Sex-biased dispersal, post-fledging care and juvenile movements in the white-throated dipper

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Abstract

Dispersal is a crucial life history trait which has profound consequences for individual fitness and population dynamics. Yet, our understanding of the spatial and temporal processes of dispersal remains poorly understood, largely due to the logistic difficulties of following and monitoring wide-ranging individuals. White-throated dippers are specialised aquatic passerines which are well-established as an important indicator of river and stream water quality, and they provide an ideal model system for studying dispersal due to their linear territories. However, little is known about the factors that underpin variation in natal dispersal distance. Furthermore, as with many passerines, behaviour during the post-fledging period has rarely been studied despite the likely influence on dispersal. Here, these issues are investigated using a long-term study population of dippers in the UK. In Chapter 2, the impact of early life conditions on natal dispersal is investigated, including the timing of breeding, brood size, population density, and body condition. The analyses also accounted for sex, a well-known determinant of dispersal distance in birds. Indeed, as with many species, sex was the most important predictor of dispersal distance in dippers, with females generally travelling further than males. However, there also appears to be a weak effect of condition, suggesting that individuals in better condition disperse shorter distances. This may reflect the benefits to settling on territories near to the natal area, including familiarity with nesting and feeding sites. No other early life effects were detected. In Chapter 3, observations during the 2021 breeding season were used to measure provisioning rates and track movements of juvenile dippers during the post-fledging period. Brood division appeared to be widespread within this population, and comparisons of mean feeding rates suggests that males contributed more to feeding the fledglings than females. Post-fledging provisioning rates were generally higher than nestling provisioning rates. On average, juveniles were first observed outside of their natal territory 30 days after fledging, but some had left as young as nine days old. Soon after leaving the natal territory, juveniles were highly mobile and able to travel relatively long distances; many individuals were observed together with birds from other broods. Together, these observations provide some of the first descriptions of behaviour during the post-fledging period in this species, and the implications for dispersal are discussed. In the final chapter, the key messages of the thesis are reviewed alongside avenues for future research, with an emphasis on the need to further study the early life determinants of dispersal and behaviour during the transience stage. Combining long-term studies of marked individuals with advanced tracking technologies offer perhaps the best opportunities.

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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.

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Chapter 1. General Introduction

Dispersal is a key process in ecology and evolution which influences the spatial and temporal distribution of populations, and has profound consequences for demography, genetic diversity and individual fitness (Greenwood and Harvey, 1982; Clobert, 2012). Furthermore, dispersal plays a key role in a species' ability to adapt to, and persist alongside, environmental change (Clobert et al., 2009; Driscoll et al., 2014). The study of dispersal is therefore of major current interest considering present-day threats to biodiversity from chief drivers such as climate change, habitat fragmentation and pollution (Clobert et al., 2009; Elliot et al., 2014). Advancing our knowledge of the behavioural and eco-evolutionary processes of dispersal will not only improve our ability to develop reliable forecasting models, but it will also aid in implementing conservation initiatives such as habitat corridors, both of which are critical for the management and conservation of biodiversity (Dobson, 2013; Driscoll et al., 2014; Bonte and Dahirel, 2017).

Dispersal is a complex process which can be strongly affected by environmental factors, for example habitat quality (Rémy et al., 2011) and density dependence (Matthysen, 2005); social pressures including sibling rivalry (Cote and Clobert, 2010; Bebbington et al., 2017) and inbreeding avoidance (Pusey, 1987; Perrin and Goudet, 2001); and individual phenotypic traits, such as size and condition (Delgado et al., 2010; Gyllenberg et al., 2011; Hewison et al., 2021). Vast amounts of research has attempted to describe and disentangle these influences, but many studies are problematic, largely due to the logistic issues of monitoring wild populations without the use of advanced tracking technologies (Sharp et al., 2008a; Suh et al., 2020). Despite a wealth of knowledge, many aspects of dispersal behaviour remain poorly understood, and empirical studies of readily observable species often include systematic bias due to the restricted extent of the study sites (Baker et al., 1995; Koenig et al., 1996; Sharp et al., 2008a). Individuals that disperse further are harder to follow, and those that disperse outside of finite study areas are usually indistinguishable from deceased individuals (Koenig et al., 1996; Clobert, 2012).

