same area as year-round residents (Tyler & Ormerod 1994; Wilson 1996; Logie 1998). Most residents are territorial, whereas many altitudinal migrants act as winter 'floaters' and only remain in a single wintering site if residents are absent (Crowther *et al.* 2018; S. P. Sharp unpublished data). This species shows signs of phenological change, with lay date having advanced by 12 days over 50 years (Woodward *et al.* 2018). Furthermore, predicted climate-driven trophic level asynchrony in freshwater habitats and reductions in invertebrate species could potentially impact reproductive success in dippers (Briers *et al.* 2004; Durance and Ormerod 2007; Thackeray *et al.* 2010). Thus, understanding how altitude impacts on the breeding ecology of these birds would not only provide a useful model of altitudinal migration but may also offer key insights into the causes of their decline.

It has been observed that upland dippers tend to breed later than lowland birds and rarely have second broods, but lay similarly sized clutches (Tyler and Ormerod 1985, 1994). A study of Scottish dippers found that lowland pairs had more breeding attempts, laid more eggs, and hatched and fledged more offspring than upland birds, although these differences were not statistically significant (Logie 1998). In the closely related American dipper (*Cinclus mexicanus*), no difference was found between residents and migrants in clutch size or brood size, but lay date was significantly later for migrants, whereas fledging success and annual productivity were higher for residents and they were also predicted to have higher lifetime reproductive success (Morrissey 2004; Gillis *et al.* 2008). Furthermore, delayed timing of breeding by migrants reduces the likelihood of second brooding, and they do not compensate for lower productivity with higher quality offspring (Morrissey 2004; Mackas *et al.* 2010). It has been suggested that migrant American dippers are subordinates and that breeding at higher altitudes is a conditional strategy whereby they breed and survive using the resources available for lack of a better alternative (Gillis *et al.* 2008; Mackas *et al.* 2010). However, there have been no similar studies in the UK of a single population comparing life-history traits and breeding success between residents and altitudinal migrants. In this chapter, I address this by analysing how the timing of reproduction, key components of breeding success and annual productivity vary with altitude in a long-term study population in the north of England.

2.3 Methods

Data were collated from a long-term study population of dippers found along rivers and tributary streams in the River Lune catchment within an 8km radius of Sedbergh, Cumbria, UK (54°19'25.0"N 2°31'41.5"W) (see Appendix Figures 1-5 for territory locations). Dippers breeding below an altitude of 200m were defined as lowland nesting and those above this altitude as upland nesting (lowland and upland habitat descriptions are given in Chapter 1). Each year from 2013-2017, the breeding population of *c.*40-45 pairs was closely observed from

February to June in order to monitor nests and measure reproductive success. In 2017, additional pairs from neighbouring upland areas supplemented the core study population in order to increase the sample of birds breeding at high altitudes. Adults were caught using mist nets or landing nets placed over nests and given a unique combination of three colour rings and the standard BTO metal ring; wing length (length of the maximum wing chord measured to the nearest mm) was measured with a wing rule and could be used to determine sex (males have longer wings; Demongin 2016). Birds which had not been ringed as nestlings could be aged as either first-year or older (‘adults’) according to the presence or absence of unmoulted juvenile coverts, respectively (Demongin 2016). Active nests were located by making frequent visits to all known and potential supplementary upland territories and observing for signs of breeding behaviour, and altitude in m was measured with a Garmin eTrex H GPS (Garmin Ltd, Switzerland) and later validated with Ordnance Survey data to the nearest 10m. Once breeding activity was established, repeat visits were made to establish lay date, clutch size, hatch date, day 9 nestling mass, fledging date and the number of fledglings for all first and second brood nesting attempts (see Chapter 1). Nestlings aged nine days old were weighed to the nearest 0.1g using an electronic balance and ringed using the same system as adults. A total of 296 breeding attempts were monitored across the study period, where a breeding attempt was taken to be the laying of at least one egg.

2.3.1 Statistical analyses

Linear mixed-effect models (LMMs) or generalised linear mixed-effect models (GLMMs) were employed to investigate the relationship between altitude and each of the following reproductive (response) variables: lay date, nestling mass, fledging success (i.e. whether or not a nest fledged at least one chick), the number of fledglings (that fledged from a nest), and annual productivity (i.e. the total number of fledglings produced by a female in one year). LMMs and GLMMs were used to analyse Gaussian and non-Gaussian data, respectively, with non-independent data (pseudoreplication) accounted for by random effects following Bolker *et al.* (2009) and Harrison *et al.* (2018). Female identity was fitted as a random term in all models to account for repeated measures across years. Territory identity was fitted as an additional random term in preliminary models but subsequently dropped because it did not explain any further variation in the data, presumably because most females remain in the same territory for multiple breeding attempts. In all models, altitude was included as a continuous fixed effect and all measures of age and wing length refer only to females.

In examining the effect of altitude (the nest site height in m) on lay date (the Julian date on which the first egg was laid, where 1=January 1st), the following fixed explanatory variables were included: year, age in years, wing length in mm (as a proxy for body size and condition), and the interactions between altitude and age, and altitude and wing length (LMM, Gaussian error structure and identity link function; n=141). For the effect of altitude on nestling mass (in g), fixed explanatory variables included year, age and wing length, brood size (the number of nestlings on the 9th day after hatching, as a measure of sibling competition), and hatch date (the Julian date on which hatching occurred, to control for seasonal variation in environmental conditions). Interactions contained in the full model included those between altitude and age, age^2, brood size, hatch date and wing length (LMM; Gaussian error structure and identity link function; n=107). A GLMM was used to examine the effect of altitude on the response fledging success (binomial error distribution and logit link function; n=199); fledging success was given as either 0 (nest failure) or 1 (nest success i.e. at least one nestling fledged). Additional explanatory variables were year, age, and wing length. For altitude and the number of fledglings, additional fixed explanatory variables included year, age, wing length, clutch size and hatch date. Preliminary analysis on number of fledglings suggested a potential quadratic effect of age, and so age^2 was also fitted as a fixed effect, and the interactions between altitude and both age and age^2, and wing length (LMM; Gaussian error structure and identity link function; n=103). Finally, for the effects of altitude on annual productivity (LMM; Gaussian error structure; n=141), additional fixed explanatory variables included year, age and wing length and lay date of the first brood. Preliminary analysis of annual productivity (total number of offspring from single or double broods) suggested potential quadratic effects and so age^2 was fitted as a fixed effect. The interactions between altitude and age, age^2, lay date and wing length; age and lay date, age and wing length; age^2 and both lay date and wing length; and wing length and lay date, were also included. In all cases, explanatory variables were fitted as continuous variables except year which was fitted as a factor.

All statistical models were constructed in the R environment, version 3.5.1 (R Core Team 2018) with relationships and interactions of variables analysed as described by Zuur *et al*. (2010); LMMs and GLMMs were run in the *lme4* package (Bates *et al.* 2015). Prior to model construction, selection and analysis, collinearity between the explanatory variables was tested using pairwise correlation and Variance Inflation Factors (VIFs) using the 'corvif' function in the AED package (Zuur *et al.* 2009, 2010). Collinearity values of VIFs were all low (<3) and pairwise correlation plots between explanatory variables were mostly weak (<0.5) and so these were all included in the models (Zuur *et al*. 2010). When explanatory variables were highly correlated, selection for final model inclusion was based on the lowest AIC estimate (Anderson *et al.* 2001; Symonds and Moussalli 2011), but primarily on how biologically informative the variable would be as a fixed effect and in interactions. To ensure interpretation and comparability of test model estimates, all fixed effect explanatory variables (and hence, interactions) were centred and standardised (non-continuous variables centred only) prior to modelling (Schielzeth 2010; Harrison *et al.* 2018). Models were validated by checks of overdispersion and by plotting the distribution of the residuals, Q-Q plots of the residuals, the residuals versus the fitted values and the residuals versus each of the covariates (Zuur *et al.* 2009). The full model was then analysed using the *lme4* package and the 'dredge' function within the *'Mumin'* package (Bartoń 2018). Candidate models were generated containing all possible variable and interaction combinations and ranked according to the lowest Akaike Information Criterion (AIC) corrected to AICc (the second order Akaike Information Criterion) for small sample sizes, including R^2 variance (Hurvich and Tsai 1989; Burnham and Anderson 2002; Nakagawa and Schielzeth 2013). Using the 'MuMin' package, models with ΔAICc <2 of the best fitting model were selected and averaged (Harrison 2018), and used to generate predictive values and plots of significant variables (plots of fledging success and with overlapping points are presented randomly offset using the 'jitter' function for clarity), and these are reported in the results.

2.4 Results

A total of 296 breeding attempts which progressed to egg laying were monitored during 2013-2017. First broods accounted for 261 attempts and second broods 35; 255 attempts were in lowland habitat and 41 were at upland nest sites (lowland habitat is defined as being below a height of 200m and upland habitat above a height of 200m, as described in Chapter 1). In cases where breeding variables and measures of dippers were absent, such as those nests that were not located until the nestling stage, or nests which failed before clutch size had been determined, the breeding attempts did not form part of the analyses. A summary of the breeding variables of lowland and upland dippers in this study is found in Table 2.1.

Table 2.1. A summary of the breeding variables of lowland and upland dippers in the River Lune catchment study site 2013-2017. Data are means ± SD (sample sizes in parentheses).

Breeding variable	Lowland (<200m): first broods	Upland (>200m): first broods	Lowland (<200m): second broods
Lay date (Julian date)*	90.19 ± 14.05 (155)	100.62 ± 10.88 (26)	129.97 ± 7.90 (33)
Clutch size*	4.75 ± 0.55 (151)	4.68 ± 0.48 (22)	4.38 ± 0.66 (32)
Hatching success (%)**	92.27 ± 14.34 (99)	94.00 ± 13.50 (10)	92.06 ± 13.24 (17)
Brood size on day 9**	3.94 ± 0.98 (127)	3.45 ± 0.89 (20)	3.19 ± 1.21 (21)
Fledging success (%)*	61.54 (169)	57.14 (28)	54.29 (35)
Number of fledglings (all nests)	2.18 ± 2.05(217)	2.21 ± 1.83 (38)	1.66 ± 1.80 (35)
Number of fledglings (successful nests)	3.82 ± 1.03 (124)	3.50 ± 0.83 (24)	3.05 ± 1.27 (19)

* Calculated only for first breeding attempts

** Calculated only for nests which hatched at least one nestling

2.4.1 Factors affecting lay date

All the best fitting LMMs of the factors associated with lay date and their effects after model averaging are shown in Tables 2.2 and 2.3. Altitude was the best predictor of lay date and was found in all of the best fitting models, with nests at higher altitude having later lay dates (Figure 2.1). Additional fixed effects retained in the best fitting models were year (in all models), with which lay date varied considerably but with no clear temporal trend (Figure 2.2), and female age and wing length, for which effect sizes were very small and unlikely to be biologically meaningful. Finally, no interactions were present in the best fitting models.

Table 2.2. The best fitting LMMs of the factors associated with lay date (i.e. those models with a ΔAICc value of 2 or less from the best fitting model). The null model is shown for comparison. (2013-2017; n=141; "+" indicates presence of a categorical variable).

Full model = lmer: lay date ~ (altitude + female age + wing length + year + altitude : female age + altitude : wing length) + (1|female identity).

Model	Intercept	Altitude	Female age	Wing length	Year	Altitude: female age	Altitude: wing length	df	Loglik	AICc	ΔAICc	Weight	R^2m	R^2c
11	104.972	5.258			+			8	-520.504	1076.1	0.00	0.267	0.460	0.558
12	103.954	5.311	-1.328		+			9	-518.754	1076.7	0.60	0.198	0.462	0.576
16	103.433	5.313	-1.795	1.454	+			10	-516.848	1077.0	0.98	0.164	0.467	0.589
15	104.883	5.256		0.909	+			9	-519.176	1077.5	1.43	0.131	0.462	0.567
1 (Null)	91.000							3	-573.683	1155.7	79.68	0.000	0.000	0.000

Table 2.3. The results of the LMMs of the factors associated with lay date after model averaging. Details of fixed effects were returned from averaging the models within 2 AICc units of the best fitting model. The random effects variance was obtained from the best fitting model.

Fixed effect	Estimate	Standard error	Adjusted standard error	Relative importance
Intercept (2013)	104.360	3.287	3.316	
Altitude	5.283	0.931	0.940	1.00
Female age	-0.733	1.072	1.077	0.48
Wing length	0.470	0.892	0.896	0.39
Year 2014	-16.676	3.602	3.635	1.00
Year 2015	-10.529	3.697	3.730	1.00
Year 2016	-3.870	3.753	3.786	1.00
Year 2017	-25.065	3.784	3.817	1.00
Random effect	**Variance**			
Female identity	26.220			
Residual	87.800			

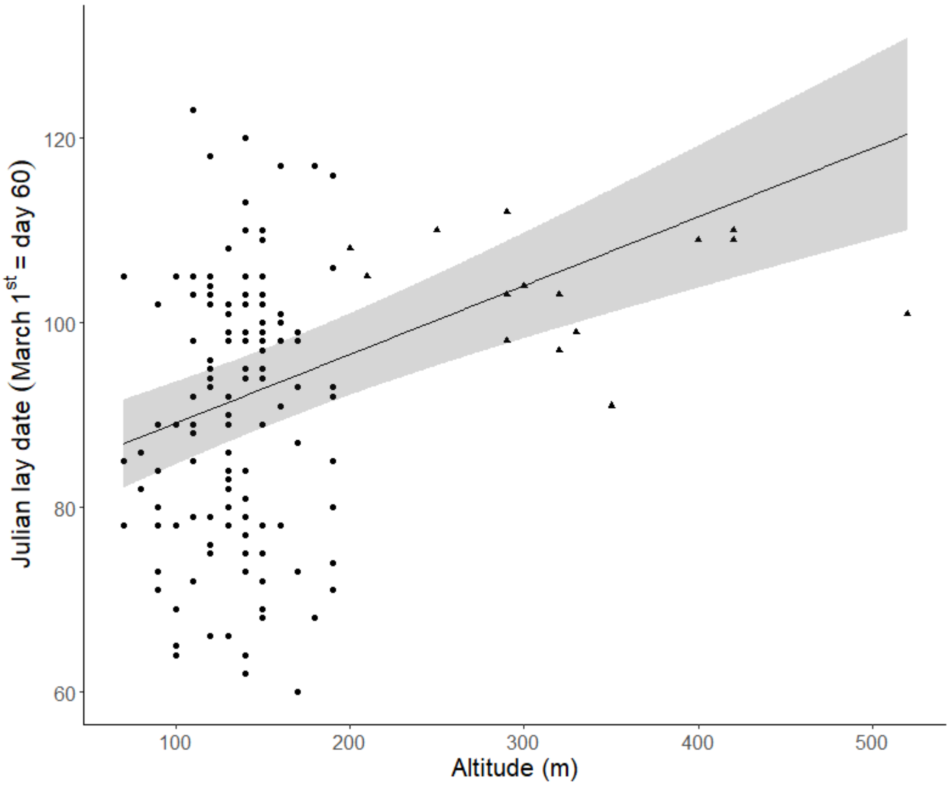

Figure 2.1. The relationship between lay date and altitude. The points represent the predicted values from a LMM after model averaging (circles = nests <200m altitude, triangles = nests >200m altitude) and the shading shows the 95% confidence intervals.

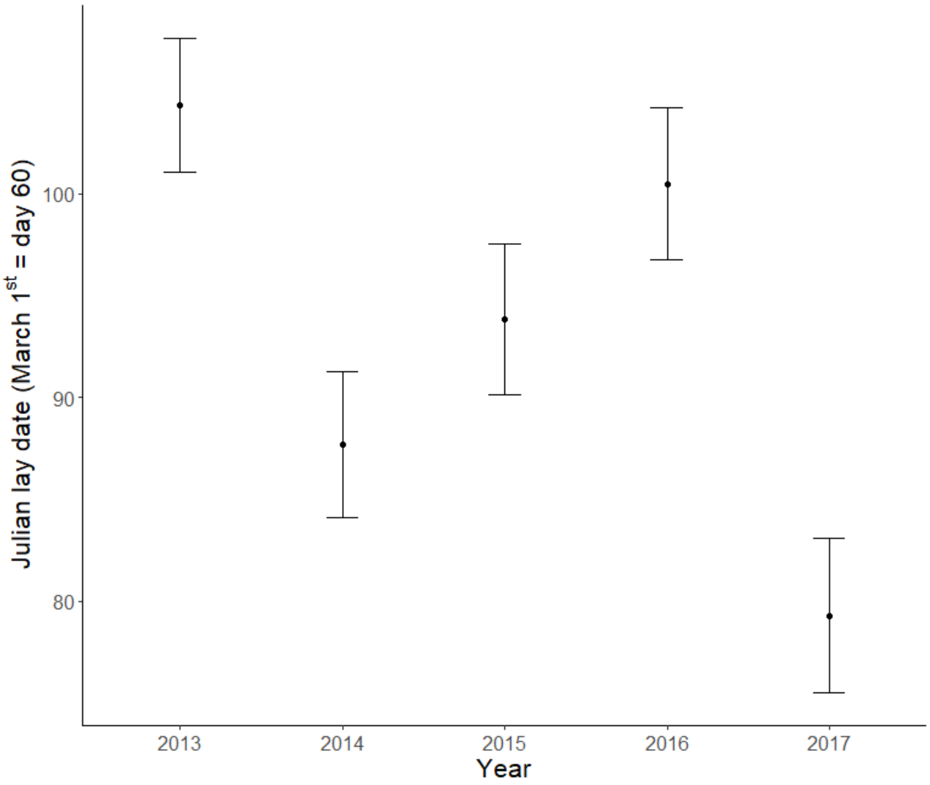

Figure 2.2. The relationship between lay date and year of breeding predicted from the average model. The points represent the predicted values and the bars represent the 95% confidence intervals.

2.4.2 Factors affecting nestling mass

Tables 2.4 and 2.5 show the estimates of all the best fitting LMMs and model averaging for the variables associated with nestling mass. Nestling mass was correlated with female age after controlling for brood size (Figure 2.3), with older females more likely to have heavier nestlings. Year was retained in the top models, with mean nestling mass varying between years but without any meaningful trend (Figure 2.4). Also retained in the best fitting models was hatching date, although the effect size was small and unlikely to be important (Figure 2.5). Variables absent from best fitting models included altitude, brood size, wing length and all interactions.

Table 2.4. The best fitting LMMs of the factors associated with nestling mass (i.e. those models with a ΔAICc value of 2 or less from the best fitting model). The null model is shown for comparison. (2013-2017; n=107; "+" indicates presence of a categorical variable).

Full model = lmer: nestling mass ~ (altitude + brood size + female age + hatch date + wing length + year + altitude : brood size + altitude : female age + altitude : hatch date + altitude : wing length) + (1|female identity).

Model	Intercept	Altitude	Brood size	Female age	Hatch date	Wing length	Year	Altitude: brood size	Altitude: female age
34	43.821			1.682			+		
42	43.546			1.699	0.404		+		
1 (Null)	38.654								

Model	Altitude: hatch date	Altitude: wing length	df	Loglik	AICc	Delta AICc	Weight	R^2m	R^2c
34			8	-310.098	647.6	0.00	0.236	0.198	0.198
42			9	-309.525	649.4	1.77	0.097	0.201	0.201
1 (Null)			3	-326.916	660.6	13.01	3.527e-04	0.000	0.090

Table 2.5. The results of the LMMs of the factors associated with nestling mass after model averaging. Details of fixed effects were returned from averaging the models within 2 AICc units of the best fitting model. The random effects variance was obtained from the best fitting model.

Fixed effect	Estimate	Standard error	Adjusted standard error	Relative importance
Intercept (2013)	43.741	1.533	1.552	
Female age	1.687	0.474	0.480	1.00
Hatch date	0.118	0.340	0.343	0.29
Year 2014	-3.566	1.827	1.849	1.00
Year 2015	-7.213	1.883	1.907	1.00
Year 2016	-5.966	1.838	1.861	1.00
Year 2017	-5.400	1.784	1.805	1.00
Random effect	**Variance**			
Female identity	0.000			
Residual	22.490			

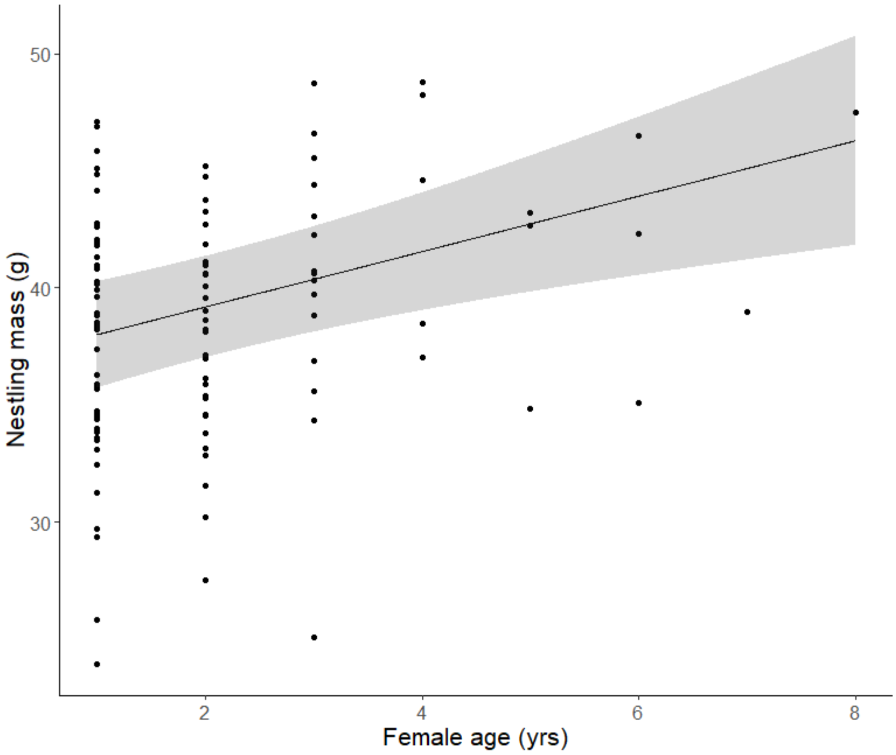

Figure 2.3. The relationship between nestling mass and female age. The points represent the predicted values from a LMM after model averaging and the shading shows the 95% confidence intervals.