Two major forms of dispersal are typically recognised. 'Natal dispersal' refers to the movement from the birthplace to the site of first reproduction (Greenwood and Harvey, 1982; Clobert, 2012); 'breeding dispersal' describes the movement that occurs between breeding sites in subsequent seasons (Paradis et al., 1998). The former, which is the focus of this study and hereafter will be referred to as simply 'dispersal', tends to involve greater distances and has a major impact on individual fitness, population structure and dynamics (Clobert, 2012). There is an accumulation of evidence to support the idea that dispersal is a non-random process,

comprising three distinct, interrelated stages: departure or emigration from the natal site; transience, the movement that occurs between leaving the natal site and reaching a new site; and settlement in a new site after the completion of natal dispersal, or immigration (Clobert et al.; Bonte et al., 2012). Individuals vary in when they leave the natal site, how they move through the environment during transience, and when and where they finally decide to settle. Identifying the factors which affect behaviour at each of these stages has become an increasingly important focus of wildlife research (Maag et al., 2018; Benoit et al., 2020; Engler and Krone, 2021).

One of the most widely studied topics in research on dispersal is the causes and consequences of sex-specific variation, both in the propensity to disperse and the distance moved. In many species, there are clear differences in dispersal between the sexes, with one sex dispersing further or more frequently than the other, including well-established patterns of predominantly male-biased dispersal in mammals and female-biased dispersal in birds (Greenwood, 1980; Clarke et al., 1997; Dobson, 2013; Trochet et al., 2016). Several hypotheses have emerged to explain these contrasting patterns, which suggest that avoidance of inbreeding and intrasexual competition act as some of the proximate drivers (Greenwood, 1980; Clobert et al., 2004; Clobert, 2012; Dobson, 2013). The *mating systems hypothesis* proposes that sex-biased dispersal occurs because of the difference between resource-defence and local-mate competition mating systems. In a resource-defence system, the territorial gender should benefit from increased philopatry and territory defence (Greenwood, 1980). For example, it is thought that in monogamous species such as many birds, it is typically the males that defend territories, and the females disperse to assess and chose a suitable breeding opportunity (Clarke et al., 1997). In local-mate competition systems, which are prevalent in polygynous species, intense intrasexual competition for access to limited mates is thought to influence dispersal propensity and, as such, male-biased dispersal is expected in mammals (Dobson, 2013). Finally, the *inbreeding avoidance hypothesis* states that individuals should disperse to move away from kin and reduce the risks of inbreeding (Pusey, 1987). However, the significance of inbreeding avoidance as a driver of sex-biased dispersal remains of considerable debate, as in the vast majority of species both sexes show some degree of dispersal, and as such inbreeding pressure should be the same across genders (Perrin and Goudet, 2001; Clobert et al., 2004; Guillaume and Perrin, 2009).

While it is widely accepted that mating systems play a role in influencing the direction of sex-biased dispersal, an array of other environmental, social, and individual factors are central to dispersal decision making. These relationships are complex and often challenging to disentangle. For example, in many species, individuals will disperse from densely populated habitats to avoid competition and perhaps to reduce inbreeding (Greenwood and Harvey,

1982; Clarke et al., 1997; Dobson, 2013; Trochet et al., 2016). In contrast, negative-density dependence, in which high population densities lead to reduced dispersal, is also known to occur, likely as a means to avoid aggressive encounters outside of the natal territory (Ims and Andreassen, 2005; Matthysen, 2005). A wealth of empirical studies have demonstrated condition-dependence in dispersal (Gyllenberg et al., 2008; Bonte and de la Pena, 2009; Clobert, 2012), including in mammals (Debeffe et al., 2012; Elliot et al., 2014), birds (Barbraud et al., 2003; Azpillaga et al., 2018), reptiles (Cote and Clobert, 2010; Clobert, 2012), insects (Bonte, 2009) and plants (Gyllenberg et al., 2008). Again, however, the nature of these effects varies. Dispersal is energetically expensive and exploratory movements are potentially costly, therefore larger, stronger or healthier individuals often have a greater dispersal propensity and capacity to withstand these costs (Barbraud et al., 2003; Debeffe et al., 2012). In contrast, there are benefits to staying local, and therefore quality individuals can compete for nearby vacancies (Hanski et al., 1991; Suh et al., 2020). Individuals should optimise dispersal decision making, depending on the varying costs and benefits of environmental conditions and phenotypic characteristics (Clobert et al., 2009; Matthysen, 2012), but further research is needed to understand these processes.