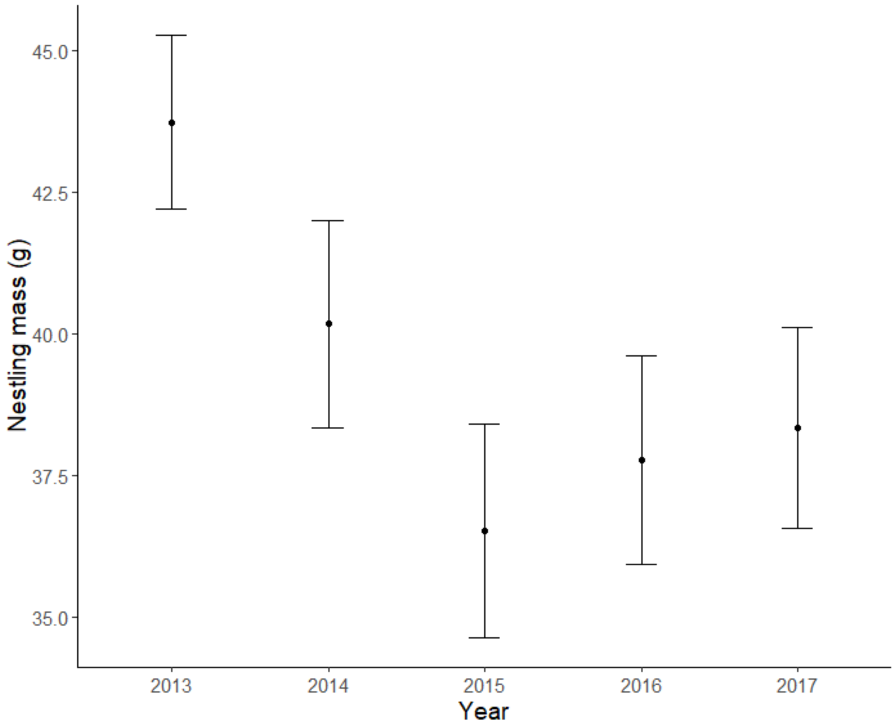

Fig 2.4. The relationship between nestling mass and year of breeding predicted from the average model. The points represent the predicted values and the bars represent the 95% confidence intervals.

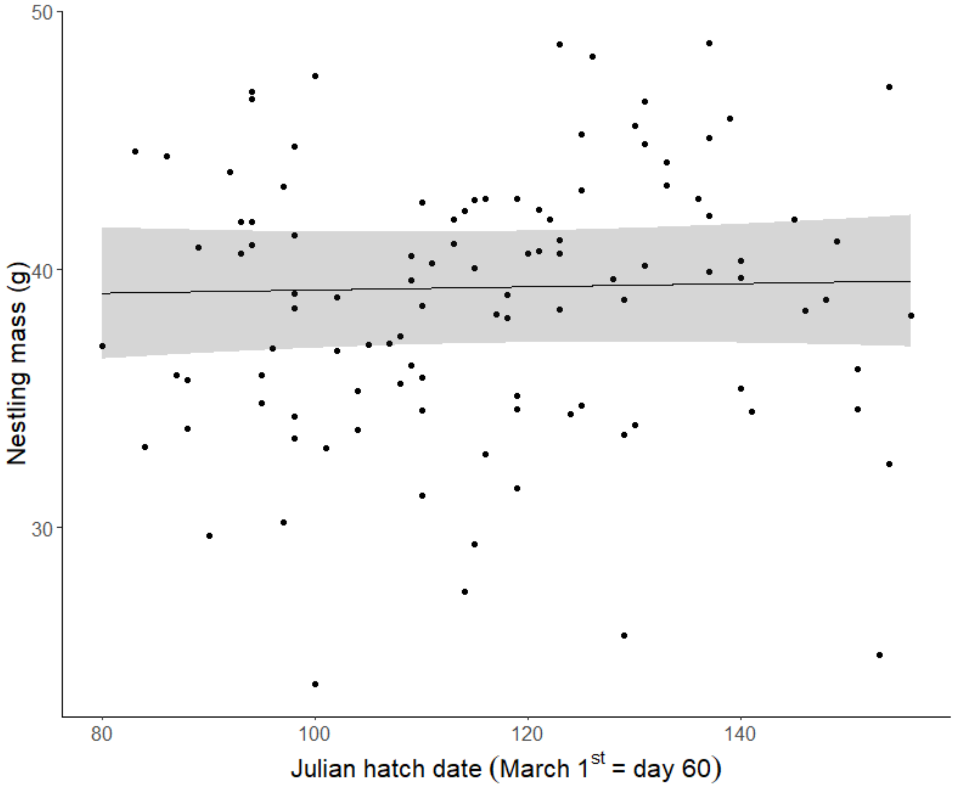

Figure 2.5. The relationship between nestling mass and hatch date. The points represent the predicted values from a LMM after model averaging and the shading shows the 95% confidence intervals.

2.4.3 Factors affecting fledging success

The estimates of all the best fitting GLMMs and model averaging for the variables associated with fledging success are found in Tables 2.6 and 2.7. Female age was found in all of the best fitting models as the best predictor of fledging success; overall, the probability of fledging at least one chick increased with female age (Figure 2.6). Other fixed effects present in the best fitting models were altitude, with nests at higher altitudes more likely to fledge successfully, but this was a small effect (Figure 2.7); and wing length, albeit with a negligible effect. Year and all interactions with altitude were not present in the best fitting models.

Table 2.6. The best fitting GLMMs of the factors associated with fledging success (i.e. those models with a ΔAICc value of 2 or less from the best fitting model). The null model is shown for comparison. (2013-2017; n=199).

Full model = glmer: fledging success ~ (altitude + female age + wing length + year + altitude : female age + altitude : wing length) + (1|female identity).

Model	Intercept	Altitude	Female age	Wing length	Year	Altitude: female age	Altitude: wing length	df	Loglik	AICc	ΔAICc	Weight	R^2m	R^2c
2	0.478		0.422					3	-130.328	266.8	0.00	0.234	0.046	0.153
6	0.478		0.464	-0.192				4	-129.748	267.7	0.92	0.148	0.053	0.154
4	0.473	0.164	0.418					4	-129.867	267.9	1.16	0.131	0.054	0.151
1 (Null)	0.470							2	132.899	269.9	3.08	0.050	0.000	0.166

Table 2.7. The results of the GLMMs of the factors associated with fledging success after model averaging. Details of fixed effects were returned from averaging the models within 2 AICc units of the best fitting model. The random effects variance was obtained from the best fitting model.

Fixed effect	Estimate	Standard error	Adjusted standard error	Relative importance
Intercept	0.477	0.188	0.189	
Altitude	0.042	0.113	0.113	0.26
Female age	0.433	0.194	0.195	1.00
Wing length	-0.055	0.129	0.130	0.29
Random effect	**Variance**			
Female identity	0.354			

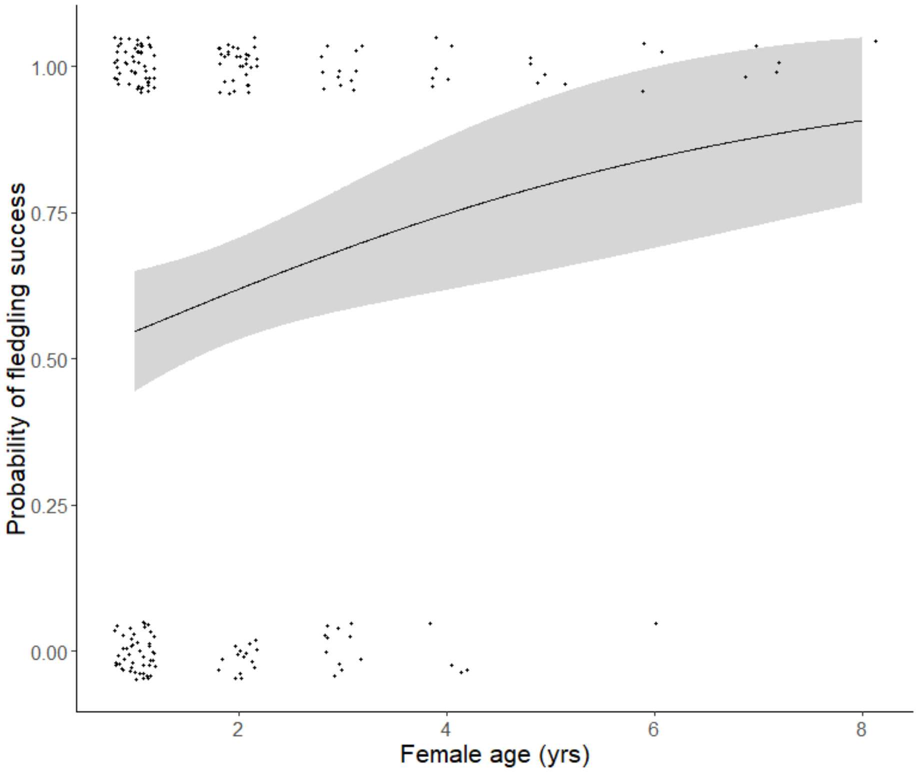

Figure 2.6. The relationship between fledging success and female age. The points represent the predicted values from a GLMM after model averaging (with overlapping points randomly offset using the 'jitter' function) and the shading shows the 95% confidence intervals.

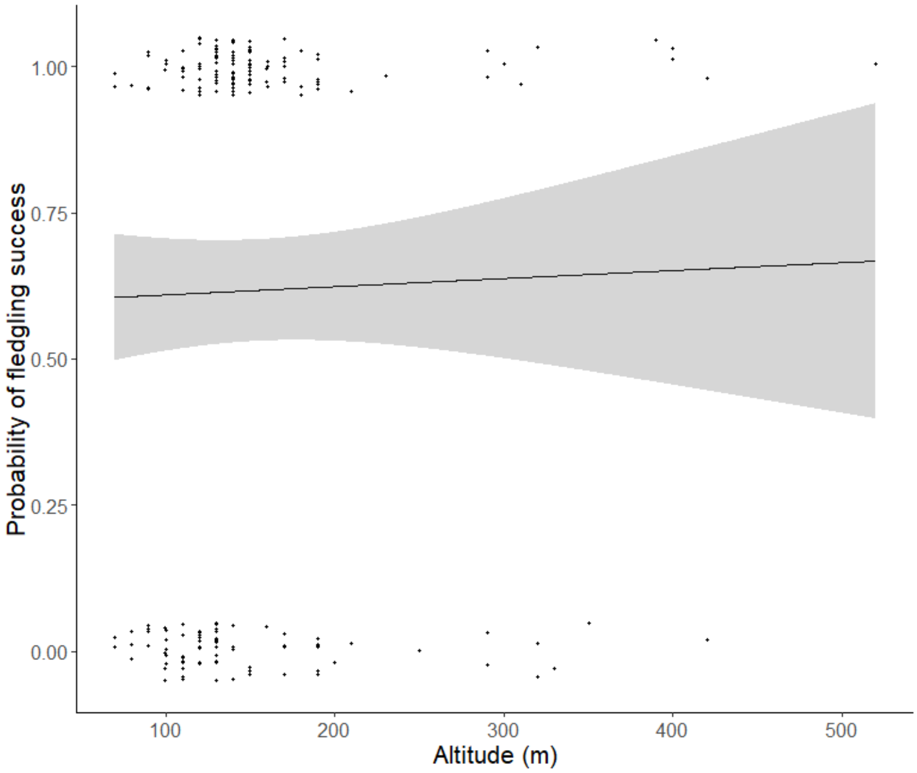

Figure 2.7. The relationship between fledging success and altitude. The points represent the predicted values from a GLMM after model averaging (with overlapping points randomly offset using the 'jitter' function) and the shading shows the 95% confidence intervals.

2.4.4 Factors affecting number of young fledged

Tables 2.8 and 2.9 show all the best fitting LMMs of the factors associated with number of fledglings and after model averaging. After controlling for clutch size, female age was the most important predictor of variation in the number of fledglings, and preliminary analyses suggested a non-linear positive relationship. Fitting the quadratic term age^2 to the model generated negative estimates, suggesting that young females produce an increasing number of fledglings with age but only up to a point, beyond which the relationship becomes negative (Figure 2.8). Wing length appeared in the best fitting models with a small positive effect size but was unlikely to be having any meaningful biological effect. Year was retained in the best fitting models but without any observable trend (Figure 2.9), and the effects of altitude, hatching date and all interactions including altitude were absent from the best fitting models.

Table 2.8. The best fitting LMMs of the factors associated with the number of fledglings (i.e. those models with a ΔAICc value of 2 or less from the best fitting model). The null model is shown for comparison. (2013-2017; n=103; "+" indicates presence of a categorical variable).

Full model = lmer : number of fledglings ~ (altitude + clutch size + female age + female age^2 + hatch date + wing length + year + altitude : female age + altitude : female age^2 + altitude : hatch date + altitude : wing length) + (1|female identity).

Model	Intercept	Altitude	Clutch size	Female age	Female age^2	Hatch date	Wing length	Year	Altitude: female age	Altitude: female age^2
76	4.290		0.472	0.171	-0.162			+		
108	4.276		0.439	0.166	-0.183		0.108	+		
1 (Null)	3.804									

Model	Altitude: hatch date	Altitude: wing length	df	Loglik	AICc	ΔAICc	Weight	R^{2}m	R^{2}c
76			10	-128.305	260.9	0.00	0.204	0.375	0.419
108			11	-129.121	262.0	1.14	0.115	0.382	0.398
1 (Null)			3	-145.594	294.8	33.90	8.866e-09	0.375	0.419

Table 2.9. The results of the LMMs of the factors associated with the number of fledglings after model averaging. Details of fixed effects were returned from averaging the models within 2 AICc units of the best fitting model. The random effects variance was obtained from the best fitting model.

Fixed effect	Estimate	Standard error	Adjusted standard error	Relative importance
Intercept (2013)	4.285	0.263	0.267	
Clutch size	0.460	0.087	0.088	1.00
Female age	0.169	0.139	0.141	1.00
Female age^2	-0.170	0.064	0.065	1.00
Year 2014	-0.559	0.297	0.301	1.00
Year 2015	-0.761	0.312	0.316	1.00
Year 2016	-0.120	0.312	0.316	1.00
Year 2017	-0.153	0.292	0.296	1.00
Wing length	0.039	0.078	0.079	0.36

Random effect	Variance
Female identity	0.017
Residual	0.624

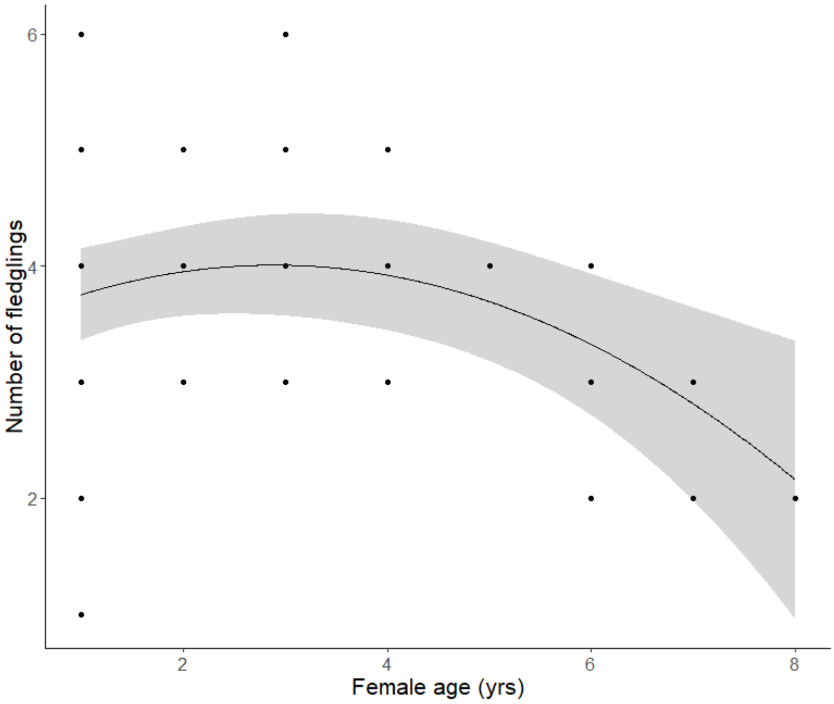

Figure 2.8. The relationship between number of fledglings and female age. The points represent the predicted values from a LMM after model averaging and the shading shows the 95% confidence intervals.

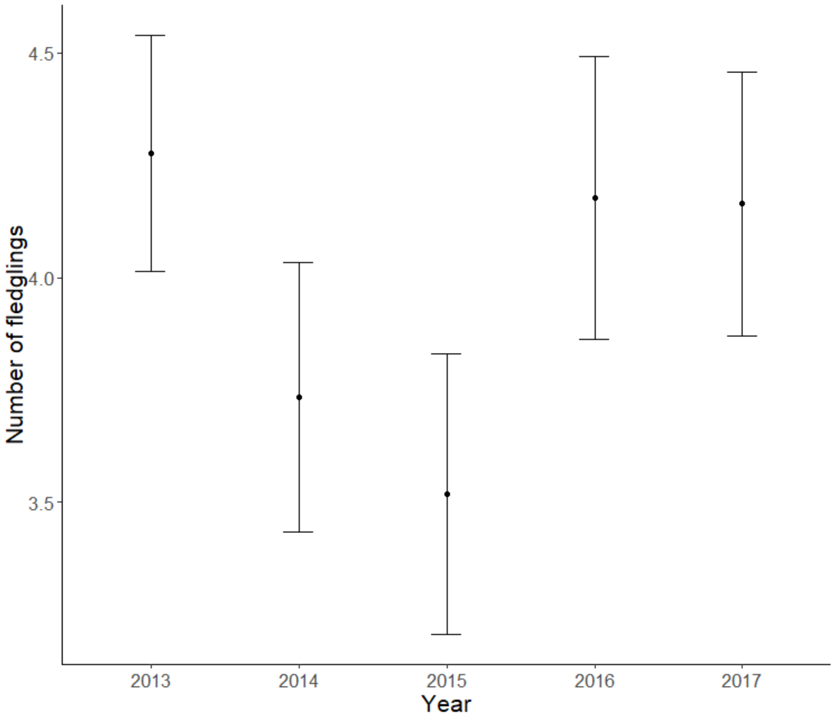

Figure 2.9. The relationship between number of fledglings and year. The points represent the predicted values from a LMM after model averaging and the bars represent the 95% confidence intervals.

2.4.5 Factors affecting annual productivity

All the best fitting LMMs of the variables associated with the total annual number of fledglings (from single and double broods) and after model averaging are found in Tables 2.10 and 2.11. Fixed effects contained in all of the best fitting models were female age, female age^2 and lay date; present in at least one of the top model set were altitude and the interactions between lay date and female age and age^2. Fitting the quadratic term age^2 to the global model produced negative estimates and a non-linear relationship with greater explanatory power. This suggested that young females produce a relatively small number of fledglings per year but that this increases with age, whereas the relationship becomes negative for older females (Figure 2.10). Annual productivity was negatively correlated with lay date, and thus, earlier breeding pairs are more likely to have higher annual productivity than birds that commence breeding later (Figure 2.11). The interaction between female age^2 and lay date generated a small positive estimate with confidence intervals that were only non-overlapping for young females. This suggests that early lay dates were more productive than later lay dates for young birds, but timing of breeding was likely to have less of an effect on annual productivity for older birds above that already predicted by female age alone (Figure 2.12). Although altitude was retained in the best fitting models, its small effect size suggests that it was unlikely to be biologically meaningful. Finally, fixed effects of wing length and year and all other interactions were not present in the best fitting models.

Table 2.10. The best fitting LMMs of the factors associated with annual productivity (i.e. those models with a ΔAICc value of 2 or less from the best fitting model). The null model is shown for comparison. (2013-2017; n=141).

Full model = lmer: annual productivity ~ (altitude + female age + female age^2 + lay date + wing length + year + altitude : female age + altitude : female age^2 + altitude : lay date + altitude : wing length + female age : lay date + female age : wing length + female age^2 : lay date + female age^2 : wing length + lay date : wing length) + (1|female identity).

Model	Intercept	Altitude	Female age	Female age^2	Lay date	Wing length	Year	Altitude: female age	Altitude: female age^2	Altitude : lay date	Altitude: wing length
12	3.092		0.813	-0.278	-0.540						
140	3.110		0.818	-0.281	-0.543						
16	3.097	0.100	0.814	-0.283	-0.563						
1036	3.088		0.805	-0.275	-0.580						
1 Null)	2.753										

Model	Female age : lay date	Female age : wing length	Female age^2 : lay date	Female age^2 : wing length	Lay date : wing length	Df	Loglik	AICc	ΔAICc	Weight	R^2m	R^2c
12						6	-303.458	612.2	0.00	0.077	0.125	0.125
140	0.160					7	-303.869	613.6	1.34	0.039	0.130	0.130
16						7	-304.102	614.1	1.90	0.030	0.127	0.127
1036			0.038			7	-304.966	614.2	1.97	0.029	0.126	0.126
1 (Null)						3	-309.796	624.3	12.10	0.018e-2	0.125	0.125

Table 2.11. The results of the LMMs of the factors associated with annual productivity after model averaging. Details of fixed effects were returned from averaging the models within 2AICc units of the best fitting model. The random effects variance was obtained from the best fitting model.

Fixed effect	Estimate	Standard error	Adjusted standard error	Relative importance
Intercept (2013)	3.096	0.216	0.218	
Altitude	0.0170	0.083	0.084	0.17
Female age	0.813	0.300	0.303	1.00
Female age^2	-0.279	0.128	0.130	1.00
Lay date	-0.551	0.181	0.183	1.00
Age : lay date	0.036	0.106	0.106	0.22
Age^2 : lay date	0.006	0.035	0.035	0.16
Random effect	**Variance**			
Female identity	1.140e-14			
Residual	4.287			

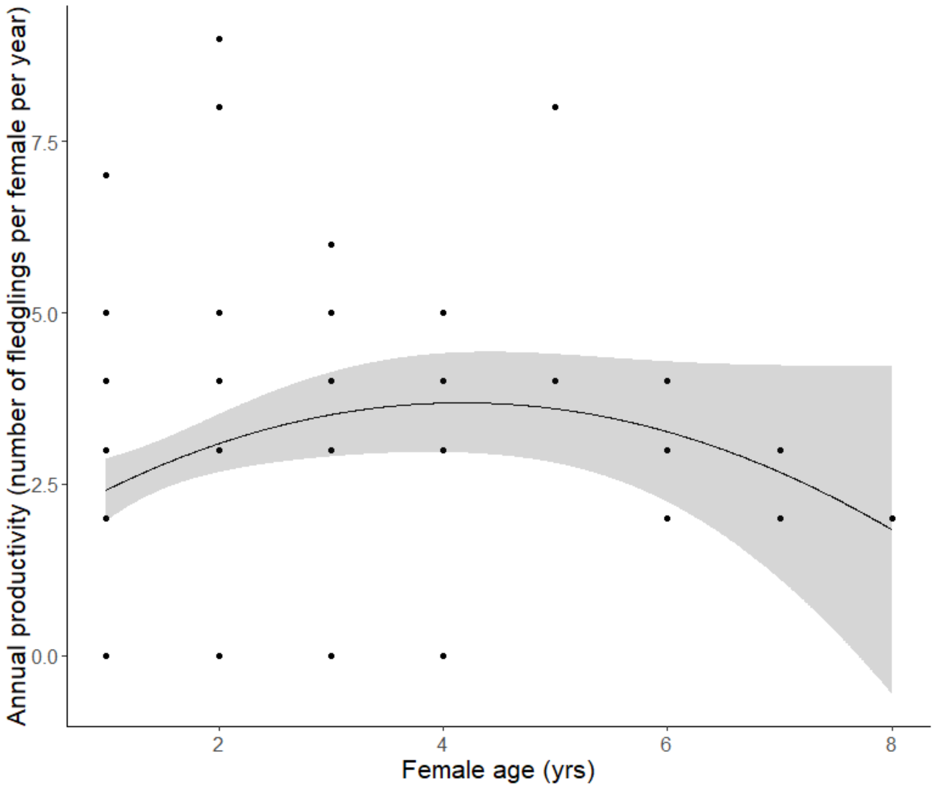

Figure 2.10. The relationship between annual productivity and female age. The points represent the predicted values from a LMM after model averaging and the shading shows the 95% confidence intervals.