Costs and benefits of dispersal

Understanding how the complex interaction between an individual and its environment drives variation in the timing of departure from its natal area, how an individual moves through the landscape, and where it finally settles, will aid in resolving the costs and benefits of dispersal, and ultimately, how populations might respond to environmental change. Selection will favour those individuals that are able to minimise the costs associated with each stage of dispersal (Maag et al., 2019). For example, in most vertebrates, juveniles of both sexes leave the natal territory soon after achieving independence but the precise timing varies according to conditions (Barbraud et al., 2003; Hewison et al., 2021). Similarly, hostile environments, habitat patch connectivity, unsuitable or distant habitats, as well as the energetic costs associated with travelling and the risks of entering unfamiliar territories, all might hinder an individual during the transience and settlement stages of dispersal (Stamps, 2001; Cote and Clobert, 2010; Bonte et al., 2012). However, most research has focussed on the net movement distances and patterns of settlement, and few researchers have investigated variation in the timing of departure from the natal area or behaviour during the transience stage (Koenig et al., 1996; Conradt et al., 2003; Elliot et al., 2014).

Timing of departure from the natal area

Variation in the timing of departure is associated with different types of costs and benefits. For example, higher population density and increased competition for breeding opportunities might select for individuals to disperse sooner or further to avoid overcrowding (Matthysen, 2005; Baines et al., 2020). Individuals that choose to disperse earlier might benefit from being the first to seek opportunities elsewhere and exploiting the best available breeding sites, whilst avoiding the costs associated with staying in the natal territory, such as kin competition (Bowler and Benton, 2005; Ronce, 2007). For example, it has been shown that eagle owls (*Bubo bubo*) which disperse earlier choose to travel shorter distances and obtain nearer breeding territories to reduce the costs encountered along the way (Delgado et al., 2010). Furthermore, in the cooperatively breeding red-cockaded woodpecker (*Picoides borealis*), individuals switch between a combination of short distance 'territory building' and long distance 'jump dispersal' strategies in order to overcome limited dispersal opportunities in the natal range, and disperse further to find available opportunities (Kesler et al., 2010). In contrast, other studies have proposed that higher population densities may favour philopatry and can delay dispersal to reduce the probability of aggressive encounters with conspecifics in a saturated environment (Matthysen, 2005). It is well known that in many cooperatively breeding species, individuals delay dispersal due to the benefits of philopatry, costs of dispersal, or constraints on independent reproduction (Ekman et al., 2004; Hatchwell, 2009), but even in non-cooperative species, individuals may benefit from delaying dispersal. In the socially monogamous brown thornbill *(Acanthiza pusilla),* for example, males which delay dispersal have higher survival and are more likely to obtain a breeding territory than those dispersing as soon as reaching independence (Green and Cockburn, 2001). However, for obligate dispersers, remaining in the natal territory might not always be an option because young are often pushed out by parents (Clobert, 2012).

Transience

Transience, the process that takes place between departure from the natal area and settlement at the breeding site, is the least well known aspect of dispersal (Koenig et al., 1996; Conradt et al., 2003; Elliot et al., 2014). This is partly because it is difficult to track and observe individuals moving through the landscape, but also due to the high mortality rates of juveniles (Anders et al., 1997; Cox et al., 2014). Yet, an individual's behaviour during the transient phase of dispersal might aid in its ability to overcome the costs incurred and impact the likelihood of obtaining a suitable breeding opportunity. For example, time and energetic costs of increased

locomotor activity and increased risk of predation might influence when and how far individuals travel, whether they make return visits to the natal site, or whether they engage in direct dispersal trajectories to the nearest vacancy (Stamps et al., 2005; Benoit et al., 2020). In several species, the transient phase has been demonstrated to be a non-random process (Clobert et al., 2004; Delgado et al., 2009; Elliot et al., 2014). For example, lions (*Panthera leo*) display sequential movement patterns, travelling in intentionally direct trajectories in search of a new territory (Elliot et al., 2014). Experimental evidence has shown that root voles (*Microtus oeconomus*) travel in fast, straight-lined movements between patches using habitat corridors (Andreassen et al., 1998). Nevertheless, investigations of individual variation in transient behaviour are few and far between.