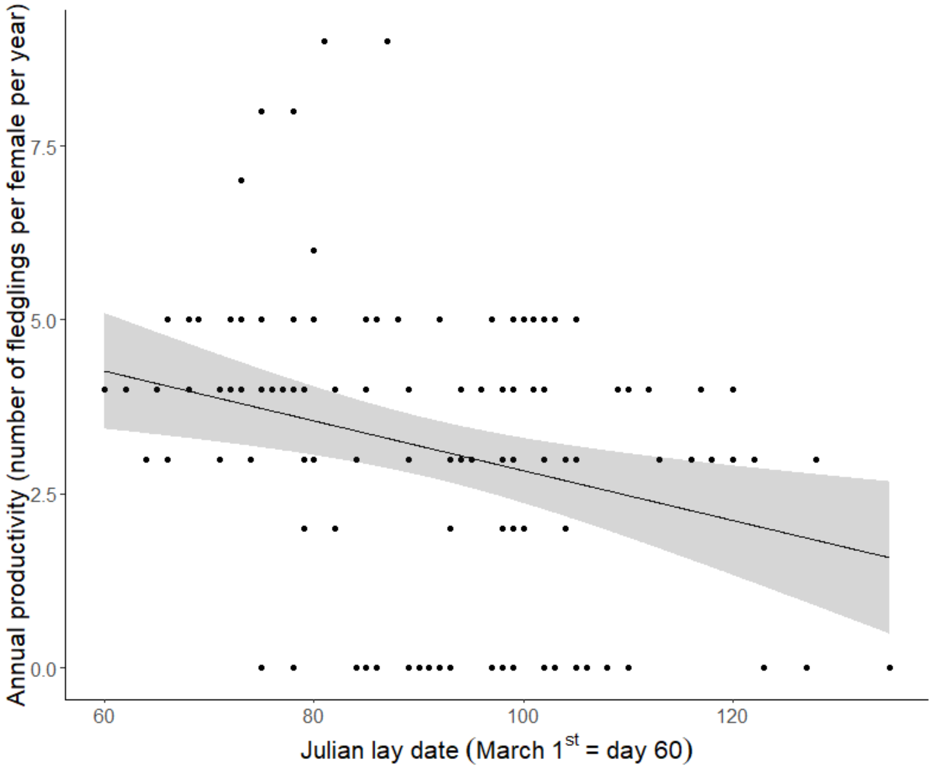

Figure 2.11. The relationship annual productivity and lay date. The points represent the predicted values from a LMM after model averaging and the shading shows the 95% confidence intervals.

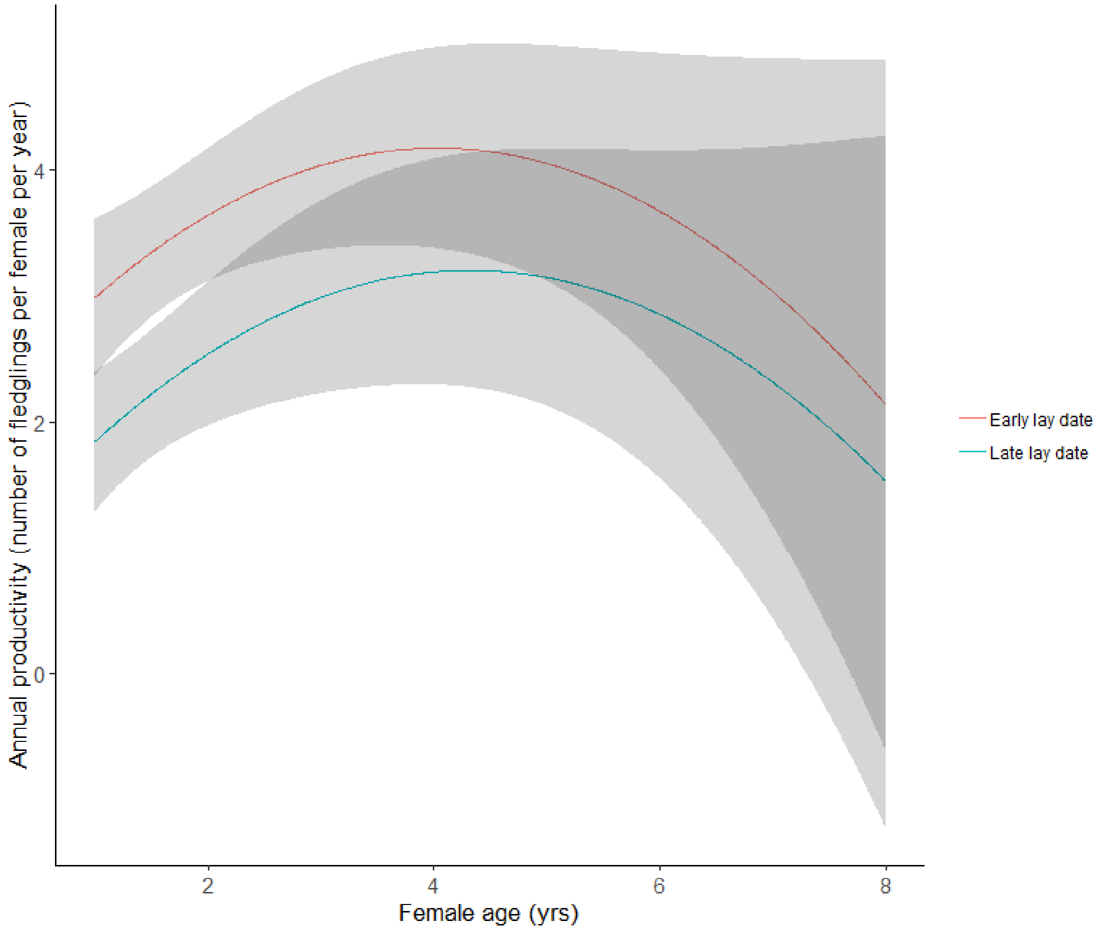

Fig 2.12. The relationship between annual productivity and the interaction between lay date and female age. The lines show the prediction from a LMM after model averaging and the shadings show the 95% confidence intervals; points are excluded for clarity.

2.5 Discussion

Together, the results of this investigation indicate that several components of reproductive performance varied with altitude, and that female age, lay date and year of breeding may be influential variables. Altitude was a strong predictor of the timing of reproduction, with birds at higher altitudes having later lay dates, but there were no clear associations between altitude and any of the measures of reproductive success. Instead, after accounting for seasonal effects, much of the variation in all of the models of breeding success was accounted for by female age. Altitude, when present in the best fitting models, had only a weak effect, which may not be biologically meaningful. Similarly, the effects of other terms present in the models were marginal, the only exceptions being clutch size, which as expected was a strong predictor of the number of fledglings, and lay date, which predicted annual productivity, with females that began breeding earlier tending to have higher reproductive success.

2.5.1 Year effects

The fact that year predicted several components of breeding indicates that there is significant inter-annual variation in the timing and outcome of reproduction and, in most years, there was no clear temporal trend; these results are consistent with other studies of dippers (Wilson 1996, Logie 1998; D'Amico *et al.* 2003). However, in 2013, lay date was later, nestlings were heavier and numbers fledged were higher than all other years. This may be because late winter and early spring weather conditions delayed breeding to a time when the peak in nestling food demands was closely matched to that in prey biomass (Shaw 1978; Ormerod 1985a). Large-scale climate effects act at the population level and can influence avian reproduction through the action of regional weather (Stenseth and Mysterud 2002, 2005; Wilson *et. al* 2007). Due to the proximity to the North Sea and further west, the Atlantic Ocean, the weather of north-west England is characterised by mild, wet and windy winters (Met office 2016), and these conditions can vary annually. Pre-breeding season weather conditions may be highly variable at the study site and weather is known to have consequences for lay date and breeding outcomes in dippers (Tyler and Ormerod 1985; Hegelbach 2001). Stochastic weather events prior to and during the breeding season such as episodic storms with high wind speeds and heavy precipitation can produce short but intense periods of localised spate and flooding on lowland rivers (Ward 1968); this occurs in the study area and is known to affect the onset of egg laying in dippers (Tyler and Ormerod 1985). Water levels and flow rates in individual higher altitude streams are less likely to be affected by heavy rainfall and recover quickly compared to lowland rivers receiving higher volumes of water discharged into them by many tributaries. Thus, foraging by upland dippers may be less impacted by spate conditions and the consequences for lowland dippers, particularly over prolonged periods, could be poorly nourished nestlings, loss of bridge and bankside nests by flooding, and less opportunity for second broods and replacement of lost nests. Spates can affect flow rate and depth, with consequences for aquatic benthic prey distribution and abundance (Chiu *et al.* 2013; Royan *et al.* 2013, 2014), which may impact foraging activity in dippers (Taylor and O'Halloran 2001). Dippers mainly forage in riffles, mostly by diving but also shallow water wading (Rabeni and Minshall 1977; O'Halloran *et al.*1990). Deeper and faster flowing water makes diving in riffles more difficult and less energetically profitable (Da Prato 1981), particularly for caddisfly which are an important dietary component for nestlings (Tyler and Ormerod 1994). Additionally, in years with harsh conditions, predators may be forced to source alternative prey to meet energetic demands (Hegel *et al.* 2010; Smith and Wilson 2010; Tablado *et al.* 2014; Fisher *et al.* 2015; Sherry *et al.* 2015; Williams *et al.* 2015), and this could impact on pre- and breeding season dipper populations, especially at lower altitudes, where avian and mammalian predators appear to be in greater numbers in the study site (RPW personal observation).

Species inhabiting temperate regions constrained by seasons must interpret environmental cues to time breeding to match optimal conditions that permit nestling growth and development (Perrins 1970). Visser *et al.* (2009) suggest temperature can act as a causal cue for lay date, and which may be delayed by late winter temperatures in dippers (Tyler and Ormerod 1985, 1994), although it is likely that many cues and responses related to temperature affect the fine-tuning of laying by birds (McNamara *et al.* 2011). Winter snow cover and low temperatures can be experienced in the Howgills and the western Yorkshire Dales, and although this did not occur over long periods during the study years, temperature conditions vary annually. In the event of late winter low temperatures, delayed lay dates could influence the likelihood of double brooding and migrant dippers may have delayed departure to upland nest sites, have later breeding and less opportunity to replace failed nests. Water temperature can influence growth and development of aquatic invertebrates (Vannote and

Sweeney 1980; Ward and Stanford 1982), advancing or delaying peak prey biomass in streams. Prolonged poor weather prior to breeding can inhibit early breeding as stored nutrient reserves diminish and affect female quality, laying physiology and nest building behaviours in a trade-off between survival and reproductive success (Rohwer 1992; Wingfield 2003; Moreno *et al.* 2015). Additionally, adverse conditions prior to incubation have been shown to affect egg volume or clutch size, or to delay hatch dates and nestling development, condition and survival, and hatching success (Monrós *et al.* 1998; Takagi 2001; Bradbury *et al.* 2003; Krist 2011; Pipoly 2013; Etezadifar and Barati 2015; Martin *et al.* 2017), and these may be felt more acutely at higher altitudes.

2.5.2 Factors affecting lay date

Lowland lay dates were typically in mid-March with the earliest being March 1st (2014 and 2017) and the latest March 20th (2016). Upland breeding was later and typically from the second week in April, with the earliest and latest first dates being March 15th (2014) and April 26th (2016), respectively. Refer to Table 2.1 for a summary of breeding variable data.

Altitude

Altitude was found to have a significant effect on the timing of breeding with lay dates being later at higher altitudes, as reported in dippers by several previous studies (Ormerod *et al.* 1991; Tyler and Ormerod 1994; Logie 1998; D'Amico *et al.* 2003). Resident, lowland dipper pairs defend territories throughout the year. During the winter, upland breeding migrants descend to rivers resulting in increases in population density and consequently, more competition at lower elevations, also observed in American dippers (Tyler and Ormerod 1994; Morrissey 2004). Territory sizes contract ostensibly to foraging areas and so full breeding territories are less aggressively defended (Tyler and Ormerod 1994; Crowther *et al.* 2018). Numbers of birds on lower elevation lowland rivers increase with the presence of upland breeding birds and juveniles (Crowther *et al.* 2018). At the end of the winter, pair-bonding, courtship and more aggressive defending of breeding territory and nest sites probably forces unpaired birds to search for vacant territories and unpaired partners, including upstream to higher altitudes, and migration resulting from competition has been reported in American dippers (Morrissey 2004, Gillis *et al.* 2008; Mackas *et al*. 2010; Green *et al.* 2015). Resident lowland pairs already occupying a territory thus commence the breeding season earlier and have increased likelihood of having second broods (Crowther *et al.* 2018), and more opportunity to replace lost nests. The quality hypothesis contends that higher quality individuals occupying better territories breed earliest (Price *et al.* 1988; Verhulst and Tinbergen 1991; Harriman *et al.* 2017). Crowther *et al.* (2018) suggested that breeding later may lead to lower fitness due to the reduced likelihood of second brooding and with poorer competing unpaired birds conceivably becoming partial migrants on upland tributary streams. Paired and unpaired dippers from upland breeding sites are seen regularly on lowland rivers during the winter (S. P. Sharp unpublished data; P. J. Mawby unpublished data), and then move to upland nests above 200m on tributary streams in late winter and early spring.

Differences in lay date between early breeding resident lowland dippers and late breeding migrants may reflect the delays caused by movement from lowland overwintering sites to upland nesting sites and then establishment of territories, courtship and nest building, and are unlikely to be the result of higher elevations *per se*. Migrations are only 1-5km distance across a small number of generally increasingly longer territories on narrowing streams and with a maximum elevation gain of about 400m. The time taken for these movements may be rapid if made in one movement during the course of a day or longer if time is spent exploring intermediate territories for a vacancy, territorial encounters and disputes, and pairing en route.

The timing of breeding in birds is likely to be influenced by intrinsic and environmental cues (Reed *et al.* 2009), as has been suggested for dippers (Tyler and Ormerod 1994), and might include responses to increasing daylength, elevated stress hormones resulting from territoriality or increased fat stores laid in preparation for reproduction, which has been described in other partial altitudinal migrants (Boyle 2011). For pairs or females that live to breed in multiple years, swapping from upland to lowland territories (i.e. within a breeding season) following a failed nesting attempt or between years, is rare (S. P. Sharp unpublished data). This suggests that the fitness benefits of territorial familiarity or natal philopatry may outweigh those to be gained from changing territories. However, this does not exclude the possibility of a genetic basis to migratory status in dippers, or, that it is dependent on an individual's condition, which could influence its dominance status and ability to acquire a territory. A preliminary analysis here appeared to show that young female dippers were not disproportionately represented at higher altitudes, suggesting that competition for lower altitude breeding territories with older females or a lack of experience are not important.

Female age

A small negative effect in the models of female age with lay date may not be biological meaningful. Logie (1998) studied a dipper population in the Ochil hills of central Scotland and suggested that a lack of a female age effect upon lay date could be accounted for by high variability between territories in quality relative to variation in age.

2.5.3 Factors affecting nestling mass

Altitude

There was no correlation between altitude and nestling mass. This suggests that lowland and upland territories separated by relatively short distances may not be subjected to large-scale differences in weather or habitat, which affect nestling growth. Food supply also seems unlikely to be having an effect on nestling mass at different altitudes (see Chapter 3), and adults may be able to compensate for any little variation that does exist. In a meta-analysis of life-history traits, no consistent difference in nestling size between high and low elevation populations was found (Boyle *et al.* 2016). Nestling mass (and reproductive success) may be an indicator of the quantity of food delivered to nestlings, rather than its quality as represented by the nutritional value of specific taxa, and reported for another high altitude insectivorous species, the alpine water pipit (*Anthus spinoletta*) (Brodmann *et al.* 1996).

Female age

Nestling mass was significantly correlated with female age, with older females producing heavier nestlings irrespective of hatch date and brood size. Older female dippers may invest more in egg production and the factors necessary for nestling development, be of good body condition, and better able to provide enhanced parental care because of previous experience. Studies of other species have shown pre-natal investment in egg development influences nestling quality (Whittingham *et al.* 2007), and that older females may lay bigger or better quality eggs (Languy and Vansteenwegen 1989), and incorporate more growth-promoting chemicals and hormones that appears to affect nestling mass (Bogdanova *et al.* 2006). Additionally, higher mortality of small individuals may occur before they breed, resulting in a greater proportion of older, bigger (and more likely better quality) breeding birds that make behavioural investments in growth and development during the nestling period (Languy and Vansteenwegen 1989). It may be that older parents may not provision offspring more than younger birds but through experience, they may be more effecient at it (Marchetti and Price 1989).

Cross-fostering experiments with tree swallows (*Tachycineta bicolor*) showed that pre-natal investment by older experienced females produced heavier fledglings and raised nestlings with greater growth rates that can influence the likelihood of fledging (Bitton and Dawson 2017). In Bluethroats (*Luscinia svecica*), older birds laid larger clutches, fed young more often, and were more likely to fledge young probably as a result of physiological and behavioural differences between age groups (Geslin *et al.* 2004). Studies of the effects of parental age and experience in other birds have reported earlier breeding, increases in the number and weight of eggs, increases in foraging effort, offspring defence and duration of parental care, and faster nestling growth which may increase reproductive success (Pugesek 1981, 1983, 1995; Coulson and Porter 1985). Investing in eggs and fledgling mass may enhance the ability of offspring to forage, survive periods of adverse weather or food shortage, or detect and avoid predators (Williams 1994; Martin *et al.* 2011; Gill and haggerty 2012; Martin 2015). Due to the risks of dipper nestlings prematurely leaving the nest after about day 13, weight measurements are not available for older nestlings in the study site, and when coupled with the low recapture rate of recently fledged birds, this makes their condition difficult to assess (Tyler and Ormerod 1994). However, well-fed dipper nestlings resulting from effective care by parents of any age are more likely to acquire quickly the skills necessary to gain independence and, in turn, survive (Yoerg 1998).

Hatch date

The small positive effect size of hatch date suggests that this may not be biologically meaningful and that development of dipper nestlings was largely unaffected by seasonal changes in ecological conditions including weather, food availability or habitat quality; indeed, the values of nestling mass compared favourably with those reported by Ormerod *et al.* (1986b). It is unlikely that temperature fluctuations in the breeding season across the short distance and elevation range were limiting, as warmth provided by brooding females and nest insulation would ensure greater trophic energy transfer was utilised developmentally, especially within the closed and dome shaped nest of dippers (Tyler and Ormerod 1994; Deeming 2016; Akresh *et al.* 2017).

2.5.4 Factors affecting fledging success

Altitude

There was a small positive effect of altitude on fledging success. While it is difficult to assess the biological significance of this, especially as the sample size for high altitude territories was relatively small, it may be that the higher probability of fledging young in the uplands reflects a change in the threats nests face. As temperature is unlikely to differ significantly over the elevational gradient, upland territories may have benefitted from reduced levels of nest loss through predation and flooding. Nest failures were not systematically analysed for causation but flooding losses were exclusive to lowland rivers and, whilst predation was suspected across much of the elevational gradient, the number of cases with strong evidence was higher on lowland rivers (S. P. Sharp unpublished data). No upland nests have been lost through flooding as most are sited high on waterfalls or banks above streams, which are protected from small increases in water volume, even after significant rainfall. In comparison, lowland nests sited in banksides and on bridges above rivers radially fed by tributary streams are often washed away during spate conditions following heavy rain. Rats near habitation probably accounted for some nest losses (Shaw 1978), along with American mink (*Neovison vison*) and otters (*Lutra lutra*) that were regularly seen on lowland rivers in the vicinity of dipper nests and are known to predate riparian species including dippers (Hewson 1969; Ormerod and Tyler 2005). Additionally, these mustelids are more likely to occur in greater number at lower elevations on larger rivers where they predate fish and white-clawed crayfish (*Austropotamobius pallipes*) (Holdich 2003), and have never been recorded in the upland territories where a lack of bankside cover and prey may limit their distribution. Evidence of nest predation in upland territories has been confined to fox (*Vulpes vulpes*) and corvids, particularly carrion crows (*Corvus corone*) (S. P. Sharp unpublished data; RPW unpublished data). Finally, due to the typically longer length of upland territories, there may be less opportunity for polygyny, so males might invest more care in a single brood to secure breeding success.

Female age

Clear differences are seen in fledging success between first year and increasingly older females. It may be that selective removal of poorer quality individuals occurs after their first year of breeding (Forslund and Pärt 1995; Martin 1995; Mauck *et al.* 2004; Steenhof and Heath 2009), leaving a stock of higher quality individuals with accumulated physiological attributes and parenting experiences from breeding, and that these aspects may continually improve with age (Nol and Smith 1987; Wooller *et al.* 1990; Pyle *et al.* 1991; Weimerskirch 1992; Brown and Roth 2009). Furthermore, habitat familiarity with repeat territory occupancy may enhance foraging and predator avoidance behaviours resulting in greater fledging success and productivity (Oring and Lank 1982; Hatch and Westneat 2007; García-Navas and Sanz 2011). Under stressful environmental conditions including reduced food supply, age related improvements in reproductive performance may be a consequence of past experiences (Bunce *et al.* 2005).

2.5.5 Factors affecting number of young fledged

Female age

The model output suggests that after controlling for clutch size, the number of fledglings a female produces increases with age up to a peak around 3 years and then declines, presumably due to senescence. Whilst the sample sizes are small, the results suggest that the maximum productivity occurs for birds having gained experience in their first and second years as breeding adults. Reproductive success in many birds is age-dependent, with older, experienced individuals, which are often in better condition and have habitat familiarity, especially if they are territory occupants, usually breeding earlier, with refined maternal care and greater brood investment (Oring and Lank 1982; Sæther 1990; Hatch and Westneat 2007; García-Navas and

Sanz 2011). This continues with age until the onset of senescence, beyond which a decrease in productivity often occurs with further increases in age (Forslund and Pärt 1995; Hammers *et al.* 2012; Potti *et al.* 2013; Zhang *et al.* 2015; Jankowiak *et al.* 2018). Over a number of reproductive years, the cumulative effect of tissue and physiological damage is thought to cause senescence and result in lowered reproductive success and survival (Monaghan *et al.* 2008). Individuals may trade-off investment in the current brood and body maintenance, and between current and future breeding attempts, and the outcome shifts with age and when resources become constraining (Kirkwood *et al.* 1979, 1991; Nussey *et al.* 2008; Bouwhuis *et al.* 2010). Further discussion of reproductive senescence is beyond the scope of this thesis, but see Curio (1983), Forslund and Pärt (1995), and Steenhof and Heath (2009), for useful reviews (of the literature on birds). There has been no study of ageing in dippers to date, but the results here suggest that this would be a useful avenue for future research.

Hatch date

Breeding early, or at a time of rising or of peak prey biomass, has been shown to increase the number of fledglings (Perrins 1970; Daan *et al.* 1989). In this study, however, hatch date was not found to predict the number of fledglings produced. Moreover, late breeding birds are not disadvantaged by a delayed breeding season in terms of the number of fledglings, but there are likely costs for annual productivity as the opportunity for second broods lessens with later breeding. Hatch dates subjected to seasonal variations in weather and episodic extreme weather events and habitat quality, possible fluctuations and declines in food availability, or losses though predation, appear to have little effect upon numbers fledged. However, studies of long-term dipper population change in Norway concluded that environmental variation affected population growth or decline, citing the effects of temperature and precipitation (Nilsson *et al.* 2011a).