Condition-dependence

There is good empirical evidence to suggest that dispersal costs can be overcome by an individual's body condition and behaviour (Cote and Clobert, 2010; Delgado et al., 2010; Debeffe et al., 2012; Hewison et al., 2021). Increased brood or litter size and greater competition between siblings for parental resources can lead to asymmetrical development within the young (Bebbington et al., 2017). As such, size and condition cues can be important for triggering dispersal decisions and may result in larger or better-conditioned individuals to disperse earlier and have better success with finding and defending territories and mates (Edelman, 2011). For example, larger male guppies (*Poecilia reticulata*) disperse further, likely as a result of being stronger swimmers and having less predation pressure from gape-limited predators (Borges et al., 2021). Contrastingly, stronger more competitively able individuals might opt for staying local, forcing the weaker subordinates to disperse (Gyllenberg et al., 2011; Clobert, 2012). In the Florida scrub-jay (*Aphelocoma coerulescens*), lower ranking females are more likely to disperse further, suggesting that intragroup competition influences dispersal distance within this cooperatively breeding species (Suh et al., 2020).

In summary, an individual's condition can have major influences on the timing of departure from the natal area and behaviour during the transience stage. Parental care, interactions with conspecifics, foraging behaviour and juvenile movements all influence condition and can therefore aid an individual's ability to overcome environmental threats such as predation and limited resources (Grüebler and Naef-Daenzer, 2008a; Naef-Daenzer and Grüebler, 2016). Integrating these ideas in future research is key to a more holistic understanding of dispersal patterns and their consequences.

The post-fledging period

Birds are perhaps the most commonly used model system for understanding dispersal. The post-fledging period of passerines includes departure from the natal site and the early stages of transience (Vitz and Rodewald, 2010; Ausprey and Rodewald, 2013), and therefore can shape the nature and outcome of dispersal. Parental care, juvenile movements and behaviour during this period can impact survival rates and have important consequences at the individual and population levels (Anders et al., 1998; Naef-Daenzer and Grüebler, 2016). In many species, fledglings continue to receive parental care after they have left the nest (Tarwater and Brawn, 2010). The level and extent of parental care can influence an individual's condition and therefore timing of departure from the natal territory, and movements during the transience stage (Naef-Daenzer et al., 2001; Grüebler and Naef-Daenzer, 2008a). Early movements may vary considerably between individuals, and in some species juveniles disperse in groups (Sharp et al., 2008b; Elliot et al., 2014). However, the post-fledging period is perhaps the least well studied life history stage in birds, mainly due to the challenges associated with tracking and monitoring individuals as they move through the environment (Cox et al., 2014; Naef-Daenzer and Grüebler, 2016). For many species, even basic descriptions of post-fledging behaviour are completely lacking.

Study Species

In this study, I investigated natal dispersal and the post-fledging period in the white-throated dipper (*Cinclus cinclus;* hereafter simply 'dipper'). The dipper is a widespread aquatic passerine which lives almost exclusively along fast-flowing rivers and streams (Tyler et al., 1990; Tyler and Ormerod, 1994). They are superbly adapted to this riverine lifestyle and are unique among songbirds in their ability to dive and swim below the surface to feed on freshwater invertebrates (Tyler and Ormerod, 1994). This establishes them as an important indicator species of water quality; they are highly sensitive to water acidity (Ormerod et al., 1991; Tyler and Ormerod, 1994) and known to bioaccumulate persistent pollutants in their eggs and other tissues (Ormerod et al., 2000; Morrissey et al., 2004; D'Souza et al., 2020). Here, the dipper provides an ideal model system for studying dispersal in a wild population (Fig. 1). They are easy to observe and survey, and they establish linear territories along watercourses, allowing for relatively simple monitoring, tracking and measuring of territory length (Tyler and Ormerod, 1994; Crowther et al., 2018).

Figure 1. Colour ringed adult dipper.

Breeding Ecology

Pairs of dippers establish territories along the watercourse, usually in upland areas up to 2500m, and will make use of natural crevices and manmade structures to build nests close to the water's edge (Tyler and Ormerod, 1994). Many birds will strongly defend a length of river or stream throughout the year and they often remain faithful to nest sites over multiple seasons (Tyler and Ormerod, 1994; Crowther et al., 2018). The rivers they inhabit are usually clean, fast-flowing, and full of shallow riffles which support the invertebrate prey upon which dippers depend; predominantly mayfly (Ephemeroptera), caddisfly (Trichoptera) and stonefly (Plecoptera) larvae, although small fish and other macroinvertebrates are sometimes taken (Tyler and Ormerod, 1994).

Dippers are typically monogamous with high mate fidelity, although sometimes polygamous males pair with two or even three females, often in adjacent territories (Tyler and Ormerod, 1994). In the UK, laying usually begins between late February and mid-March, and first clutches of up to six eggs (usually four or five) are laid asynchronously, one per day. Once the final egg has been laid, the female begins incubation and this lasts for approximately 16 days, giving rise to synchronous hatching (Shaw, 1978; Tyler and Ormerod, 1994). Both parents feed the nestlings until they are ready to fledge at 20-24 days old (Shaw, 1978). When they have left the nest, fledglings continue to depend on parental provisioning and will remain within the natal territory for between one and two weeks until they have reached independence, or

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are driven out of the territory by the parents (Tyler and Ormerod, 1994; Yoerg, 1998). At this point, some of the pairs that started breeding earlier in the season will attempt to raise a second brood.

Aims

In this study, I investigate how early life conditions impact patterns of dispersal in dippers, and provide some of the first observations of behaviour during the post-fledging period in this species. Analyses of a long-term individual-based dataset collected between 2013 and 2021 are combined with field observations from the 2021 post-fledging period. In dippers, juveniles take on different foraging strategies compared to adults, with many relying heavily on small prey items, although some individuals do take larger prey items and this may result in independence being reached sooner (Yoerg, 1998). Upon reaching independence, juveniles are thought to disperse randomly, upstream or downstream, rarely further than 10km from the natal site, and natal dispersal is thought to be completed by the autumn (Tyler et al., 1990). With the exception of altitudinal migrants, which abandon their upland breeding territories in the winter months (Tyler and Ormerod, 1994), most adults remain sedentary and, as such, it is believed that juveniles must disperse to find a vacant territory depending on adult mortality (Tyler et al., 1990). In a Welsh population of dippers, sex-biased dispersal has been suggested to be the result of females dispersing further to obtain a male territory, with males opting for the advantages of staying within familiar areas in the hope of acquiring a local vacancy (Tyler et al., 1990). A Swiss study suggested that temporary emigration might be a form of exploratory movement used during the transience stage to assess potential future territories (Becker, 2014). However, the different stages of dispersal in this species, and in particular behaviour during the post-fledging period, require further study.

In this thesis, the specific objectives of Chapter 2 were to: (1) determine whether early life conditions (timing of breeding, brood size, population density, and body condition) influence dispersal distance; and (2) compare different measures of dispersal, with and without accounting for the actual distance moved along the watercourse, in order to investigate whether the relationship between early life conditions and dispersal might differ between methods. In Chapter 3, I used field observations of colour-ringed birds to describe and quantify provisioning behaviour and juvenile movements during the post-fledging period, giving insights into how these processes might influence dispersal.

Chapter 2. The impact of early life conditions on natal dispersal distance in the white-throated dipper

Introduction

Natal dispersal, the movement between an individual's place of birth and the site at which it first attempts to breed, is a fundamental process in ecology and evolution (Greenwood, 1980; Greenwood and Harvey, 1982; Clobert, 2012). Yet, despite its importance for individual fitness, population structure and genetic diversity, our understanding of the underlying determinants which cause variation in dispersal behaviour remains poor (Clobert, 2012; Claramunt, 2021). This is partly because most field studies are subject to the biases associated with finite study site boundaries (Koenig et al., 1996; Sharp et al., 2008a; Clobert, 2012), but is also due to the difficulties of following individuals from early life through the spatial and temporal process of dispersal itself.

To better understand the ecology and evolution of dispersal, it is necessary to identify the underlying causes of variation (Sharp et al., 2008a; Clobert et al., 2012). In birds, a major determinant of dispersal patterns is sex (Greenwood, 1980; Clarke et al., 1997; Trochet et al., 2016). In most species, females disperse further and more frequently than males, which is often thought to be due to their predominantly resource-defence mating systems, in which males are territorial and benefit from remaining nearer the natal area and typically females disperse further to assess and choose a suitable mate or breeding vacancy (Greenwood and Harvey, 1982; Clarke et al., 1997). Indeed, male-biased dispersal does occur but is generally more prevalent in non-passerines with different mating systems (Clarke et al., 1997). Other important influences on dispersal propensity include body size (Barbraud et al., 2003; Dawideit et al., 2009), body condition (Delgado et al., 2010; Azpillaga et al., 2018) and flight efficiency (Claramunt, 2021).