Clutch size

Larger clutch size had a significant positive effect on the number of fledglings, suggesting that sibling competition and parental ability to provision larger broods did not compromise the number of nestlings fledged. Larger clutch sizes (and ultimately brood sizes) may be perceived as higher value and receive greater investment in parental care enhancing the likelihood of a larger number of fledgings (Trivers 1972; Clutton-Brock 1991; Hainstock *et al.* 2010). Breeding performance correlates with the ability to adequately provision developing nestlings to ensure growth and survival. Care of large broods is heavily energy dependent and parents may adjust clutch size to account for food availability (Wellicome *et al.* 2013). In this study, the demands of raising large broods had little effect on nestling quality (in terms of nestling mass), apparently contradicting experimental studies of other birds showing a decline in nestling mass with increasing brood size (Nur 1984; Gard and Bird 1992; Sanz 1997; Pichorim and Monteiro-Filho 2008). This suggests that adults could respond to increasing brood size by adjusting levels of parental care, and this will be explored further in the following chapter.

2.5.6 Factors affecting annual productivity

Altitude

There was a small positive effect of altitude upon annual productivity, despite upland breeding birds never having second broods and being less likely to have replacement clutches. It therefore seems that productivity of first broods is marginally higher at altitude or, more likely, that this result is not biologically meaningful. The latter would suggest that there is no clear advantage to being either a resident or an altitudinal migrant dipper and that the fitness payoffs are similar, at least in the short-term. However, there may be long-term differences in survival and lifetime reproductive success between resident and migrant dippers especially if the costs of reproducing successfully vary with altitude. Resident American dippers have been shown to have higher annual productivity resulting from earlier lay dates, larger clutch sizes and higher first brood successes, and higher probability of replacing failed nests and having second broods than migrants (Morrissey 2004; Gillis *et al.* 2008). Migrants are predicted to have a lower lifetime reproductive success than residents because despite higher annual survival, this is insufficient to compensate for the lower annual productivity (Gillis *et al*. 2010). Furthermore, it has been suggested that migrant American dippers produce poorer quality offspring with low first winter survival, and so lifetime reproductive success is potentially lower (Mackas *et al*. 2010).

Female age

Annual productivity increased for birds up to a maximum of about 4 years of age, and included birds double brooding and those raising high single brood numbers, and then declined as females aged further. This may be explained by few birds living longer than 4 years (or having breeding data available) (n=18; 5 years=6; 6 years=4; 7 years=6; 8 years=1). Additionally, breeding early that enables double brooding to occur (and discussed further in Chapter 4), being phenotypically high quality individuals in good condition, or, being in resource rich breeding habitat, also influence productivity (Verhulst and Nilsson 2008). Finally, annual productivity will be limited by the effects of senescence and is described earlier for the number of fledglings produced.

Lay date

Annual productivity decreased with lay date. As hatch date had no effect on the number of fledglings, this suggests that early initiation of breeding may provide sufficient time for second broods or for replacement of failed nests. The time between first lay date and the lay date of a second clutch is, on average, 54 days in this study site, and so there must be sufficient time for the first brood to fledge and receive post-fledging parental care, and then for second brood completion before adult moult occurs. Moreover, territories would need to retain sufficient prey biomass in order to support second brood provisioning. Since prey availability appears not to be limiting at the study site (see Chapter 3), it is possible that other intrinsic and extrinsic cues inform further brood decision-making. A weak interaction between female age and lay date suggested that early breeding birds up to about 4 years old were most productive probably because of high numbers of single brood fledglings and with some second brood success, and later breeding birds contributed fewer nestlings to annual productivity most likely because of being unable to fit in a second brood or replace failed nests into a shortened breeding season. Although there were only a few old, early and late breeding females, the results do not preclude the possibility that lay date is important for them in order to have second broods, or that they are affected by senescence and declining fecundity, as described earlier for number of fledglings.

Of 296 breeding attempts between 2013 and 2017, 12.1% were second broods, and of 155 breeding attempts producing fledglings, 23.2% were second broods, which is higher than the proportion reported in comparable studies of dippers elsewhere in the British Isles (Smiddy *et al.* 1995; Tyler and Ormerod 1985; Newton 1989; Wilson 1996). Across the study period, on average, double brooding pairs had first lay dates of March 18th and second brood lay dates of May 10th, and birds making replacement breeding attempts following nest failure, of April 28th. Repeat attempt dates following breeding failure occur beyond the limit of the majority of second brood dates presumably due to the absence of energetic investment through raising an initial brood. Over the study period, of 109 failed lowland nesting attempts, 29.4% had replacement nests, compared to 35.7% replacement nests in the uplands following 14 failed breeding attempts. Although these results are difficult to interpret, birds with early lay dates have been found to be more likely to have double broods, have replacement nests after first breeding attempt failure, and higher productivity (including when the interval between broods is shorter) (Bohning-Gaese *et al.* 2000; Pakanen *et al.* 2014; Jackson and Cresswell 2017). There has been no recent study of productivity in dippers, but the results here suggest that this could be a valuable line of enquiry for future research particularly in the context of climate change and the trend of advancing lay date.

2.6 Conclusion

Increasing altitude is associated with later breeding but has either little or no effect on reproductive success, at least not the measures investigated here. Year had no effect upon fledging success or annual productivity, but there was significant interannual variation in lay date, nestling mass and the number of fledglings, albeit with no clear trend over time. Weather conditions immediately prior to the breeding season may influence lay date with sustained low temperatures limiting prey development acting as a cue to delay breeding to correspond with peak benthic biomass. Food supply throughout the breeding season and across altitudes does not appear to be limiting (see Chapter 3), and nestling mass across the monitoring period and altitude also appears to be unaffected and in line with that reported by other dipper studies (Ormerod *et al.* 1986b; O'Halloran *et al.* 1992). It may be that over the relatively short distance and height difference between lowland and upland sites, climatic and water conditions are not sufficiently different to have any meaningful effect upon, for example, thermal costs or food supply. What remains unknown are the effects of flow events including spate, flood and drought, and levels of predation along this elevational gradient. Thus, altitude *per se* may not influence lay date but that breeding is initiated later is most likely caused by factors governing when altitudinal dispersal from overwintering grounds commences, followed by time migrating, exploring, and establishing a territory and mate acquisition.

Higher altitude breeding dippers were predicted to have a marginally higher fledging success than those at lower elevations but altitude had no apparent effect on the number of first brood fledglings. Annual productivity does not appear to be influenced by altitude but later breeding is probably limited by a foreshortening of the breeding season. This allows little opportunity for repeat attempts after nest failure or second brooding due to the constraints of summer moult and a possible reduction in post-peak prey biomass as larval and nymphal stages of key EPT prey items emerge as aerial adults.

Older females tend to produce heavier nestlings and were more likely to fledge a nest, but after a peak in fledgling production around 2-4 years old they showed a decline in productivity, most likely due to senescence. A similar pattern is shown by annual productivity, with birds about 4 years old being most successful and a decline occurring thereafter. No older birds were found to have a second brood, which goes some way to explaining this decline; body condition in later years may preclude second brooding, with females instead investing more in their single brood and consequently producing heavier offspring, which are more likely to fledge. As birds age it is likely that prior experience in parenting, improved foraging efficiency and predator awareness translate into higher quality nestlings that are more likely to fledge and survive the early juvenile period.

Altitudinal migration is likely to be an alternative migratory tactic resulting from competition for lowland nest sites. Breeding success for dippers at different altitudes may be a consequence of: typically earlier breeding dippers on lower altitude rivers being influenced by higher risks of flooding and predation but compensated by opportunities for double brooding and replacement of failed nests; versus later breeding at higher altitudes with only single broods and less opportunity to replace failed nests, but with lower risks of nest losses to flooding and predation. Breeding conditions do not appear to be better at lower altitudes and this suggests that altitudinal migration persists because the fitness payoffs of both strategies are similar, although the longer-term fitness consequences remain unclear.

2.6.1 Further work

Dipper populations in the UK have recently undergone a decline, and a clearer understanding of their life-histories could help to arrest this situation. Future study could examine the factors that cue altitudinal migration, and why some birds habitually return to breed at higher altitudes if breeding conditions do not differ across the elevational range. Investigating the conditions required for double brooding would help to explain why, despite early lay date and lower altitudes appearing to be prerequisites, some adjacent territories experiencing similar habitat quality and environmental conditions may, or may not, have second broods. Allied to this is the need to determine what the fine-scale habitat requirements are for breeding success (Sim 2012). Additional work could examine brood size and parental investment costs, particularly those involving parental age, and their impact on the quality of fledglings across the elevational gradient. This could further explore post-fledging and first winter survival, dispersal, recruitment and subsequent breeding success, and could help towards a better understanding of the population ecology and the lifetime reproductive success of residency versus altitudinal migration. Determining the nature and extent of predation could suggest appropriate control measures, particularly of non-native species. Examining the effects of weather on habitat quality and the impact of variable and extremes of flow regime on prey availability and reproductive success across altitudes could provide key insights into providing mitigating measures for the consequences of climate change.

Chapter 3

Altitude and its effect upon provisioning rate in dippers (*Cinclus cinclus*)

3.1 Abstract

In many populations of migratory birds, only some individuals migrate but others remain as residents, and this is known as partial migration. Migration along an altitudinal gradient, whereby some individuals move to higher altitudes to breed, can have important fitness consequences. Understanding how parental care varies with altitude is important for predicting how populations may respond to environmental change. Here, I undertook a field study of an altitudinal partial migrant and aquatic passerine, the dipper (*Cinclus cinclus*), in order to investigate how offspring provisioning rates varied across an elevational gradient. Dippers feed exclusively on aquatic invertebrates and small fish, but whether upland migrants on small streams are able to feed nestlings at a similar rate to residents on lowland rivers was previously unknown. Mixed effect models were used to examine how provisioning rates varied across an altitudinal range of 90-520m, while controlling for brood size, nestling age and local prey availability. Provisioning rates decreased with altitude in both sexes. This likely reflects the increased travelling time to ever more distant foraging sites on higher altitude streams as nestling prey items are removed closest to the nest first, although whether prey size, load and species varies is not clear. In females, the impact of altitude on provisioning rate was greater when nestlings were older, presumably because females spend a lot of time brooding younger nestlings, and the costs of distant foraging; higher provisioning rates of older nestlings may act to safeguard female investment in offspring and maintain fitness. In contrast, the relationship between male provisioning rates and altitude varied with brood size, and there may be less opportunity to vary rates when brood size is large, especially if female provisioning rate is relatively low, which may serve to safeguard female survival. Provisioning rates were positively correlated with partner rates and may ensure fitness and play a role in lowering the risk of nest predation. This study therefore provides evidence that breeding at higher altitudes influences parental care but that the effects vary between the sexes. Future research should determine the relative costs and the long-term fitness consequences of offspring provisioning strategies at different altitudes and hence, the benefits of altitudinal migration versus residency for partially migrating populations.

3.2 Introduction

Birds living in seasonal environments often synchronise reproduction with the peak abundance in their food supply, which usually coincides with favourable weather conditions, in order to maximise offspring fitness (Perrins and McCleery 1989; Van Noordwijk *et al.* 1995; Sparks *et al.* 2002; Cresswell and McCleery 2003). Provisioning of nestlings at these times has evolved to meet thermo-energetic demands and the energy requirements for developmental and growth stages leading to fledging, post-fledging survival and independence (Weathers 1992; Birkhead *et al.* 1999; Gilbert 2001; Weathers *et al.* 2003; Monaghan 2008). The ability of parents to provision nestlings is dependent upon many factors, including those that influence habitat quality, such as climate, phenology and seasonality, and parental condition, but primarily by the abundance of, and accessibility to, food resources (Johnson 2007; Piersma 2012; Stevens *et al.* 2015). However, even during peak abundance, many factors influence food availability at a finer scale, including weather conditions (Dawson *et al.* 2005; Öberg *et al.* 2015), foraging distance (Staggenborg *et al.* 2017; Evens *et al.* 2018), threat of predation (Lima and Dill 1990; Brown and Kotler 2004), and human disturbance (Verhulst *et al.* 2001; Glądalski *et al.* 2016). Understanding how variation in these conditions impacts offspring provisioning is therefore vital for predicting the fitness consequences of changes in the climate and habitat quality.

In altitudinal migration, populations consist of sedentary residents and migrants that make short-distance seasonal movements between breeding and non-breeding locations at different elevations (Cade and Hoffman 1993; Dingle and Drake 2007; Norbu *et al.* 2013), and the ecological drivers and evolutionary consequences of this have been the subject of a number of studies (Boyle *et al.* 2016 ; Barçante *et al.* 2017 ; Boyle 2017 ; Hsiung *et al.* 2018). Temporal variation in food availability is thought to be an important influence alongside other factors such as predation pressure, climatic conditions and population density (Barçante *et al.* 2017; Boyle 2017; Hsiung *et al.* 2018).

Breeding outcomes may be driven by quantity rather than quality of prey, but environmental conditions that affect prey availability may have negative impacts on reproductive success (Lamb *et al.* 2017). Variations in territory quality and food availability may also affect the quality of nestling diet, in turn impacting growth rates and post-fledging success (Naef-Daenzer and Grüebler 2016). Parents may adjust the level of care they provide to their offspring according to local conditions (Wilkin *et al.* 2009), so changes in food availability across elevational gradients may affect parental care, with consequences for nestling development and survival (Badyaev and Ghalambor 2001).

Badyaev and Ghalambor (2001) compared life-history traits for species or subspecies breeding at different elevations and found differences in fecundity and parental care. Their results suggested that as altitude increased, fewer offspring were raised and the duration of parental care was longer. Additionally, there was no difference in total provisioning rate across elevations but males provisioned more than females at higher altitudes. There have been relatively few studies of variation in provisioning rates across elevational gradients, but higher provisioning rates have been reported in populations of species at high elevations compared with low elevation conspecifics (Johnson *et al.* 2007; Zeng and Lu 2009; Lee *et al.* 2011, 2016). Studies of sex-specific provisioning rates have produced conflicting results; males have higher provisioning rates than females at high altitudes in some species (referenced by Badyaev 1997, in Badyaev 1993, 1994), but the converse is true in others (Lee *et al*. 2011) and no difference between the sexes across elevational gradients has also been reported (Johnson *et al.* 2007). However, these studies are from discrete populations distributed along a continuous elevational gradient rather than single populations of partial altitudinal migrants. Very few studies have investigated how parental care, and offspring provisioning in particular, varies between altitudinal migrants and lowland residents.

Dippers (*Cinclus cinclus*) are a specialised bird species of rivers and streams feeding almost exclusively on aquatic invertebrates and small fish and mostly found in hill and mountain regions in the UK in populations containing altitudinal migrants (Tyler and Ormerod 1994; Ormerod and Tyler 2005). Dipper populations have decreased in recent years but little is known of the causes for these declines, although a number of threats from anthropogenic sources including climate change are thought to be important (Ormerod and Tyler 2005; Nilsson *et al.* 2011a, 2011b; Eaton *et al*. 2015). Further information about dippers is provided in Chapters 1 and 2.

Dippers are early spring breeders with occasional second broods. Adults provision nestlings almost entirely on aquatic macroinvertebrate prey, mainly mayfly and stonefly nymphs and caddisfly larvae, but also small fish, molluscs and crustaceans foraged within linear breeding territories. Most prey is foraged below turbulent surface water flow known as riffles (Ormerod 1985b, 1987, 1988; Ormerod and Edwards 1987; Wade *et al.* 1989; Ormerod and Tyler 1991; Tyler and Ormerod 1994; Hong *et al.* 2018a). Aquatic larval and nymphal growth stages increase in size and mass prior to emerging as reproductive aerial forms, which often occurs en masse. Emergence is thought to be triggered by cues of water temperature and photoperiod causing swarming, but the process can occur continually from spring until late summer (Dewalt *et al.* 1994). It has been suggested that dippers synchronise first breeding with cues from prey abundance and quality in order to match brood demand with peak food resources (Shaw 1978). This early breeding may enable a second brood to exploit remaining prey later in the spring (Da Prato and Langslow 1976; Shaw 1978; Thorne and Harvey 1978), particularly if first broods are provisioned on a still rising and sub-peak biomass macroinvertebrate food resource.

Populations of dippers overwinter at low elevations that contain year-round residents and breeding migrants that travel to higher elevations to breed in early spring. Higher altitude uplands in comparison to lowlands typically have delayed phenology, are colder with more extreme weather conditions and have shortened seasonality (Körner 2007). Upland streams are typically narrow with steep gradients, variable flow rates, depths and substrates. The distribution and abundance of aquatic invertebrates can be influenced by differences in stream structure, hydrology and environmental conditions at differ altitudes (Lewin *et al.* 2015; Li *et. al*. 2018), and could have consequences for dipper prey availability.

Insect community structure has been found to change with altitude and latitude and with decreasing temperature (Ormerod and Edwards 1987; Palmer *et al.* 1994; Jacobsen *et al.* 1997; Leunda *et al.* 2009), and clear patterns of altitudinal zonation for different mayflies, stoneflies and caddisflies (Dodds and Hisaw 1925; Minshall 1969). A pH <5.7 has been found to limit a wide range of taxa (Sutcliffe and Carrick 1973). Longitudinal uniformity of stream benthos communities has been linked to constancy of river topography and type of substrate (Wise 1976), whereas seasonal distributions of some mayfly species have been associated with lower and upper catchment water temperatures (Macan 1960, 1961; Wise 1976). Finally, climatic effects have been shown to affect ecological conditions experienced by upland stream biota, and models projecting temperature rises resulting from climate change predict declines of aquatic macroinvertebrate abundance (Durance and Ormerod 2007).

A previous study of American dippers (*Cinclus mexicanus*) found altitudinal migrants fed their offspring less fish and compensated by higher rates of the provisioning of invertebrates than lower elevation residents (Mackas *et al.* 2010). These sedentary residents fed offspring less often but with more fish and a higher energetic provisioning rate and produced better quality offspring than altitudinal migrants did. However, there have been no similar studies in the UK that compare life-history traits in a single population consisting of residents and migrants, and dippers offer an excellent model system to examine the effects of altitude on provisioning rates. In this chapter, I address this by analysing how male and female provisioning rates vary with altitude in a dipper population in the River Lune catchment in the north of England.

3.3 Methods

Data were collected during the 2017 breeding season from a colour-ringed population of dippers distributed along lowland rivers and upland streams in the River Lune catchment within an 8km radius of Sedbergh, Cumbria, UK (54°19'25.0"N 2°31'41.5"W) (see Appendix Figures 1-5 for territory locations). Dippers nesting below an altitude of 200m were defined as lowland breeding and those above this altitude as upland breeding (lowland and upland habitats are described in Chapter 1). This population has been the subject of a long-term monitoring project, but in order to increase the sample of upland birds, the study area was enlarged by searching suitable habitat for occupied territories within the catchment immediately outside the core site. A total of 37 breeding pairs were monitored, of which 25 pairs were in habitat described as lowland and a further 12 pairs were at upland sites. Birds which were unringed at the start of the season were caught in mist nests or hand nets placed over the nest; these individuals were colour ringed, sexed according to their wing length (maximum chord measured to the nearest mm with a wing rule) and aged as first-year or older (‘adults’) by the presence or absence of unmoulted juvenile coverts, respectively (Demongin 2016; see Chapter 1). Once active nests were located, altitude in metres above sea level to the nearest 10m was determined with a Garmin eTrex H GPS (Garmin Ltd, Switzerland), and verified with Ordnance Survey data. Nests were closely monitored through to fledging or failure in order to determine lay date and the different components of breeding success; nestlings were colour ringed and measured when nine days old (for further details of the nest monitoring and ringing process, see Chapter 1).

3.3.1 Provisioning rate

Offspring provisioning rates for each parent were measured once in each of the three weeks of the nestling period, usually on day 2, day 10 and day 18 (where the day of hatching is day 0), but sometimes a day either side due to logistic constraints. Observation sessions were carried out during daylight hours before 11am and were made using Opticron 10x42mm ED roof prism binoculars and a Kowa 20-60 x 77mm zoom telescope. Most sessions were made from behind the cover of bankside features and at least 15m from the nest to avoid influencing natural feeding behaviour; in the absence of suitable cover, a portable camouflaged hide was used. Where direct nest observations were not possible, for example if the nest was in a culvert or hidden under a riverbank, a Panasonic HC-V160 video camera with zoom focussing was instead used to record provisioning. Review of video recordings with slow-motion playback and freeze frame capability enabled determination of parental identity from colour ring combinations. All sessions, whether manual or recorded via video, were one hour long starting from when birds displayed ‘normal‘, undisturbed behaviour. Adults which are wary of the observer, hide or camera typically alarm call, ‘bob’ frequently and make ‘test flights’ to the nest without actually feeding the nestlings; in some cases the adults will eat the food which they have brought to the nest area. These behaviours are rare when the observation site chosen is appropriate, but measurements did not start until offspring provisioning took place and no signs of wariness were apparent. Provisioning rates for each parent were measured simply as the number of feeds made in one hour. It was assumed that females returning to the nest to brood young nestlings had brought food with them, as this is almost always the case when the bird is seen well enough. Two visits to the nest in quick session made with the same food load were recorded as a single feed.

3.3.2 Prey availability

In order to measure prey availability, aquatic macroinvertebrates were sampled on day 10 (+/- 1 day) of the nestling period from a riffle in the territory where the parents were regularly observed foraging or where a high density of droppings indicated a major feeding site. Sampling site location and altitude (to the nearest 10m) were recorded using a Garmin eTrex

H GPS (Garmin Ltd, Switzerland), and cross-checked with Ordnance Survey data. Samples were obtained following the Standardisation of River Classifications (STAR) framework and Freshwater Biological Association (FBA) sampling protocols (STAR 2005; FBA 2017). Briefly, a standard three-minute kick sample was taken in the riffle using a 1.5m handled D-shaped metal-framed net with a cross sectional area of 557cm^2 and a 1mm polyester mesh held downstream, with the rim on the stream bed. Kicking and shuffling of the substrate dislodged fauna that was swept by the current into the net. On site, net contents were hand sorted to remove stone debris and to record and release any small fish. Specimens were completely immersed in a preservative solution of 1:1 methanol and water in labelled and sealable polythene bags. The net was then rinsed clean and visibly checked for animals before subsequent use at further sites.

In the laboratory, samples were hand sorted to remove remaining stream debris with any finer material passed though stacked sieves of mesh sizes 4mm and 0.5mm. Specimens were identified and counted using identification guides of freshwater invertebrates (Croft 2012; Dobson *et al.* 2012) using a Leica S4E 20 X 0.63-3.0 (Leica L2 light unit) zoom binocular microscope. Specimens were sorted into Ephemeroptera (mayfly; E), Plecoptera (stonefly; P), Trichoptera (caddisfly; T) and all other animal taxa; the former three make up the majority of the diet of nestling dippers (Ormerod 1985a; Ormerod *et. al* 1987; Tyler and Ormerod 1994) and their combined dry biomass, hereafter known as ‘EPT’, was used as an index of prey availability. Excess liquid was removed from the samples by blotting for 1 minute on tissue, and specimens were then dried to constant weight by heating at 70^{o}C for 48h in a thermostatically controlled Gallenkamp Size 1 Economy Incubator and weighed using an OHAUS Pioneer digital electronic balance to 0.01g.