The conditions an individual experiences in early life can have major long-term consequences for growth, survival, and behaviour (Metcalfe and Monaghan, 2001; Krause et al., 2009; Spencer and MacDougall-Shackleton, 2011; Magoolagan et al., 2018), and there is some evidence that they may be a cause of intraspecific variation in dispersal (Hardouin et al., 2012; Azpillaga et al., 2018). However, the interplay between individual state (e.g. sex), early life conditions and dispersal requires further study, ideally taking spatial biases into account (Koenig et al., 1996; Sharp et al., 2008a). Factors such as environmental conditions and sibling competition may be important through their impact on nestling body condition (Benard and McCauley, 2008; Monaghan, 2008; Bonte and de la Pena, 2009); local population density

might affect the movements individuals make soon after leaving the natal area (Ausprey and Rodewald, 2013). Understanding these processes will provide key insights into variation in dispersal behaviour and may be vital for predicting how populations will respond to environmental change.

Timing of Breeding

Parental decisions about the timing of breeding determine the environmental conditions their offspring will experience in early life, with consequences for reproductive success and survival later on (Lindström, 1999; Grüebler and Naef-Daenzer, 2008a). In many birds, earlier breeding is associated with more favourable conditions, for example higher food availability (Verhulst and Nilsson, 2008). Furthermore, breeders often reduce parental effort towards the end of the season and focus more on their own needs, such as preparing to moult or migrate. As such, individuals which hatch earlier in the year may be in better condition than those which hatch later in the season (Saino et al., 2012). Assuming that dispersal is costly (Bonte et al., 2012; Clobert, 2012; Maag et al., 2019), earlier hatched birds might therefore be more likely to disperse further distances. Alternatively, birds born earlier in the season might be more dominant and competitively able to secure favourable breeding territories nearby.

Sibling Competition

Competition between individuals from multi-offspring broods can have wide ranging fitness consequences. Nestmates compete for access to parental care (Mock et al., 2009; Bebbington et al., 2017), and competition for resources continues through the early post-fledging period (Tarwater, 2012). Reduced nutritional intake during early life can hinder growth and development, which in turn may affect condition at fledging and competitive ability (Emlen et al., 1991; Royle et al., 2001; Bebbington et al., 2017). Consequently, brood size might influence an individual's dispersal propensity or distance (Tarwater, 2012). For example, individuals from smaller broods may obtain greater benefits from the natal territory and therefore be better able to compete for higher quality breeding territories (Smiseth et al., 2007; Tarwater, 2012). Individuals from larger broods might disperse sooner or further to avoid kin competition (Suh et al., 2020).

Population Density

Local population density can be a good indicator of the current level of competition and may therefore inform dispersal decisions (Clobert et al., 2004). These effects can be either positive or negative. For example, high population densities suggest that intraspecific competition is intense, and so individuals may choose to disperse out of the locally crowded area (Bowler

and Benton, 2005; Matthysen, 2005). This may be compounded by sibling competition. However, densely populated areas might also act as a proximate cue for habitat quality, and as such appeal to more competitive individuals (Matthysen, 2005). In many species, there are benefits to remaining close to the natal area, such as familiarity with nesting or feeding sites (Ekman et al., 2004; Kingma et al., 2016). Furthermore, simultaneous positive and negative density-dependent dispersal has been demonstrated within the same population (Kim et al., 2009), and the effects of population density likely depend on other environmental conditions.

In this study, I investigate the impact of early life conditions on natal dispersal distance in the white-throated dipper (hereafter 'dipper'). Dippers are freshwater specialists and spend much of their lives along rivers and streams (Tyler and Ormerod, 1994). In the UK, dippers are resident (although altitudinal migration occurs in some populations), and individuals invariably move along watercourses rather than crossing between them (Tyler et al., 1990). Dispersal distance was therefore measured in two ways: the Euclidean distance, by far the most commonly used metric in studies of avian dispersal; and 'instream distance', the shortest route along the watercourse, which is likely to be a closer approximation of the true distance each bird travelled.

Previous research has found that female dippers disperse further than males and that both sexes disperse further than would be expected if they were to settle at the first vacant territory (Tyler et al., 1990; Becker, 2014). Tyler et al. (1990) only measured Euclidean distance, but the results nevertheless suggest a trade-off between the costs and benefits of settling near the natal territory and searching for breeding sites elsewhere. However, the effects of early life conditions on dispersal have never been explored in this species. Here, the specific objectives were to: (1) determine the relationship between natal dispersal Euclidean distance and instream distance; and (2) investigate the relationship between each measure of natal dispersal distance and the early life conditions experienced by birds of known sex and body condition. In particular, I focused on the timing of breeding, sibling competition and population density.