3.3.3 Statistical analyses

Generalised linear mixed-effect models (GLMMs) in the *lme4* package (Bates *et al.* 2015) were used to investigate the relationship between altitude and the response variable provisioning rate (i.e. the number of food deliveries to a nest in a 1h period) of adult male and female dippers. GLMMs were used because the data were non-Gaussian and to account for non-independence (pseudoreplication) by fitting random effects (following Bolker *et al.* 2009 and Harrison *et al.* 2018). Models of male and female provisioning rates were run separately, with individual identity fitted as a random term to account for repeated measures of provisioning rate at different stages of nestling development.

For models of the relationship between altitude and male provisioning rate, provisioning rate was fitted as the response variable with the following fixed effects included: altitude (in m), nestling age (as week 1, 2 or 3 of provisioning rate observations after hatching), brood size (the number of nestlings on day 9), EPT (total dry biomass of Ephemeroptera, Plecoptera and Trichoptera in g), male age as age category (first years or all other ages as adults), female provisioning rate (measured during the same one hour provisioning watch) and watch date (the Julian date on which the provisioning watch occurred). Nestling age and brood size are important determinants of provisioning rate in most species (Goodbred and Holmes 1996; Chamberlain *et al.* 1999; MacColl and Hatchwell 2003; Bowers et. al 2014; Čech and Čech 2017); EPT was fitted as a measure of prey availability; and male age, female provisioning rate and watch date were fitted to control for their possible influence. Interactions between altitude and each of the other fixed effects were also fitted, and male identity was fitted as a random term (GLMM; poisson error structure and log link function; n=30). Models of female provisioning rates were constructed in the same way but with the provisioning rate of females and males fitted as the response variable and a fixed effect, respectively, and with female identity fitted as a random term (n=30). In all cases, explanatory variables were fitted as continuous variables. Model construction and selection, model averaging and validity checks were carried out as described in Chapter 2.

3.4 Results

A summary of the breeding variables of the lowland and upland dippers in 2017 is given in Table 3.1 (n=37 pairs). For the analyses of provisioning rates, complete data were available for 30 breeding attempts; 22 in lowland habitat and 8 in the uplands.

Table 3.1. A summary of the breeding variables of lowland and upland dippers in the River Lune catchment study site in 2017. Data are means ± SD (sample sizes in parentheses).

Breeding variable	Lowland (<200m): first broods	Upland (>200m): first broods	Lowland (<200m): second broods
Lay date (Julian date)*	77.18 ± 12.92 (33)	94.50 ± 9.72 (8)	127.50 ± 6.14 (12)
Clutch size*	4.50 ± 0.62 (34)	4.71 ± 0.49 (7)	4.00 ± 0.43 (12)
Hatching success (%)**	87.82 ± 18.13 (29)	100.00 ± 0 (3)	88.13 ± 12.80 (8)
Brood size on day 9**	3.88 ± 0.91 (32)	3.38 ± 1.06 (8)	2.90 ± 0.99 (10)
Fledging success %*	69.44 (36)	70.00 (10)	50.00 (12)
Number of fledglings (all nests)	2.42 ± 1.99 (48)	2.77 ± 1.74 (13)	1.33 ± 1.50 (12)
Number of fledglings (successful nests)	3.74 ± 1.03 (31)	3.60 ± 0.84 (10)	2.67 ± 0.82 (6)

* Calculated only for first breeding attempts

** Calculated only for nests which hatched at least one nestling

3.4.1. Factors affecting male provisioning rate

All the best fitting GLMMs of the factors associated with male provisioning rate and their effect sizes model averaging are found in Tables 3.2 and 3.3. Male provisioning rate was predicted by altitude, brood size and female provisioning rate; together with the interaction between altitude and brood size, these terms were present in all of the best fitting models. Male provisioning rate was negatively correlated with altitude (Figure 3.1) and positively correlated with brood size (Figure 3.2). However, the relationship between provisioning rate and altitude varied with brood size; for small broods, males fed their chicks at a lower rate with increasing altitude, but the converse appeared to be true for large broods, although the confidence interval for this effect was large (Figure 3.3). Finally, the provisioning rate of males was positively correlated with that of their partners (Figure 3.4). The interaction between altitude and female provisioning rate was included in the best fitting model set, but the effect size was small and unlikely to be biologically meaningful. Finally, the fixed effects of EPT, male age, nestling age, and provisioning watch date and all other interactions were not present in the best-fitting models.

Table 3.2. The best fitting GLMMs of the factors associated with male provisioning rates (i.e. those models with a ΔAICc value of 2 or less from the best fitting model. The null model is shown for comparison (n = 30).

Full model = glmer: male provisioning rate ~ (altitude + brood size + EPT + female provisioning rate + male age + nestling age + watch date + altitude : brood size + altitude : EPT + altitude : female provisioning rate + altitude : male age + altitude : nestling age + altitude : watch date) + (1|male identity)

Model	Intercept	Altitude	Brood size	EPT	Female prov. rate	Male age	Nestling age	Watch date	Altitude: brood size	Altitude: EPT	Altitude: female prov. rate
557	1.723	-0.323	0.268		0.168				0.620		
2605	1.708	-0.352	0.267		0.144				0.634		-0.077
1 (Null)	1.639										

Model	Altitude: male age	Altitude: nestling age	Altitude: watch date	df	LogLik	AICc	ΔAICc	Weight	R^2m	R^2c
557				6	-209.821	432.7	0.00	0.148	0.656	0.668
2605				7	-209.331	434.1	1.40	0.074	0.655	0.668
1(Null)				2	-230.305	464.8	32.02	1.610e-08	0.000	0.000

Table 3.3. The results of the GLMM of the factors associated with male provisioning rate after model averaging. Details of fixed effects were returned from averaging the models within 2 AICc units of the best fitting model. The random effect variance was obtained from the best fitting model.

Fixed effect	Estimate	Standard error	Adjusted standard error	Relative importance
Intercept	1.718	0.070	0.071	
Altitude	-0.333	0.086	0.087	1.00
Brood size	0.268	0.087	0.089	1.00
Female provisioning rate	0.1600	0.051	0.052	1.00
Altitude: brood size	0.624	0.158	0.160	1.00
Altitude: female provisioning rate	-0.025	0.058	0.058	0.33
Random effect	Variance			
Male identity	0.058			

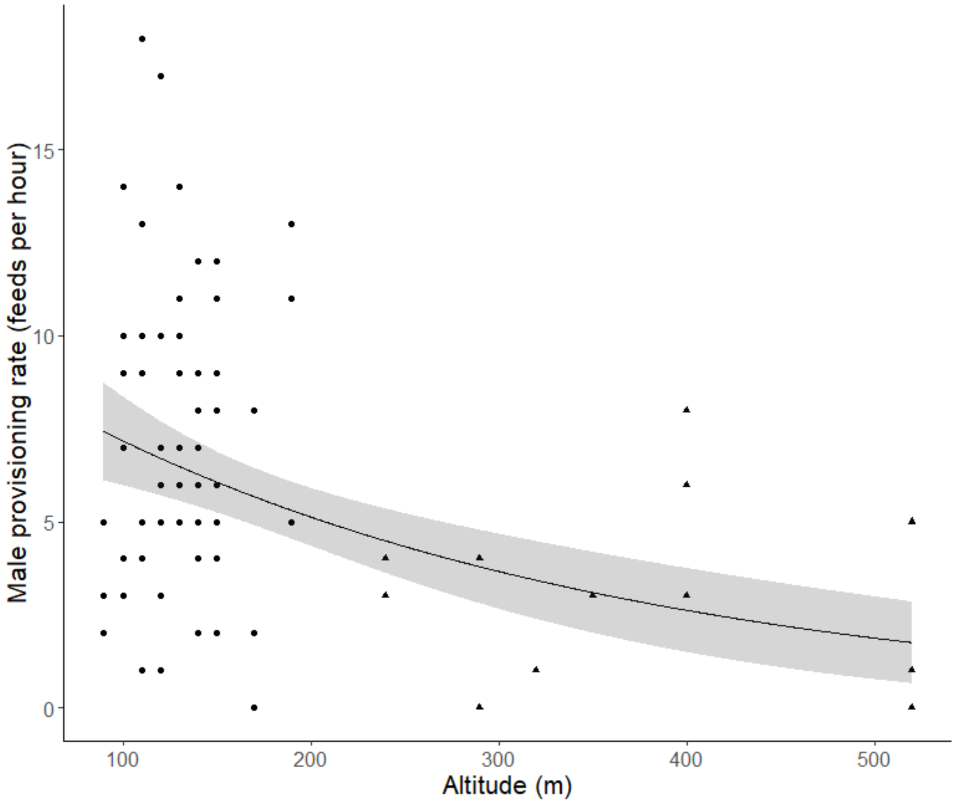

Figure 3.1. The relationship between male provisioning rate and altitude. The points represent the predicted values from a GLMM after model averaging (circles = nests <200m altitude, triangles = nests >200m altitude) and the shading shows the 95% confidence intervals.

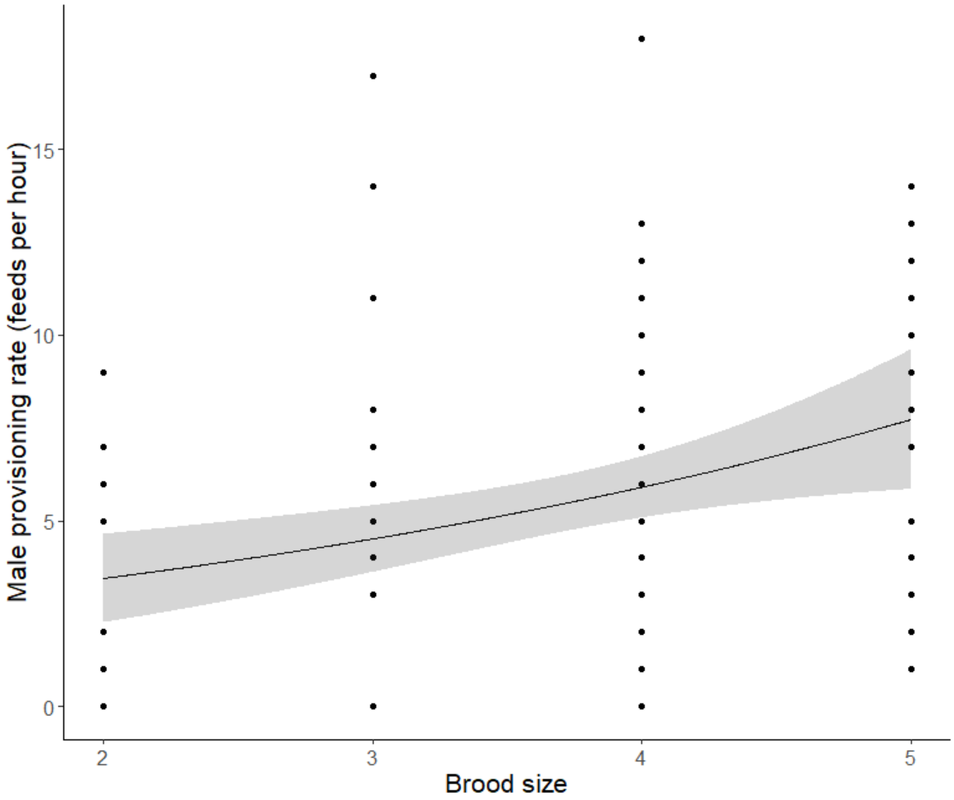

Figure 3.2. The relationship between male provisioning rate and brood size. The points represent the predicted values from a GLMM after model averaging and the shading shows the 95% confidence intervals.

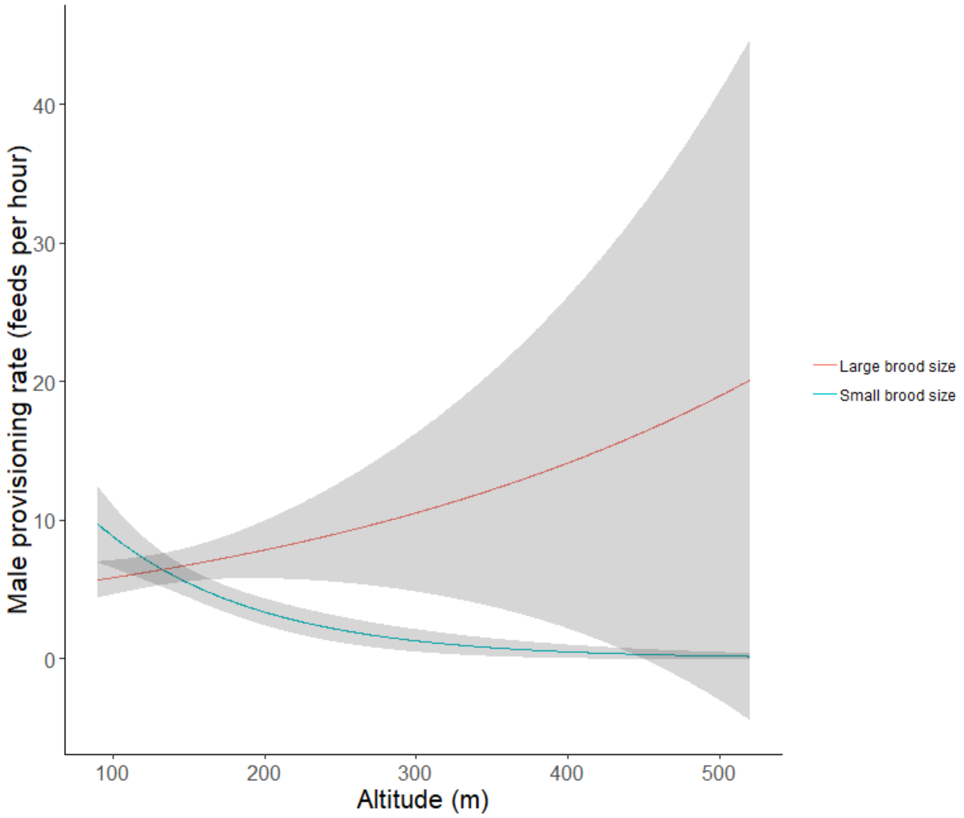

Figure 3.3. The relationship between male provisioning rate and the interaction between brood size and altitude. The line shows the prediction from a GLMM after model averaging and the shading shows the 95% confidence intervals; points are excluded for clarity.

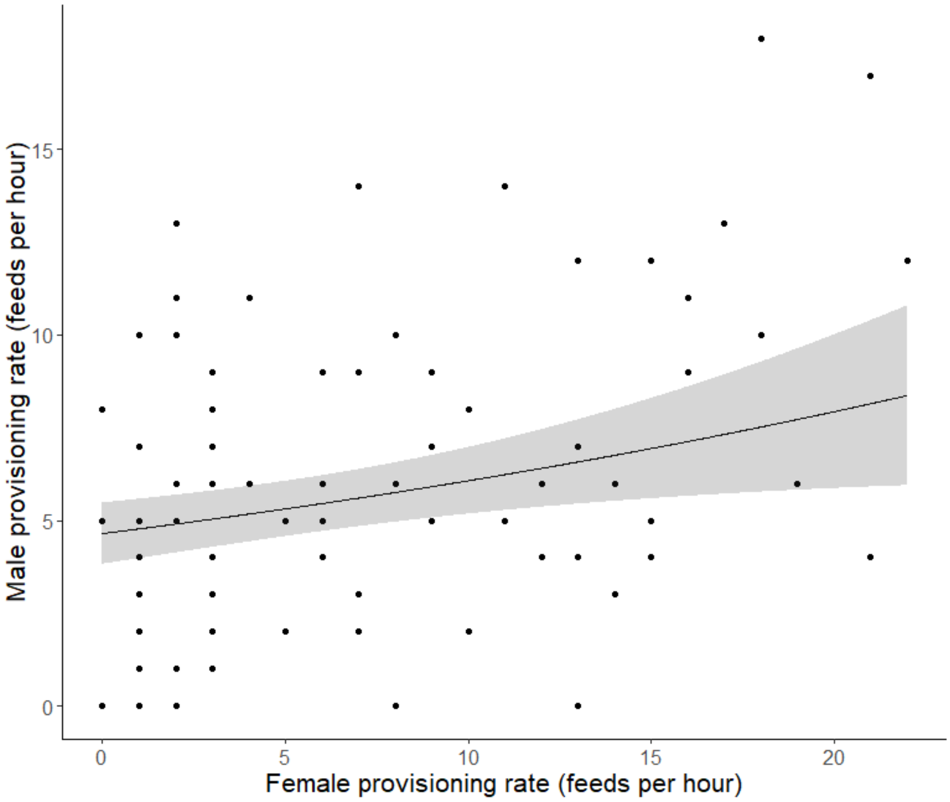

Figure 3.4. The relationship between male provisioning rate and the provisioning rate of the female (partner). The points represent the predicted values from a GLMM after model averaging and the shading shows the 95% confidence intervals.

3.4.2 Factors affecting female provisioning rate

All the best fitting GLMMs of the factors associated with female provisioning rate and their effect sizes after model averaging are found in Tables 3.4 and 3.5. Altitude, nestling age and male provisioning rate were important predictors of female provisioning rate, being present in all of the best fitting models. Female provisioning rate was negatively correlated with altitude (Figure 3.5), but unlike male provisioning rate, increased with nestling age (Figures 3.6 and 3.7). There was again a positive correlation between the provisioning rates of partners (Figure 3.8), and an interaction between altitude and nestling age (Figure 3.9). Brood size, EPT and female age category each appeared in one of the best fitting models but their effect sizes were very small and considered unlikely to have any biological significance. Provisioning watch date was the only variable absent from best fitting models, as were all other interactions.

Table 3.4. The best fitting GLMMs of the factors associated with female provisioning rates (i.e. those models with a ΔAICc value of 2 or less from the best fitting model). The null model is shown for comparison (n = 30).

Full model = glmer: female provisioning rate ~ (altitude + brood size + EPT + female age + male provisioning rate + nestling age + watch date + altitude : brood size + altitude : EPT + altitude : female age + altitude : male provisioning rate + altitude : nestling age + altitude : watch date) + (1|female identity)

Model	Intercept	Altitude	Brood size	EPT	Female age	Male prov. rate	Nestling age	Watch date	Altitude : brood size	Altitude: EPT	Altitude: female age
71	1.704	-0.198				0.184	0.506				
72	1.702	-0.186			0.185	0.191	0.509				
79	1.703	-0.186	0.077			0.180	0.505				
87	1.705	-0.174		0.073		0.184	0.505				
327	1.706	-0.185				0.182	0.495				
Null	1.779										

Model	Altitude: nestling age	Altitude: male prov. rate	Altitude: watch date	df	Loglik	AICc	ΔAICc	Weight	R^2m	R^2c
71				5	-260.327	531.4	0.00	0.062	0.525	0.535
72				6	-259.632	532.4	0.93	0.039	0.546	0.556
79				6	-259.877	532.8	1.42	0.030	0.535	0.544
87				6	-259.925	532.9	1.52	0.029	0.533	0.543
327	-0.050			6	-260.086	533.3	1.84	0.025	0.514	0.524
Null				2	-320.527	645.2	113.78	3.226e-26	0.000	0.000

Table 3.5. The results of the GLMM of the factors associated with female provisioning rate after model averaging. Details of fixed effects were returned from averaging the models within 2 AICc units of the best fitting model. The random effect variance was obtained from the best fitting model.

Fixed effect	Estimate	Standard error	Adjusted standard error	Relative importance
Intercept	1.704	0.081	0.082	
Altitude	-0.188	0.089	0.090	1.00
Brood size	0.013	0.043	0.044	0.16
EPT	0.011	0.041	0.042	0.16
Female age	0.039	0.103	0.103	0.21
Male provisioning rate	0.184	0.054	0.054	1.00
Nestling age	0.505	0.057	0.057	1.00
Altitude: nestling age	-0.007	0.031	0.032	0.13
Random effect	**Variance**			
Female identity	0.101			

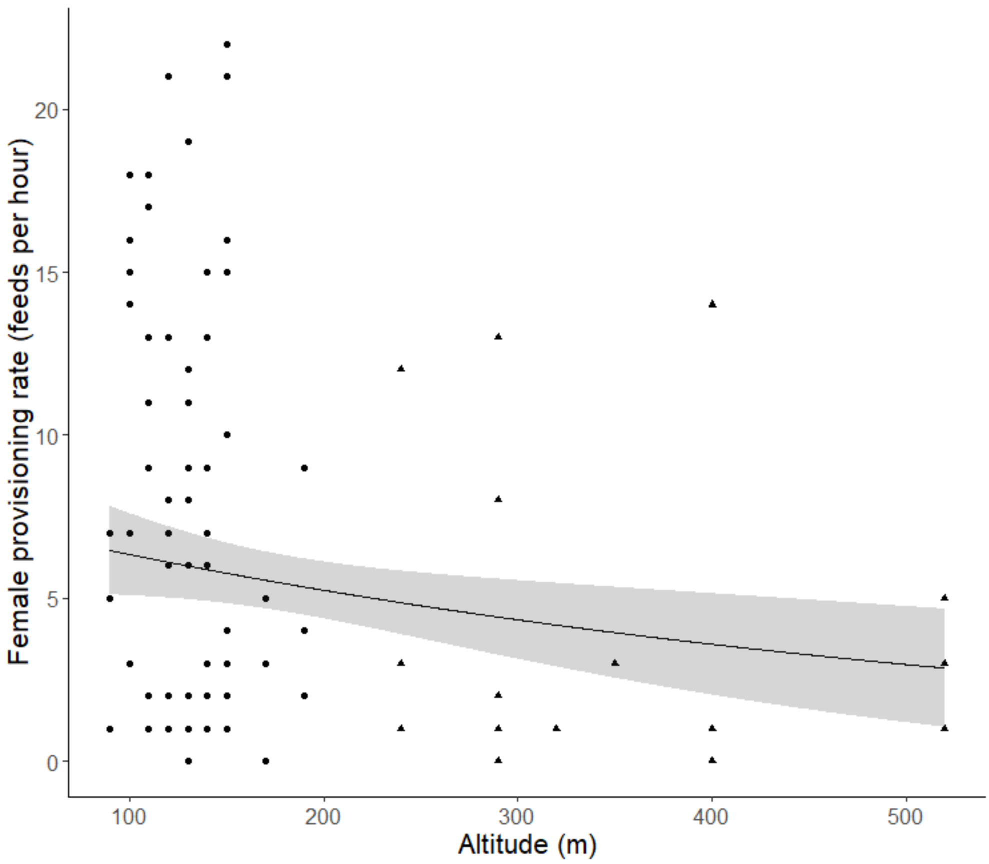

Figure 3.5. The relationship between female provisioning rate and altitude. The points represent the predicted values from a GLMM after model averaging (circles = nests <200m altitude, triangles = nests >200m altitude) and the shading shows the 95% confidence intervals.