Methods

Study Population

All data were collected within the Yorkshire Dales National Park as part of a long-term study of dippers in the River Lune catchment within an approximately 6km radius of Sedbergh, Cumbria, UK (54.323°N, 2.528°W), between 2013 and 2021 (Fig. 2). The site consists of four

main rivers and their associated tributaries: the Lune, Rawthey, Clough and Dee. Since 2013, almost all birds in the population have been individually marked with three plastic colour rings and a British Trust for Ornithology metal ring and monitored closely from birth or immigration through to death or disappearance from the site. Each year, all unmarked adults that have immigrated into the study site are trapped and ringed using mist nests placed across the watercourse or with a hand net placed directly over the nest. Birds are sexed according to wing length measurements, taken with a wing rule (± 0.5mm; Demongin, 2016); other measurements include tarsus length, measured using dial callipers (± 0.1mm), and body mass, measured with digital scales (± 0.1g). Breeding takes place between February and July, and all nests are found and closely monitored from laying through to fledgling or failure, allowing key life history, population and behavioural data to be recorded (see Crowther et al., 2018; Magoolagan et al., 2019). These include the timing and outcome of each nesting attempt, and population size. All nest sites are recorded to within 10m using a Garmin eTrex H GPS unit (Garmin Ltd., Switzerland). Most nestlings are ringed when 9 days old and the same measurements are taken as for adults; a small number each year are ringed and measured when older than this, for example if the nest was previously inaccessible. The majority (> 90%) of first year birds that were ringed as nestlings and recruit into the breeding population are re-trapped so that their adult measurements can be taken. Those that are not captured can be sexed from their breeding activity (e.g., only females incubate the eggs, Tyler and Ormerod, 1994) and because the sex of their partner is typically known.
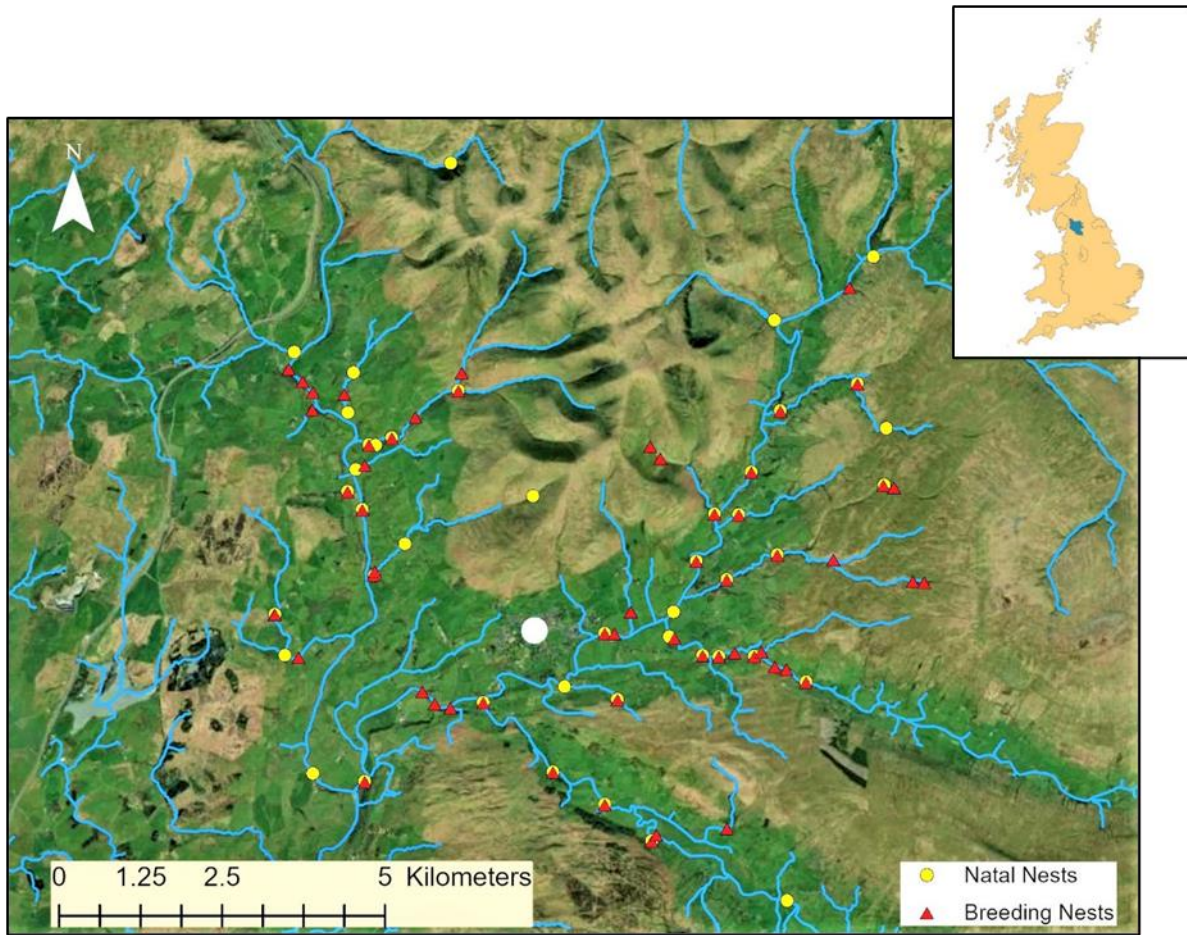
Figure 2. Natal and first breeding territories of dippers located along the watercourse within the study area in Yorkshire Dales National Park (highlighted in blue on map of Great Britain, top right), UK, 2013-2020. The town of Sedbergh is indicated by the white dot. Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User community.