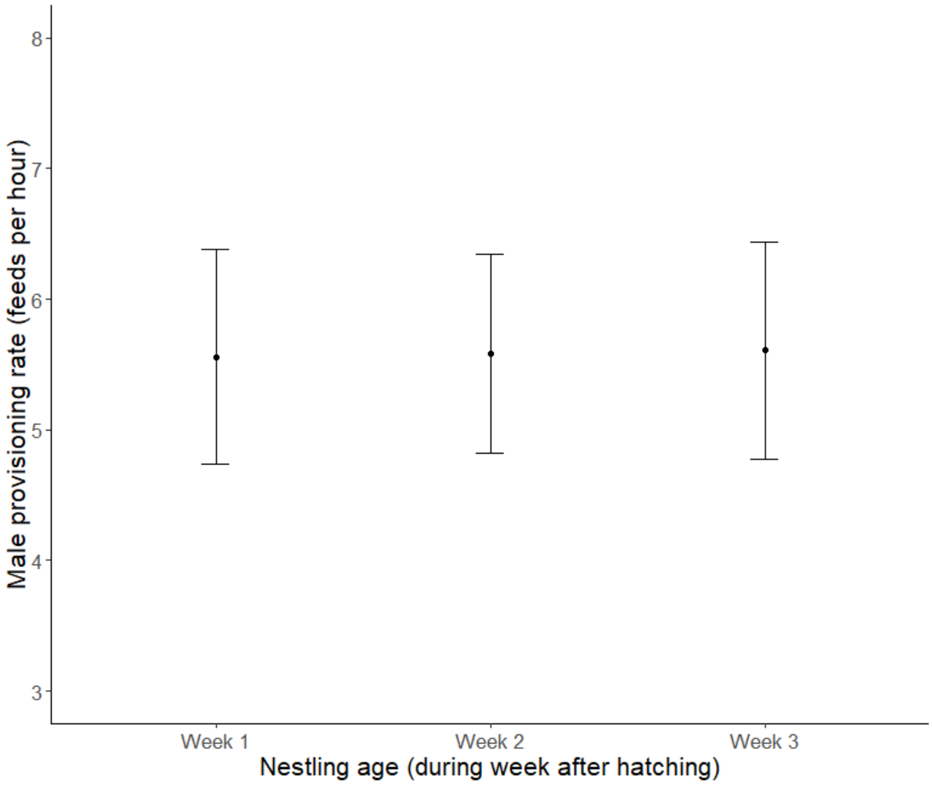

Figure 3.6. The relationship between male provisioning rate and nestling age. The points represent the predicted values from a GLMM after model averaging and the bars represent the 95% confidence intervals.

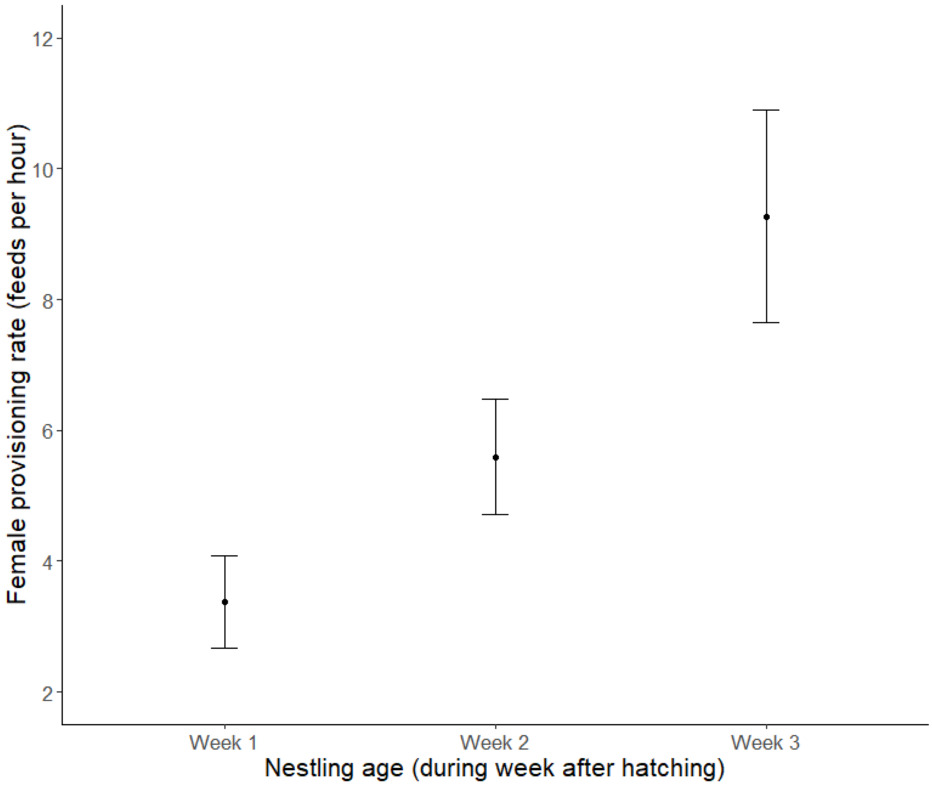

Figure 3.7. The relationship between female provisioning rate and nestling age. The points represent the predicted values from a GLMM after model averaging and the bars represent the 95% confidence intervals.

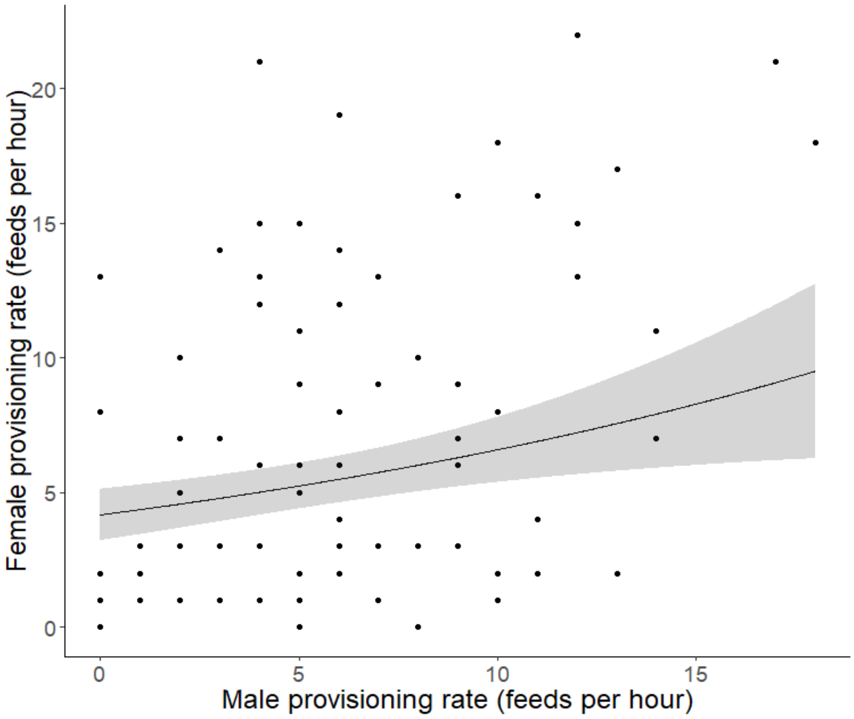

Figure 3.8. The relationship between female provisioning rate and the provisioning rate of the male (partner). The points represent the predicted values from a GLMM after model averaging and the shading shows the 95% confidence intervals.

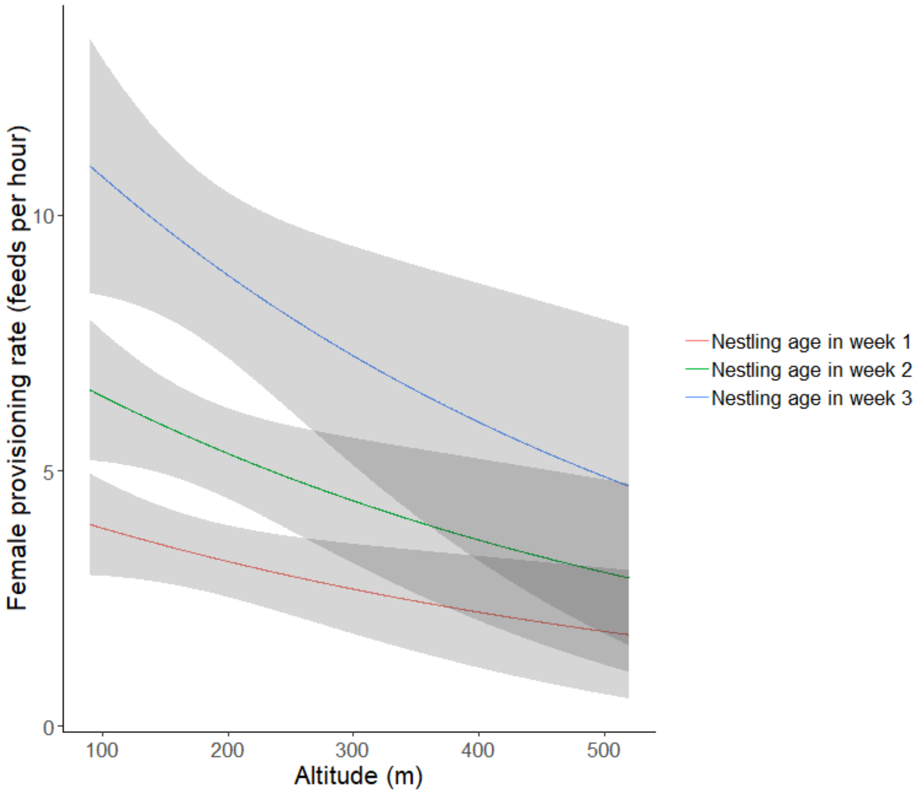

Figure 3.9. The relationship between female provisioning rate and the interaction between nestling age and altitude predicted from the average model. The lines show the predictions from a GLMM after model averaging and the shading shows the 95% confidence intervals; points are excluded for clarity.

3.5 Discussion

The results of this study suggest that offspring provisioning rates in dippers vary with altitude and a number of other variables, but these effects differ between males and females. Altitude was an important predictor of provisioning rate in both sexes and, in males, the effect varied with brood size, whereas in females, the effect varied with nestling age.

Provisioning rate was negatively correlated with altitude in both sexes. At higher elevations, streams typically become narrower and major foraging sites in riffles are fewer, have less area and are often distributed over greater distances from nests compared to lowland territories. Riffle area was the most important factor affecting territory length in brown dippers (*Cinclus pallasii*), was positively correlated with breeding performance variables, and was better at predicting food availability than territory area (Chen and Wang 2009; Hong *et al.* 2018a). Estimates of the energy requirement and territory size for dippers suggest that breeding success may be dependent upon riffle area (Bryant *et al.* 1985, 1988; Ormerod and Tyler 1991), and total riffle area required to raise a brood on higher elevation streams could be distributed over longer distances than for lower elevation rivers. Caddisfly are found in abundance in riffles and have been found to contribute the most to nestling diet in dipper species, with increasingly larger larvae taken as nestlings develop (Ormerod 1985b; Ormerod *et al.* 1987; Tyler and Ormerod 1994; Chiu *et al.* 2009; Hong *et al.* 2018a). Brood sizes were similar for lowland and upland territories and comparable to those reported elsewhere (Tyler and Ormerod 1994; Smiddy *et al.* 1995), and mean nestling mass does not differ between the two habitats (see Chapter 2), suggesting that food availability *per se* (and delivery to nestlings) may not be limiting for nestling growth. In 2017, preliminary analyses indicated that measures of local prey availability as separate E, P and T, or, EPT combined, did not vary with altitude or over the breeding season, suggesting that no particular taxa were likely to be limiting (RPW unpublished data). Provisioning appears to be adequate across all altitudes for nests to successfully fledge young and with little difference in the number of fledglings (see Chapter 2). It may be that because caddisfly and other prey are quickly predated from small, widely distributed riffle areas close to nests first, the lower provisioning rate at higher altitudes may reflect more time spent travelling to increasingly distant foraging riffles and prey handling costs. At lower altitudes, the converse of this may occur alongside either effective or less discriminating prey selection and smaller prey loads. The trade-off between the time and energy costs of distant foraging versus the declining food benefits in nearby feeding sites (Orians and Pearson 1979; Wetterer 1988), may be compensated by high intensity feeding bouts and higher prey loads per journey with either many small or a few large prey items, or selection of nutritionally higher quality food (Stephens and Krebs 1986; Cuthill and Kacelnik 1990; Tremblay *et al.* 2005; Chiu *et al.* 2009). In 2017, adults at higher altitudes were observed making return provisioning flights in excess of 1km and carrying visibly large stonefly nymphs (RPW unpublished data), despite these having highly chitinous exoskeletons similar to some terrestrial insect species (Wiebe and Slagsvold 2014, 2015), and likely being of lower nutritional value compared to less sclerotised caddisfly. If caddisfly availability were to decline, a dietary shift toward stonefly may provide an acceptable food source during early nestling stages at higher altitudes, particularly smaller and less sclerotised instars. A trade-off between utilising sub-optimal nutritional taxa and nestling growth requirements may allow dippers to overcome the scarcity of food resources as riffles near to nests become depleted of preferred prey at higher altitudes (Ormerod 1985b; Orłowski *et al.* 2017; Vilches *et al.* 2018). Dippers at higher elevations may forage opportunistically irrespective of prey taxa or size, as differences in invertebrate assemblage composition, abundance and biomass were not detected in preliminary analyses. These birds may be compensating for higher travelling costs to distant foraging sites by selecting for habitat quality i.e. riffles and thus food availability, a phenomenon observed in starlings (Heldbjerg *et al.* 2017). At higher altitudes, larger prey may be less abundant but more obvious to detect and to offset travelling costs incurred, dippers may return larger prey items and higher total prey load per foraging trip.

Nest predation can account for significant egg and brood loss (Efteland and Kyllingstad 1984), and has occurred across the study site in all years (S. P. Sharp unpublished data), with likely predators including American mink (*Neovison vison*) and other mustelids, corvids and foxes (*Vulpes vulpes*) (Shaw 1978; Tyler and Ormerod 1994). Nestling begging calls are a cue for parental provisioning but are also likely to alert predators (Kilner and Johnstone 1997; Leech and Leonard 1997; McDonald *et al.* 2009), and dipper nestling calls are relatively loud (Shaw 1978). However, responding to begging with more provisioning activity at the nest can result in a greater likelihood of predation (Martin *et al.* 2000). Dippers may trade-off distant foraging and fewer nest visits with higher prey loads per trip, which may reduce vocal nestling begging, and, together, these may avoid alerting predators. Reductions in parental visits have been shown to lower rates of nest predation (Eggers 2002; Eggers *et al.* 2005), and this may happen at higher altitudes in dippers as a response to an increased threat of predation. It is not known whether predation pressure is higher in upland territories, but there is less predator control on land that is primarily grazed by sheep (*Ovies aries*) and not managed for game bird shoots. At higher altitudes, lower male provisioning rates with small broods may provide more time for predator surveillance, whereas with larger broods, males may trade-off more conspicuous visits that sate noisy nestlings versus fewer visits but audible begging calls from hungry nestlings. The data presented for large brood sizes suggests less confidence than for small broods but this does not preclude this from being a real effect. At lower altitudes, if high provisioning rates occurred over short periods that sated rather than left nestlings hungry, noisy and conspicuous to predators, this may provide additional time for territory vigilance by parents.

It was not possible to account for parental activities other than provisioning, but nest security is a trade-off between predator vigilance, nest guarding and foraging time, and exacerbated when food is limited (Komdeur and Kats 1999; Verdolin 2006; Bell *et al.* 2009), and is possibly mediated by higher altitude habitat having less bankside cover for dippers.

Male provisioning rate was positively correlated with brood size and further influenced by the interaction between brood size and altitude, whilst small model estimates for females (and the absence of an interaction) were not thought to be biologically meaningful, suggesting investment in provisioning is consistent across altitude regardless of brood size. Brood size and provisioning rate are directly related to total nestling demands and reported in a number of species and from experimental studies (Conrad and Robertson 1993; Wright *et al.* 1998; Chamberlain *et al.* 1999; Magrath *et al.* 2007; Low *et al.* 2012; Čech and Čech 2017). Male provisioning may respond positively to food shortage, nestling demand and threat of predation to ensure rapid nestling growth (Grundel 1987; Mizuta 2005). Male dippers may also respond more than females to the noisy nestling begging of larger broods by increasing provisioning frequency to reduce alerting predators, and possibly by opportunistic foraging of sub-optimal prey at higher altitudes as described earlier. Small broods tend to produce less loud begging calls than larger broods (Ottosson *et al.* 1997; Leonard *et al.* 2000), and the lower male dipper provisioning rates may be enough to satisfy nestling food requirements, and provide more time to invest in safeguarding smaller brood survival with territorial surveillance. Males with higher provisioning rates than females may obviate low breeding success, or, with a greater certainty of paternity, may invest more in parental care as a strategy to maximise brood and lifetime reproductive success that may outweigh the potential benefits of extra-pair matings (East 1981; Trémont and Ford 2000; Nakagawa *et al.* 2007). Additionally, lower female provisioning rates may reduce the opportunity to vary rates by males. Given that the costs in egg production and brooding are entirely met by female dippers, it might be supposed that female provisioning rates would increase in line with brood size to maximise current and lifetime reproductive success. However, parental care is likely to result in lowered survival for males (Santos and Nakagwa 2012), whereas females may remain unaffected possibly by transferring costs of reproduction to offspring by prioritising their own condition (Linden and Møller 1989). Female dippers may spend more time feeding themselves because of the energetic investment made after incubation and brooding, and their post-brooding condition and ability to provision may not satisfy nestling demand during periods of rapid growth without an increase in provisioning by males, particularly for large brood sizes. An absence of a strong provisioning response to increasing brood size or across altitudes by female dippers may be to minimise adverse long-term effects of high provisioning rates upon female post-reproductive survival (Bryant 1991; Pärt *et al.* 1992; Hanssen *et al.* 2005), and may lower the reproductive costs required for subsequent breeding attempts. Alternatively, females may have different foraging strategies to males (Moreno 1995), or take longer to travel to feeding sites but offset this by returning with higher prey loads (Grundel 1987), or by engaging in additional territorial duties, predator vigilance or self-maintenance.

Male provisioning rates did not differ with nestling age whereas that of females' did. In contrast, American dippers showed no increase in provisioning rate with nestling age, although nestlings regularly eat more biomass as small fish, which is less usual in white-throated dippers (Tyler and Ormerod 1994; Mackas *et al.* 2010; RPW unpublished data). Male dippers delivered more feeds than females during week 1 provisioning watches as females were brooding but female provisioning rates significantly exceeded those of males in weeks 2 and 3 after brooding. Higher altitudes negatively affected female provisioning rates across all nestling ages but most markedly during week 3, and this may be explained by altitude effects upon habitat, foraging and defence as described earlier. During brooding, females have few periods of recess, after which they are assumed to return and feed young, and so males undertake most of the provisioning. Low provisioning rates soon after hatching at all altitudes probably result from small nestlings having a limited gape size that determines prey selection, the volume of food that can be ingested, how quickly nestlings are sated, and the rates of digestion and transit within the gut. Growth, development and energy requirements may not be constant for dipper nestlings, but provisioning must be sufficient for them to gain around 3-4g per day until growth rate plateaus after about day 13/14 (Tyler and Ormerod 1994). Provisioning rates typically increase linearly with nestling age and level off in the later stages or decline slightly before fledging, which may be an inducement to fledge or reduce predation risk close to fledging (Grundel 1987; Yasukawa *et al.* 1990; Adler and Ritchison 2011). Enhanced levels of female care during week 2 and 3 may reflect the brood investments made, whereas males may undertake other protective duties and both are described earlier. Bigamous matings may be reflected in less male parental investment concomitant with questionable paternal certainty (Chaine *et al.* 2015), and whilst polygyny occurs in the study site, it is not common (S. P. Sharp unpublished data).

The provisioning rates of both sexes appeared to match that of their partner's and this is noted in a range of other species (Nordlund and Barber 2005; Hinde and Kilner 2007; Meade *et al.* 2011). Dual increase in food delivery may arise independently in both parents in response to nestling begging, or, increased partner provisioning rate prompted by observational cues (Hinde and Kilner 2007; Harrison *et al.* 2009; Bebbington and Hatchwell 2016). Brood size and then rate of partner deliveries have been shown to influence provisioning rate in adults, with nestling begging calls having only a small effect (Hinde and Kilner (2007). Since there was no significant effect of brood size on the provisioning rate of female dippers this suggests they may respond to increases in male provisioning rates mediated by nestling demands. Increases in male provisioning rates could result from the demands of larger broods and in response to increased female provisioning rates elicited by their (males) initial rate of provisioning. The negotiation model of parental care asserts that as conditions change, parental care investments are adjusted and each parent's contribution is modified by their partner's effort (Johnstone and Hinde 2006; Nakagawa *et al.* 2007; Harrison *et al.* 2009). The current and post-fledging benefits to a brood from mutually increased parental food deliveries must be traded off against the impact upon a subsequent brood (namely, early breeding lowland dippers that are more likely to second brood), adult condition pre-moult, and a greater risk of predation with more parental activity at the nest (Martin *et al.* 2000; Leniowski and Węgrzyn 2018). There may be no measurable effects on nestlings but if parents differ in their work effort, it may have consequences for their survival or reproductive success in the following year.

EPT was only present as a weak positive effect for females and may not be biologically meaningful, so any effect on EPT due to phenology, seasonal weather conditions, or other taxa that could influence provisioning rates remained largely undetected, and EPT communities do not appear to be constrained by prevailing water conditions (described in Chapter 1). Moreover, as nestling mass across altitude and date of breeding did not appear to differ (see Chapter 2), all of these results suggest that food availability is not limiting and that distribution of macroinvertebrates at different altitudes, particularly in riffles, may be an important determinant of provisioning rates. Stonefly nymphs appeared to predominate at some upland sites and a delayed emergence from streams containing a range of nymph sizes may provide an acceptable food source for later breeding dippers at higher elevations. EPT community structure has been shown to require particular environmental conditions (Brittain 1982, 1990; Füreder *et al.* 2005; Brand and Miserendino 2011; Kalaninová *et al.* 2014), but over the short distance elevational change of 430m in the study area there may be insufficient change in altitude and stream conditions to affect invertebrate populations. Rivers and streams in the study area appear to provide equitable conditions for macroinvertebrate populations that can sustain dipper populations (see Chapter 1), but how conditions influence specific habitats and the taxa within them may be difficult to determine (Ormerod and Edwards 1987).

3.6 Conclusion

EPT do not appear to be limiting across altitude or with time of breeding and reflects high water quality that promotes abundant benthic communities across the study site. Altitude appears to affect negatively provisioning rate in dippers, although, nestling mass remains unaffected (see Chapter 2). The gender effects suggest that males may play a greater part in provisioning at higher altitudes. Upland streams tend to be narrower with small feeding riffles distributed over long distances than lower elevation rivers. This would suggest that habitat quality measured by time travelling to forage might be driving provisioning rates, and may cause migrant dippers to forage opportunistically, alter prey loads and handling costs, and produce a shift in nestling diet. As only one breeding attempt is made at higher elevations (see Chapter 2), males may adopt alternative investment strategies: for large broods higher provisioning rates are more likely to deliver sufficient food to maximise brood success; whereas small broods can be sated with fewer feeds and surplus time could be devoted to safeguarding nestling survival. Males may also respond with higher provisioning frequency to increased brood size possibly to compensate for lower female provisioning, which may be a strategy of females to enhance post-reproductive survival and lower future breeding costs. Female dippers provision more as nestlings' age compared to males possibly in response to their investment made through egg production, incubation and brooding, to ensure fitness, and is mediated by the effects of altitude that may cause a lowering of provisioning rate that without which, might impact female body condition and energetic costs and have fitness consequences pre- and post-moult. Provisioning rates are positively correlated with partner rates and as females do not increase provisioning rates with brood size it would suggest that they cooperate and follow male provisioning rates, who in turn further reciprocate the female's actions and / or respond to begging broods. Dippers may also make foraging decisions based on the threat of predation by trading-off foraging distance, increasing prey load and potentially noisy nestlings versus frequent, predator alerting visits but quieter nestlings, mediated by habitat quality resulting from the physiographic effects of altitude. With potentially fewer opportunities for extra-pair matings and so greater confidence in their nestlings' paternity, males may invest more in breeding success. Females at higher altitudes may select higher quality mates that are willing and capable to invest more in parental care in a demanding environment and, in return, deliver paternal certainty and reproductive success.

3.6.1 Further work

Future research could investigate if habitat quality is determined by how stream characteristics at different altitudes affect the distribution and size of foraging riffles and benthic communities, parental foraging behaviour and nestling diet and development, and if this has fitness consequences for resident and migrant dippers. Further study could also examine how stochastic events such as weather can affect flow conditions and influence provisioning rate and nestling development across altitudes. Predator simulation experiments could investigate the strategies that dippers adopt to counter the threat of predation such as compensatory feeding, the role of synchrony or asynchrony of nest visits, and nestling behaviour.

Chapter 4

General discussion

4.1 Altitude and its effect upon breeding success in dippers

The breeding population of dippers (*Cinclus cinclus*) in the River Lune catchment appears to have two migratory life-history tactics: yearlong residency on relatively low altitude rivers and an altitudinal migration to upland tributary streams for breeding from wintering sites alongside residents. Previous studies elsewhere in the UK have recognised partial altitudinal migration in dipper populations (Shaw 1978; Tyler and Ormerod 1985; Logie 1998), but this is the first investigation of reproductive success along an altitudinal gradient within a watershed. Dippers at higher elevations breed later, have fewer second broods and may be less likely to replace failed clutches. Resident birds, on the other hand, might have higher lifetime reproductive success if they were regularly having multiple broods, as early successful first clutches allow time for second breeding attempts. Altitude appeared to have little or no effect on nestling mass, number of first brood fledglings and annual productivity. However, fledging success (i.e. the probability of fledging at least one chick from a brood) increased with altitude, albeit with a small effect, and this may be because of a lower risk of flooding and predation. It is likely that migrants are temporally constrained to single broods but not limited by food to raise typical brood sizes, whilst residents probably sustain greater losses through flooding and predation with the shortfall made up by replacement nests or second broods.

Seasonal variation in ecological conditions across the elevation gradient does not appear to affect habitat quality or breeding outcomes, with no apparent seasonal decline in prey biomass or provisioning rates, number of fledglings or nestling mass at increasing altitudes. Upland birds provision young less often even though food does not appear limiting, but neither nestling mass nor the number of chicks fledged in first broods varied with altitude. As physical and chemical measures of water quality across the study site (including pH) are highly suitable for aquatic invertebrates, their distribution might vary with changes in stream physiography at altitude, such as a reduction in the number of foraging riffles that support key nestling food items (Tyler and Ormerod 1994). It may be that birds at higher altitude occupy streams that have more disparate foraging areas, which require longer flight times, and lead to fewer provisioning visits. However, these longer feeding trips may be compensated for by larger prey items per delivery and prey loads, lower prey handling costs through more efficient foraging, more intense foraging or a greater diversity and / or higher value food in prey rich riffles. For example, it was observed that dippers repeatedly delivered large stonefly nymphs at upland nests and it is possible they represent a good alternative food source for nestlings' once large caddisfly larvae have been effectively removed from feeding riffles (Ormerod 1985b). The diet of nestling dippers across the British Isles and Europe shows considerable variation in composition (Tyler and Ormerod 1994), and it is probable that at Sedbergh localised variation of prey diversity and abundance may vary temporally in individual streams and be further affected by altitude, which in turn influences provisioning rates for different brood sizes and as nestlings' age. It may be that birds at lower altitudes have greater access to small fish, which commonly supplement nestling diets (Tyler and Ormerod 1994).

The rivers and streams in the study site have rarely, if ever, been ice-bound, but stochastic unseasonal cold weather events can lower water temperatures, and this may influence the timing of breeding. However, in some cases, residents on the main rivers and migrants on streams actually nest at similar elevations yet the latter still breed later. Habitat structure of rivers and streams can determine invertebrate richness and abundance (Barnes *et al.* 2013), and variable flow rates on different orders of streams may also affect invertebrate diversity and densities by influencing size of substrate and riffle habitat structure (Strahler 1952, 1957; Shreve 1966; Downes *et al.* 1993; 1995), and composition of aquatic plants and detritus (Egglishaw 1969). Alternatively, it may be that elevation itself is not affecting lay date but that later reproduction is simply the outcome of the time taken by individuals to leave lowland overwintering sites and reach higher elevations, acquire mates and establish territories as has been suggested for American dippers (Morrissey 2004).

Despite annual mortality potentially ‘freeing-up’ territories, and natal and breeding dispersal in dippers being typically short distance movements (Tyler *et al.* 1990; O'Halloran *et al.* 2000; Ormerod 2002), competition for nest sites possibly forces some individuals to travel more widely in order to locate a territory, to remain as unpaired lowland ‘floaters’ and defer breeding, or, to migrate altitudinally along tributary streams. Similar processes have been described in other species (Rabenold and Rabenold 1985), including American dippers (*Cinclus mexicanus*) (Gillis *et al.* 2008). Failed competition for nests sites would suggest that migrants are subordinate to residents due to age, quality or inexperience. However, in comparing residents breeding <200m and migrants >200m across all study years, juveniles successfully established a similar proportion of lowland and upland territories (lowland: 45.5%, n=154 breeding attempts; upland: 50.0%, n=26; RPW unpublished data), and were capable of breeding successfully in their first year regardless of migratory status.

Migrant American dippers breed later, have shorter breeding seasons and fewer second broods (Morrissey 2004; Gillis *et al.* 2008), supporting the results shown here, and residents have higher annual productivity and lifetime reproductive success than migrants (Gillis *et al.* 2008). This suggests that altitudinal migration has lower fitness payoffs in this species, and is perhaps a ‘best of a bad job’ strategy, an idea supported by Mackas *et al.* (2010), who showed that migrants do not compensate for lower productivity with higher quality offspring as their offspring are less likely to survive the first winter (Green *et al.* 2015). Green *et al.* (2015) found that migrant American dippers do not gain from the reduced costs of single brooding or from not having to defend and be restricted to yearlong territories during food-limiting floods, as any possible survival benefits were offset by an increased risk of predation. Gillis *et al.* (2008) noted that some migrants repeatedly used the same strategy and had lower productivity than residents yet had higher annual survival, albeit not by enough to offset lower productivity and balance lifetime reproductive success. Altitudinal migration in this species probably results from competition and is likely a strategy by subordinate individuals unable to acquire breeding territories in the overwintering sites (Green *et al.* 2015). By contrast, migrant (white-throated) dippers do not seem to differ from residents in their annual productivity, and Logie (1998) found no difference in lifetime reproductive success. However, in the current study, survival is not easy to determine as the population is not closed and dispersal of colour-ringed birds outside the monitored site is not uncommon (S. P. Sharp unpublished data).

Residency and migration in the same population could be the result of a fixed genetic dimorphism whereby each strategy has equal pay-offs, producing an evolutionarily stable state, or it may be that annual variation in whichever migratory strategy is best creates fluctuating direction of selection (Gillis *et al.* 2008). Alternatively, environmental or social conditions could influence switching of migratory tactics but this would only apply if an individual's competitive ability changes over time (Gillis *et al*. 2008). If being a migrant is condition-dependent, then the resident and migrant strategies would coexist but with unequal fitness outcomes, with subordinate competitors accepting poorer breeding prospects over no breeding at all. Unlike Gillis *et al.* (2008), this study found no difference in productivity with altitude, which would suggest that a fixed genetic dimorphism could persist. However, since there is no analysis of annual survival in residents and migrants or their offspring, lifetime fitness cannot be assessed. Partial migration in European robins (*Erithacus rubecula*), for example, is suggested to be a conditional strategy with resident males having higher survival, higher mating success with earlier settling date, higher probability of breeding and higher lifetime reproductive success than migrant males that make the 'best of a bad job', although a genetic basis for migratory tendency was not excluded (Adriaensen and Dhondt 1990).

In this study, sample sizes are too small to compare reproductive success in each year for alternative breeding strategies. However, there are cases of juveniles from upland breeding parents becoming lowland breeding residents and vice versa (S. P. Sharp unpublished data). This does not preclude the existence of a genetic propensity for altitudinal migration, but it is suggestive of migratory status being condition dependent. If juveniles disperse from natal uplands to lowland overwintering sites where they become breeding residents, they must be capable competitors, or else are able to attain residency during years when many territories are vacant. There are only two examples during the study period of individual birds switching between being migrants and residents. If migratory strategy is condition-dependent, switching might be expected to occur more frequently as individuals make decisions depending on their current state and environmental circumstances before each breeding season. Gillis *et al.* (2008) suggest that failure to switch migratory tactics would result from no change in competitive ability over time, or if changing tactics provided no increased fitness benefits over philopatry. Passerines tend to show nest-site fidelity (Greenwood and Harvey 1982), and benefit from familiarity with feeding areas which helps provide protection from predators (Hinde 1956). Long-lived species with mate fidelity can enhance fitness resulting from shared knowledge and experience without the costs of mate acquisition and territory establishment (Banda and Blanco 2014). Philopatry is more likely to match beneficial adaptive genetic combinations of individuals with those of breeding partners and, consequently, the genotypes of their offspring are more likely to match their natal environment (Weatherhead and Boak 1986). If food supply across the study site is not limiting then the most likely driver of competition is the availability of nest sites. Less competitive individuals must search for vacant territories, including those on upland streams, or abandon breeding. As the results here show, the fitness benefits of breeding in the uplands are likely to far exceed those of delaying reproduction. The benefits of site fidelity then presumably outweigh those associated with breeding dispersal. Alternatively, migrant dippers may prospect vacant sites, irrespective of dominance rank, and make informed choices to breed in the uplands because of cues related to accessible foraging sites containing abundant prey, low predator numbers, lower disturbance and enhanced nest security.

Migrant dippers appear to have life-history traits that conform to neither the slow pace of life of increased parental care, as provisioning outcomes for nestlings are no different to residents, nor that of a fast pace of life, as fecundity appears unaffected by altitude (Promislow and Harvey 1990; Ricklefs and Wikelski 2002). Additionally, the absence of data for survival rates, longevity and lifetime reproductive success makes it difficult to place dippers in the pace of life framework. However, the contrasting life-history traits of resident and migrant dippers suggest novel positions outside of the slow-fast continuum (Hille and Cooper 2015). Furthermore, allopatric dipper populations could contain elements of each of the 'high reproductive', 'survivor' and 'bet-hedging' species categorised by Sæther *et al.* (1996). As survival rates remain unknown, any shift from a high reproductive life-history strategy at low altitudes, to increased investment in parental care producing fewer, but higher quality offspring, and an increased survival life-history strategy at higher altitudes, cannot be concluded nor dismissed (Badyaev and Ghalambhor 2001). The conflicting evidence for life-history traits suggests altitudinal migration in dippers is likely to be an alternative migratory tactic driven by competition for resources. Subordinate individuals seek breeding opportunities in vacant territories at higher altitudes in order to retain fitness (comparable to alternative reproductive tactics described by Taborsky *et al.* 2008) and respond accordingly to prevailing ecological conditions. Additionally, consistent behavioural and personality differences among individuals (Réale *et al.* 2010; Gangloff *et al.* 2017) are likely mediated by territory familiarity and philopatry, and may contribute to the reproductive tactics of dippers.

Some points to note: there are a number of pairs that stay together for several years and breed successfully; it is not clear what happens to juveniles and the degree of dispersal out of the study site, or, the extent of first year mortality. It may be that first year mortality is high but, if individuals survive the first year of breeding, there is a greater likelihood of living longer. If, individuals live long enough, they only need to produce the occasional surviving fledgling to replace themselves. Alternatively, post-fledging and first winter survival are high, and dispersal is over a much greater distance in the Sedbergh area than would normally be expected for dippers.

4.2 Double brooding

Double brooding provides short-lived and seasonally constrained but early breeding species, like dippers, with the opportunity to increase productivity (Mulvihill *et al.* 2009; Jacobs *et al.* 2013). The likelihood of double brooding is probably influenced by early timing of the first brood and food availability (Morrisson and Bolger 2002; Moore and Morris 2005; Nagy and Holmes 2005a, 2005b; Batey 2018). However, factors influencing double brooding in dippers are not well understood and its incidence varies across Europe and within the British Isles (Tyler and Ormerod 1994), and interannually in the Sedbergh population (S. P. Sharp unpublished data). This suggests that there is some environmental component directing double brooding (Nagy and Holmes 2005a; Husby *et al.* 2009). In the UK, the timing of the first clutch together with the quality and abundance of aquatic macroinvertebrates are likely to be important factors in double brooding (Da Prato and Langslow 1976; Shaw 1978; Tyler and Ormerod 1994).

The mean time elapsed between the lay date for corresponding first and second broods in Sedbergh is 53.8 days (SD=4.36; median=53; n=32; range 49-72) and concurs with that of 7½ weeks for the area noted by Mawby (1961); the number of second brood attempts for each year from 2013-2017 was 2, 11, 6, 5, and 12, respectively. Each year, a small number of nests may have disproportionately early lay dates, but a more reliable predictor of second brooding is generated from median values. Median lay dates and the number of second broods are seen in Figure 4.1 and general trends indicate that later lay dates for lowland breeding lead to less second brooding, and later laying migrants never second brood. Annual median lay dates in lowland territories are generally mirrored in upland territories albeit later. This suggests environmental conditions across the study area such as late winter weather could act upon water temperature, flow velocities and heights, and influence prey development, and that these may cue for timing of breeding.

There is no evidence of any year-round residents at high altitude, and the timing of migrants moving from winter quarters to upland streams at Sedbergh is not known, nor is whether this results from a single movement or increasingly distant forays over some time until a critical distance or previously held or vacant territory is encountered. There is evidence that commuting between upland nest sites and lowland rivers during stalled nest-building occurs because of poor weather (Mawby 1961; S. P. Sharp unpublished data), but recording of lay dates is the only absolute evidence of actual breeding.

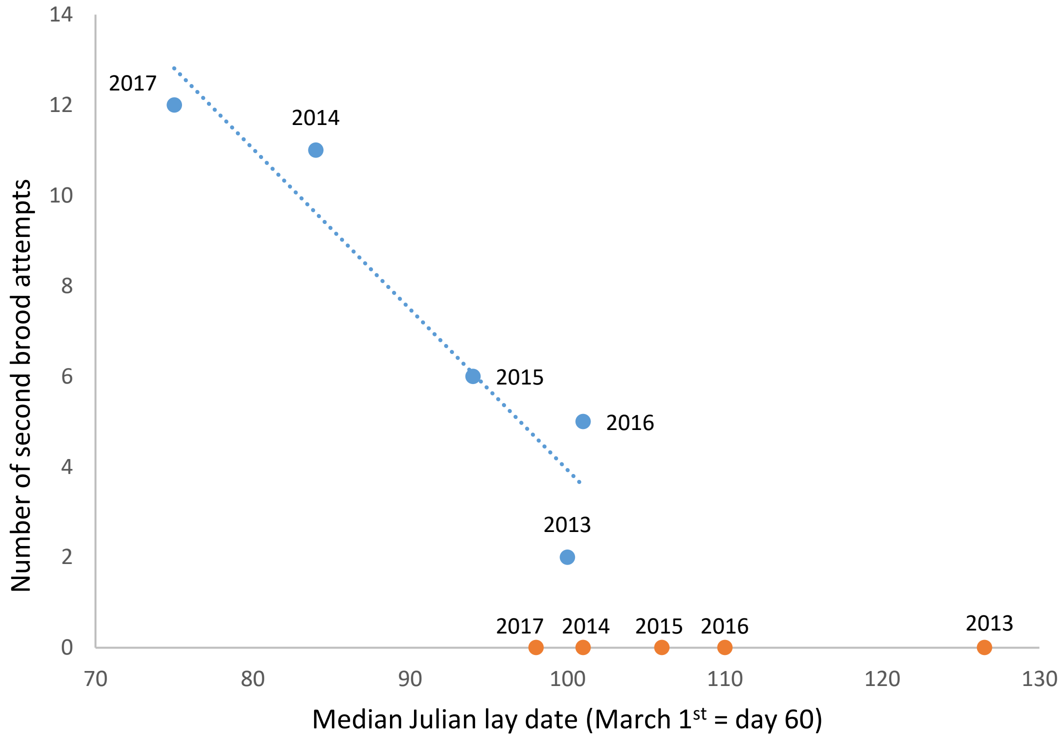

Figure 4.1. The relationship between the number of second brood attempts made in each year and the median first lay dates at lowland (<200m) and upland (>200m) nest sites in 2013-2017. Blue points = lowland nests, orange points = upland nests.

A 'rule of thumb' for the study site is that second brood attempts only occur if first lay dates are before April 1st (Julian date 91). Twenty lowland pairs made successful first breeding attempts with a lay date earlier than April 1st but did not attempt to raise a second brood (with known age categories of 10 adult and 9 first year females). The earliest lay date for a successful second brood was April 20th and the latest was May 22nd. With time apparently being available following a successful first brood for these twenty lowland pairs, this suggests that timing of first lay date alone cannot predict which pairs attempt a second brood. Second brooding may also be limited by episodic extreme weather producing either high or low flow conditions, declining food availability or territory quality, regular incursions by predators, and an individual's quality, condition and level of parental investment in first broods (Moore and Morris 2005; Nagy and Holmes 2005a, 2005b; Husby *et al.* 2009; Jacobs *et al.* 2013; Carro *et al.* 2014; Royan 2014; Woodworth *et al*. 2017). Some adjacent or nearby territories across the study site often have pairs of birds that double brood in the same year whilst elsewhere in the study site other nearby territories each subject to the same general environmental conditions have only one pair that second broods despite very similar first lay dates. This may be accounted for by variation in habitat quality between territories, for example riffle area with abundant mayflies, stoneflies and caddisflies, individual quality or age-related experience playing some role in limiting the number of breeding attempts, or, possibly a preference for retaining fitness by trading off lower annual breeding costs with higher investment in survival and greater lifetime reproductive success (Jacobs *et al.* 2013; Hoffmann *et al.* 2015).

4.3 Brood reduction

During 2013-2017, mean % hatching success for lowland (n=99) and upland (n=10) nests was >92%, and mean % hatched brood survival to day 9 of 94.6% (n=78) for lowland and 88.8% (n=8) for upland nests. However, some lowland nests with clutch size data but without hatching data had reductions to day 9 survival of 70.6% (n=36), and for corresponding upland nests of 67.3% (n=9). Mean brood nestling mass in all cases was >38g and comparable with values obtained in other studies (O'Halloran *et al.* 1992; Tyler and Ormerod 1994). Mawby (1961) found lower hatching rates for dippers at Sedbergh following adverse weather, suggesting this led to egg infertility. Since hatching success for known nests is higher than 90%, and assuming this reflects hatching outcomes generally, the clutch to day 9 reductions may be due to some females having reduced egg fertility because of poorer individual quality or body condition or because of reduced habitat quality resulting from adverse ecological conditions. Alternatively, in addition to egg infertility, brood reduction may occur. Hatching asynchrony is possible in dippers (Rankin and Rankin 1940; Tyler and Ormerod 1994), and that may produce intra-brood hierarchies and nestlings of marginal size or quality relative to siblings (Stokland and Amundsen 1988; Viñuela 1996), and may be an adaptive response to follow unpredictable food supplies (Pijanowski 1992). Declining food availability could result in the loss of inferior quality nestlings by passive starvation through sibling competition (Mock 1994; Ricklefs 2002), sibling infanticide (Godfray and Harper 1990; Mock *et al.* 1990) or parental action (Zieliński 2002; Moreno 2012), and compounded by rain and low temperatures (Reynolds 1996; Hong *et al.* 2018a). Brood reduction has been observed in brown dippers (*Cinclus pallasii*) in nests with variation in nestling body size located on territories with low food availability, and the weakest nestlings were lost (Hong *et al.* 2018a). This brood reduction may safeguard remaining siblings and parental fitness but, in its absence, provide a reproductive dividend when food is plentiful (Forbes 1991; Forbes and Mock 1996; Forbes *et al.* 2001, 2002), and a ‘reproductive insurance policy’ in the event of premature nestling mortality (Mock and Forbes 1995; Zieliński 2002).

4.4 Climate and weather

Large scale climate processes, particularly winter North Atlantic Oscillation (NAO) index values, are a significant influence on population ecology (Hallett *et al.* 2004), and whilst localised variations in weather may be a better predictor for local populations, these tend to reflect general regional trends (Nilsson *et al.* 2011a). Possible negative effects of high NAO index values, warming sea temperatures and milder but wetter winters in the UK include reduced food availability and breeding success for some species and asynchrony of summer migrant arrival and resource phenology (Leech *et al.* 2004). Changes to climate patterns that have become apparent since the mid-1970s suggest a time-lag effect on local conditions affecting timing of breeding and food abundance in subsequent years (Hinsley *et al.* 2016). In this study, interannual variation in the timing of lay date was most likely related to adverse weather conditions delaying egg laying, which by contrast may be advanced in more benign conditions (Price and Bock 1983; Tyler and Ormerod 1985; Tyler and Ormerod 1994). Interannual variations in invertebrate abundance may act as a cue to mediate initiation of breeding, parental investment and possibly brood reduction.

Durance and Ormerod (2007) obtained results for upland stream invertebrates in Wales that supported hypotheses that the NAO and climate change had identifiable ecological effects, and that aquatic invertebrates vary with winter climate. High positive NAO indices and warmer, wetter phases lowered between-year similarities in stream benthos, and circumneutral streams with projected +1 to +3°C temperature changes were shown to have potential reductions of abundance of 21% in macroinvertbrate populations for each 1°C rise in temperature (Durance and Ormerod 2007). These predictions illustrate the sensitivity and vulnerability of upland stream habitats to relatively small rises in temperature.

An increase in the frequency of extreme weather events is predicted with climate change (Beniston *et al.* 2007; Woodward *et al.* 2016), and flooding could prevent dipper species accessing foraging areas, eliciting changes in feeding behaviour (Taylor and O'Halloran 2001; D'Amico and Hémery 2007; Chiu et al. 2013). Additionally, flooding can potentially alter the diversity and abundance of benthic prey assemblages (Da Prato 1981; O'Halloran *et al.* 1990; Feeley *et al.* 2012; Chiu et al. 2013; Woodward *et al.* 2015; Sánchez *et al.* 2017; Hong *et al.* 2018b). Increased late winter and early spring rainfall could produce high flow conditions, which may prevent or be energetically constraining for foraging in riffles, particularly for caddisfly, which are an important component in nestling diet (Ormerod 1985a; Tyler and

Ormerod 1994; Crooks *et al.* 2009; Sayers *et al.* 2015). Shifts in diet and foraging behaviour were observed in Irish dippers during higher water levels, and with some climate change models predicting higher precipitation or altered rainfall patterns and producing increased risk of spates and floods, this could affect the diet, survival and productivity of dippers (Taylor and O'Halloran 2001; Sæther *et al.* 2004; Nillson *et al* 2011a). Additionally, higher flows threaten dipper nests located low down on riverbanks or on walls and bridges, and several such nests have been lost by flooding over the study period (S. P. Sharp unpublished data).

A study of Norwegian dippers found that whilst there is uncertainty about the impacts of climate change, it could produce milder winters and possible population growth as a result of potentially greater access to foraging, quicker prey growth rates, cueing for earlier lay dates and enhanced winter survival (Sæther *et al.* 2004; Nillson *et al.* 2011a). Alternatively, extremes of weather producing harsh winters may cause repeated severe population declines impacting population dynamics and territory occupation (McPeek *et al.* 2001; Beniston *et al.* 2007; Nilsson *et al.* 2011a). Extreme winter flooding episodes were found to affect some dippers in northern Iberia, with lower survival in the subsequent breeding season, but the impact at the population level appeared to be weak (Sánchez *et al.* 2017). Resident dippers display winter territoriality (Crowther *et al.* 2018), and resident American dippers have higher site fidelity and defend winter territories, but migrants may be more able to move to better habitat conditions during high flow periods (Whitehorne 2010).

4.5 Further work

Some experienced adults return annually to breed at upland sites whereas inexperienced first years can establish and hold lowland territories. Since little is known of the factors that drive migratory tendency in dippers, monitoring of individuals within winter lowland populations for physical condition, hormonal levels, territorial encounters and responses could provide insights into the causes, timing and modes of migration to high altitude nests (Schwabl 1992; Landys *et* *al.* 2010). The use of telemetry could provide detailed information on individuals' foraging and migratory behaviours, and an overview of tracking systems for birds is provided by López-López (2016). The use of genetic markers could provide roles in determining if there is a genetic basis to migratory behaviour (Garant and Kruuk 2005; Wink 2006; Ellegren and Sheldon 2008), and in investigating the effects of polygyny versus monogamy (Hartley 1991; Johnson and Burley 1998; Kvarnemo 2018), and to determine if these have fitness consequences for resident and migrant dippers. Studies of the American dipper found no fitness benefit in becoming a migrant and negative effects on productivity and offspring quality (Gillis *et al.* 2008; Mackas *et al*. 2010; Green 2015), but in this study and a previous study of (white-throated) dippers (Logie 1998), there was no impact of altitude on reproductive success. A longer-term study is now required to investigate post-fledging and adult survival and lifetime reproductive success to give a more complete picture of the fitness consequences of migratory status, particularly when associated with detailed measures of habitat quality. Replicating the work on brown dippers by Chen and Wang (2009) and Hong *et al*. (2018a) would quantify aquatic invertebrate composition and abundance in riffles, and establish total food availability and territory size as a measure of habitat quality for dippers at different elevations. Detailed observations of foraging strategies of residents and migrants including flight distances to feeding sites, prey composition and loads, and handling costs, may provide evidence for the effects of habitat quality and parental effort on breeding success. Furthermore, examining temporal variation in stream prey composition and relating this to nestling diet by faecal examination, stable-isotope analysis or DNA barcoding (Taylor and Halloran 1997; Fox and Bearhop 2008; Rytkönen *et al.* 2019) would help to determine responses in nestling growth, development and breeding success at increasing altitudes and with varying conditions influenced by climate change. If the studies of brown dippers by Chen and Wang (2009) and Hong *et al*. (2018a) hold true for white-throated dippers, then territory size is determined by total high-density prey riffle area.

Competition for nest sites has been suggested as the cause of migratory behaviour in dipper species (Price and Bock 1983; Tyler and Ormerod 1994; Mackas *et al.* 2010). Dipper nests constructed in tree branches are rare (Tyler and Ormerod 1994), as they are likely to be conspicuous to predators, but one such nest was made during the study in 2017 (shown in Figure 4.2), suggesting that nest-site availability and not territory size may limit lowland breeding densities.

Figure 4.2. Dipper nest in branches above the River Lune in Lune Island territory 2017. (Photograph by Richard Wilkinson).

Experimentally increasing nesting sites with artificial habitat features or nest boxes in territories at all elevations would help to test this theory. Whilst clutch size did not appear to show any variation across elevations, this suggests agreement with the individual optimisation hypothesis that females lay clutch sizes that maximise offspring recruitment based on parents' abilities to produce eggs and care for young, and food availability in the territory provision of food (Perrins and Moss 1975; Högstedt 1980; Coulson and Porter 1985). Since the number of fledglings also appears to be the same across elevations, brood manipulation experiments may reveal if pairs at any elevation are approaching their maximum capacity to raise offspring at equitable developmental rates or if there is residual capacity for more offspring production. This has fitness consequences for the cost of reproduction (Williams 1966; Charnov and Krebs 1974; Harshman and Zera 2007), and influences trade-offs between current and future reproduction and survival. This, in turn, has implications for lifetime reproductive success. Brood manipulation experiments could illustrate future effects of changing environmental conditions at different altitudes on population dynamics.

Another area that requires investigation to determine the lifetime fitness benefits of being a resident or migrant is the consequences of losses to predation and flooding. Climate change is projected to increase weather variability in the UK and to affect river and stream flow regimes (Watts *et al.* 2015). Weather data from the Met Office and National River Authority flow measurements could be used to investigate if raised water levels and flood events affect nest survival or disrupt foraging activity and brood provisioning, and consequently, nestling development (Chiu *et al.* 2008, 2013; Hong *et al.* 2016). The effects of predator threat could be simulated by the use of models or by using playback of the calls of known predators to determine the short-term effects upon parental care, nestling development, fledging and consequences of predator-induced dispersal (Yoder *et al.* 2004; Coslovsky and Richner 2011; Chiavacci *et al.* 2015; Goullaud *et al.* 2018; Payo-Payo *et al.* 2018).

4.6 Conservation challenges

Despite recovery from acidification by atmospheric pollution (Battarbee *et al.* 2014), dipper populations in England and in the UK as a whole have declined between 1975 and 2016 (Eaton *et al.* 2015; Woodward *et al.* 2018). There is still work to do to lower chemical contamination of rivers and improve their ecological status (Morrissey *et al.* 2013, 2014; Environment Agency 2018) and water abstraction and construction may alter flow regimes, but the greatest potential threat to dippers and other wetland bird species is probably from climate change (Crick 2004; Wormworth and Mallon 2006; Erwin 2008; Carey 2009). Lay dates for dippers have advanced by more than 10 days over the last fifty years (Woodward *et al*. 2018), and little is known of climate induced phenology effects on aquatic prey taxa. For poorly known dipper populations breeding on higher altitude streams under harsher ecological conditions, anthropogenic effects including climate change may be more pronounced and might require novel interventions to counter (Wilby *et al.* 2010; Thomas *et al.* 2015, 2016; Bussi *et al.* 2018; Riley *et al.* 2018) .

Future responses of river bird communities to floods and droughts in climate change models should take account of the timing, frequency and magnitude of high and low river flows. A projected decrease in dippers by the end of the 21st century is driven by a decrease in daily flow magnitude and low flow rate variability (Royan *et al.* 2015). Additionally, rapidly decreasing habitat suitability in western Britain illustrates a possible mechanism by which climate change may mediate range shifts in birds and other riverine biota (Royan *et al.* 2013, 2015). Hayhow *et al.* (2017) highlight trends consistent with climate change bringing earlier arriving migrants, advanced lay dates, shifts in abundance and distribution of breeding and overwintering, and further increased pressure on declining species. Birds with low fertility and limited dispersal may not be able to cope with the effects of climate change by shifting their ranges and this is likely to be exacerbated by high annual mortality rates. However, species may adapt to climate affected local conditions by microevolution or phenotypic plasticity processes (Pelletier *et al.* 2009; Jenouvrier and Visser 2011; Jenouvrier 2013). Furthermore, differing interspecific and intraspecific adaptive responses to climate change strengthen the need for continuing autecological studies (Parmesan and Yohe 2003; Balbontín *et al.* 2009) in addition to those of populations, communities and ecosystems at all spatial and temporal scales to understand the responses to environmental change. Proactive measures to ameliorate the threats to wetland birds species must provide long-term sustainable environmental management alongside current land use and projected socioeconomic demand, and inform policy decision making to address mismatches between short- and long-term demands on the environment (Cardador *et al.* 2015; Durance *et al.* 2016; Ormerod and Ray 2016).

This investigation in the eastern uplands of Cumbria provides an insight into the life-history strategies of a dipper population with partial altitudinal migration. It is through the monitoring of such populations and the use of long-term data that the population dynamics of species can be examined against variations in environmental conditions, particularly climate change (Larsen *et al.* 2018; Van Looy *et al.* 2019). An understanding of the effects of such change at individual, population, community and habitat levels are important steps in the search for providing mitigating measures for conservation (Vaughan *et al.* 2007; Reid *et al.* 2018b). A forward to *Silent Summer: The State of Wildlife in Britain and Ireland* (Maclean 2010) is apposite:

> ‘How do you know which way to go if you do not know where you are? And how can you plan for the future if you do not know the state of the present? If we are concerned about the environmental future of Britain and Ireland, then we must know as much as possible about its present condition’.
>
> Sir David Attenborough 2010

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Appendix

Appendix

Orientation of study site maps showing location of dipper territories

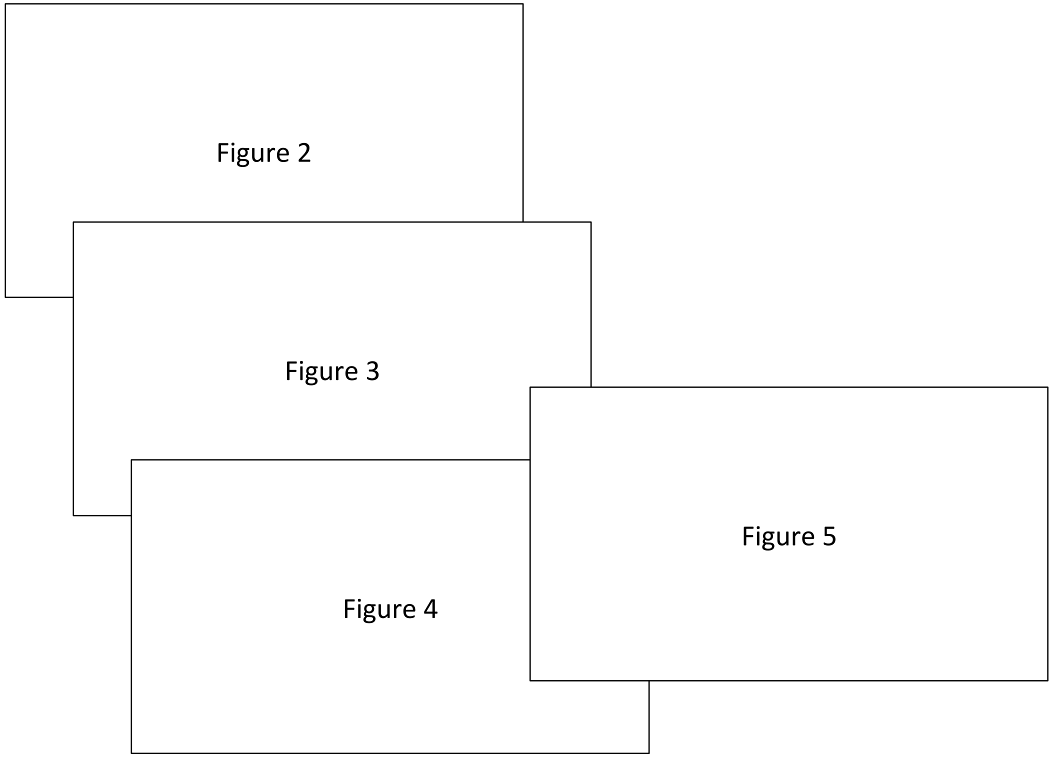

Figure 1. Study site dipper territory location sheets orientation.

Sedbergh area dipper territory maps legends access

OS 1:50 000 scale map legends available at:

https://www.ordnancesurvey.co.uk/docs/legends/50k-raster-legend.pdf

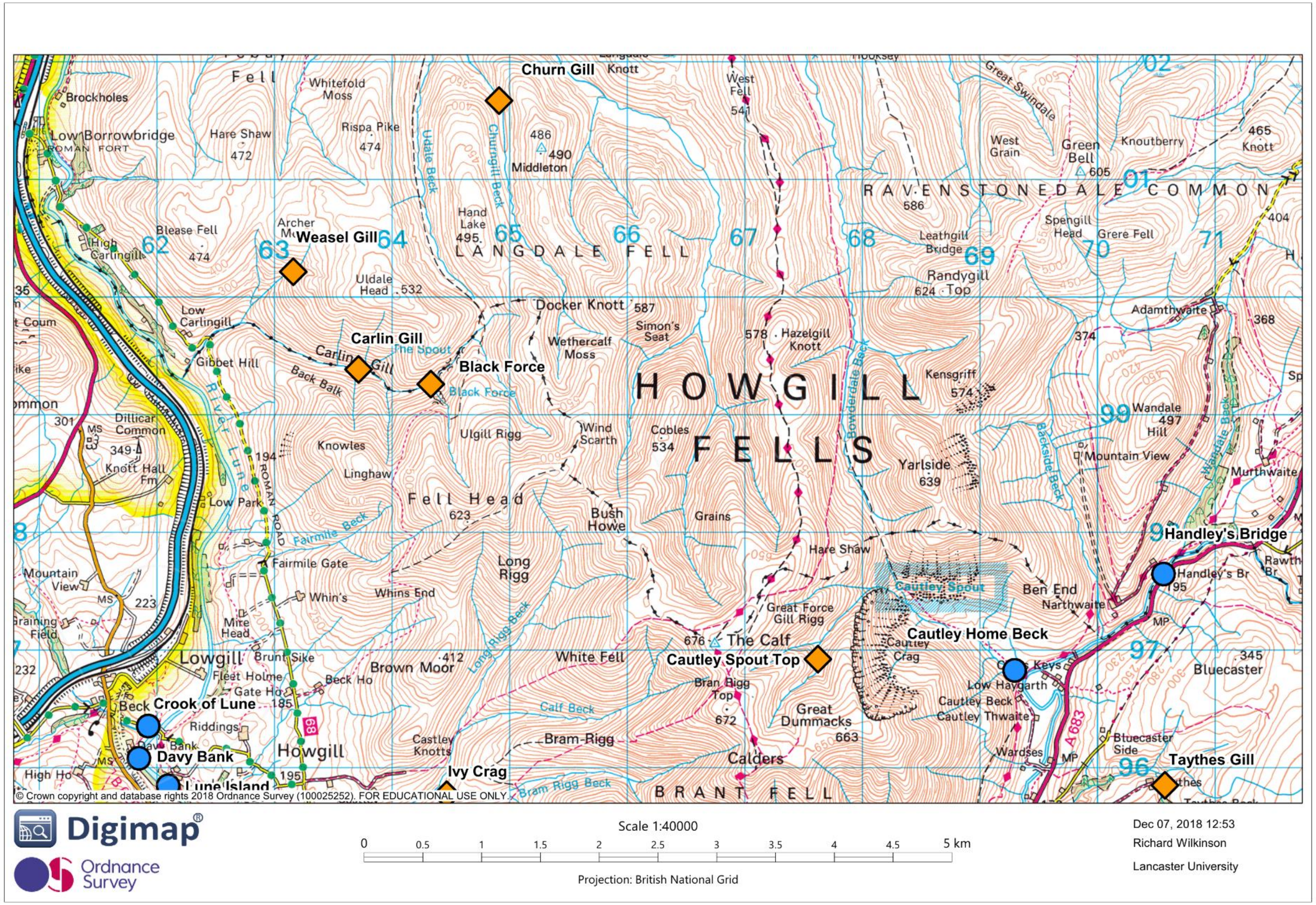

Figure 2. Study site dipper territory locations. Lowland territories ● ; upland territories ◆ . (Digimap University of Edinburgh at: https://digimap.edina.ac.uk/).

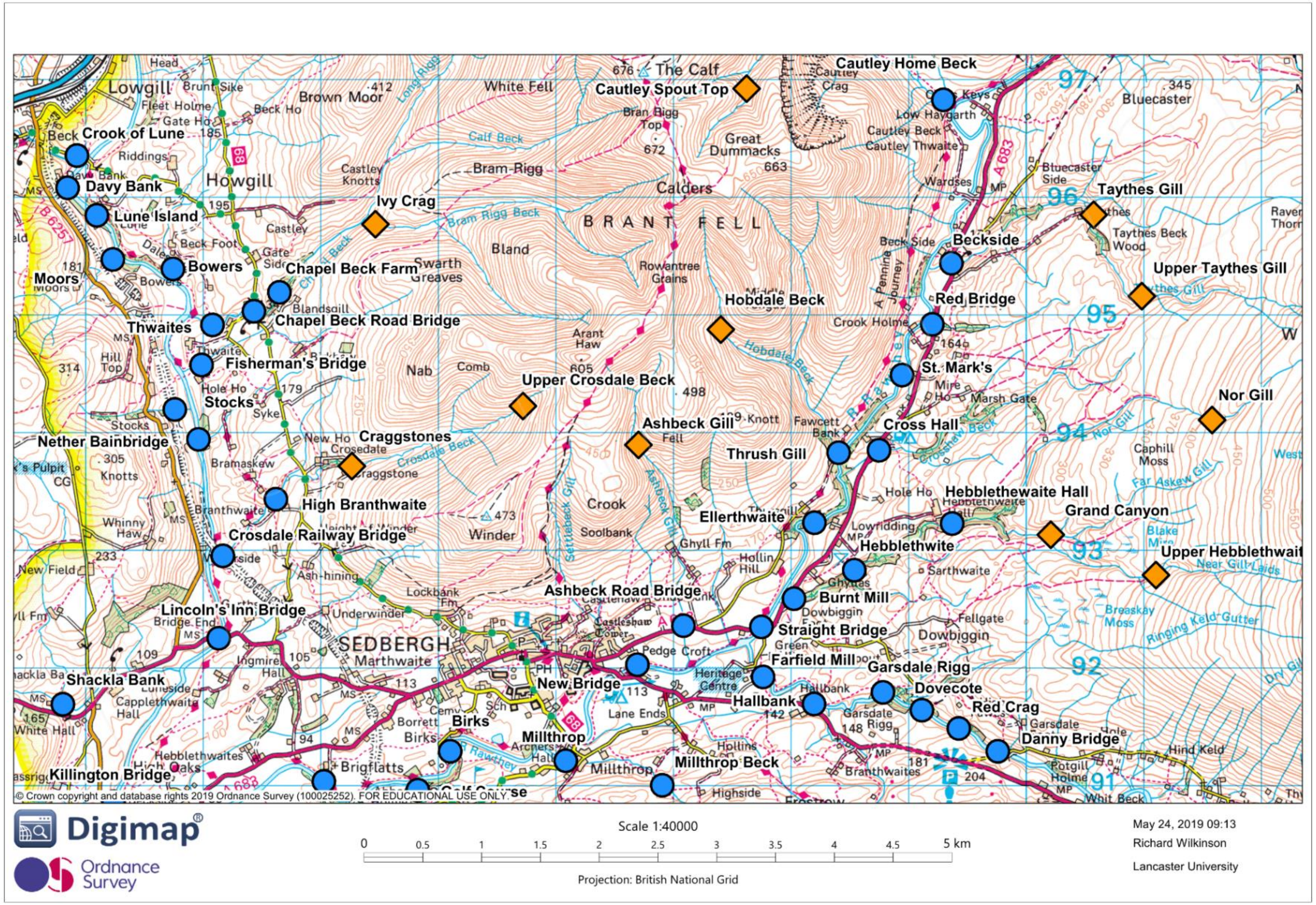

Figure 3. Study site dipper territory locations. Lowland territories ● ; upland territories ◆ .
(Digimap University of Edinburgh at: https://digimap.edina.ac.uk/).

Figure 4. Study site dipper territory locations. Lowland territories ● ; upland territories ◆ .
(Digimap University of Edinburgh at: https://digimap.edina.ac.uk/).

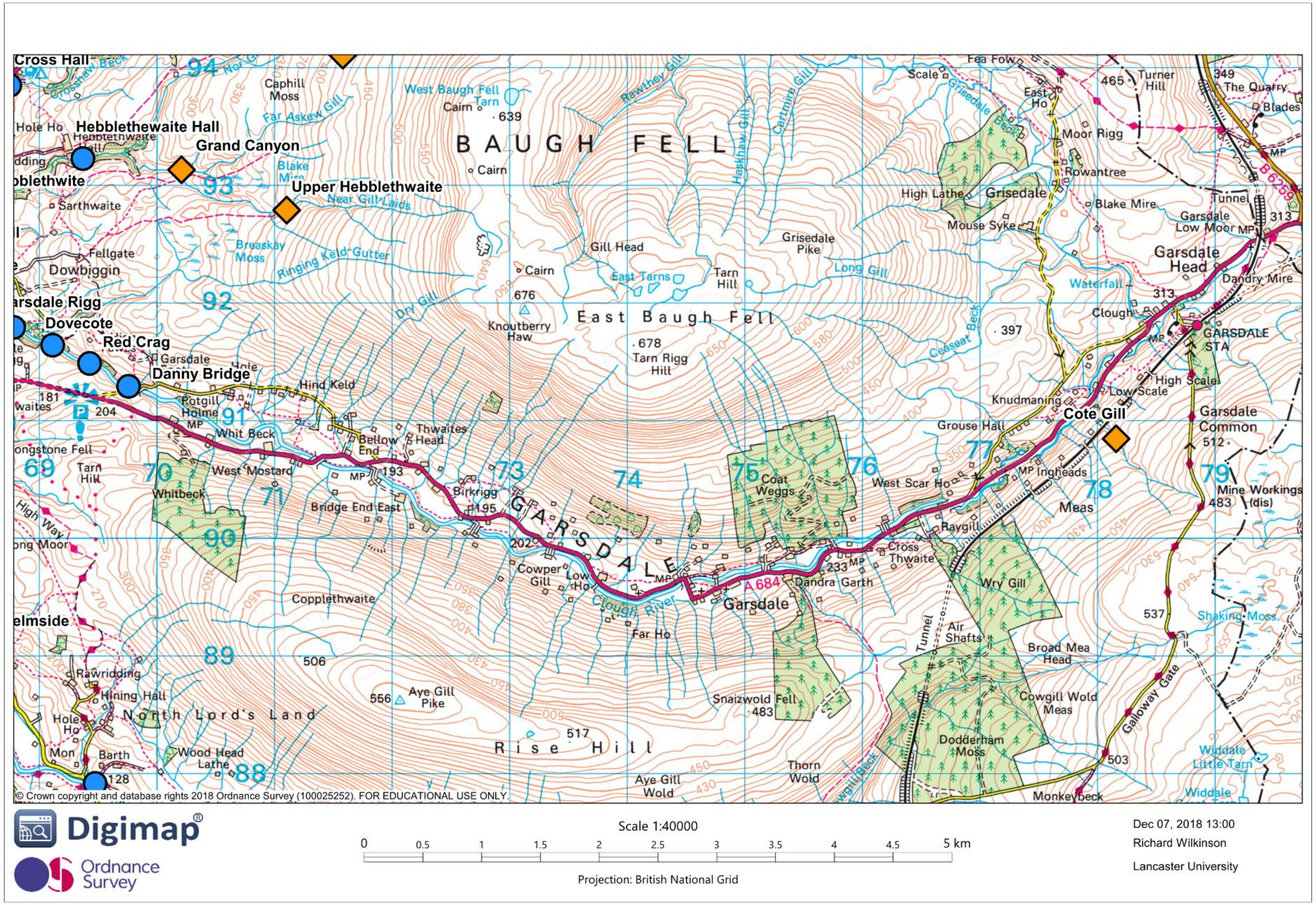

Figure 5. Study site dipper territory locations. Lowland territories ● ; upland territories ◆ .
(Digimap University of Edinburgh at: https://digimap.edina.ac.uk/).