Dispersal Distance

Natal dispersal distance (in m) was measured for 85 individuals (52 male, 33 female) born between 2013 and 2020 (and breeding between 2014 and 2021). A bird was only considered to have attempted breeding if its nesting attempt got at least as far as the laying stage. Dispersal distances were measured in two ways: the Euclidean distance (EDD), derived from the GPS data, and the instream distance (IDD), that is the shortest possible distance along watercourses between the natal and breeding nests. IDDs were obtained using the 'measure' tool in ArcGIS Pro 2.5.1 (Esri, 2020). Dippers begin breeding in their first year after birth, therefore dispersal distances were measured between the year in which an individual was born and the first nesting attempt in the following year (birth year + 1). Both measures of dispersal distance were calculated for all 85 individuals. Several individuals (n = 10; 8 males, 2 females) were apparently absent or were not known to breed in the study site in the year

after birth, but subsequently recruited into the population in the following year. These birds may have bred outside of the site boundaries in their first year, and most were found nesting close to the boundary in the subsequent year, although non-breeding 'floaters' are known to occur (SP Sharp, pers. comm.). Analyses including and excluding these individuals produced very similar results, with no bias evident; only those analyses in which they were included are presented here. Similarly, a small increase in the study area between 2013 and 2014 was found not to have biased dispersal distances, and all of the 2013 cohort were included. Finally, there was some non-independence in the sample because a small number of individuals had been raised in the same natal nest (eleven pairs of siblings and one trio). However, because the majority of birds (71%) were the only individual from their nest to have recruited into the population, mixed models with the identity of the natal nest fitted as a random term were not appropriate, and the effects of the non-independence on dispersal distance were considered small.

Statistical Analyses

All analyses were carried out in the R environment version 4.0.3 (R Core Team, 2020). Generalised linear models (GLM) were used to analyse the relationship between dispersal distance and early life conditions, controlling for sex. Dispersal distance distributions are inherently skewed therefore a Gamma distribution and log link function provided the best fit for continuous, positive data (de Freitas Costa et al., 2021). Each measure of dispersal distance (EDD and IDD) was modelled separately and fitted as the response variable. Sex was fitted as an explanatory variable due to its known impact on dispersal. In addition, the following explanatory variables were fitted to reflect early life conditions: hatch date (as a proxy for the timing of breeding), brood size (to represent sibling competition), and population size. Finally, body condition as a nestling was included as this is likely to be influenced by early life conditions and, in turn, affect dispersal. Hatch dates were converted to Julian dates where 1st January = 1. Brood size was based on the number of nestlings present at the time of ringing (day 9, where day 0 = hatch date). This varied from one to six, but in the vast majority of cases was between three and five. Brood size was therefore fitted as a categorical variable relative to the sample mean of 4.19: 'small' (one to four; n = 46) or 'large' (five to six; n = 39). Population size was measured as the number of breeding pairs in the year of birth. Body condition was measured using a scaled mass index, following Peig & Green (2009). Briefly, body mass was scaled according to the relationship between body mass and tarsus length in the sample. The scaling index was calculated separately for males and female due to size dimorphism in this species, with tarsus length standardised to the mean. Birds that were ringed and measured

after day 9 were excluded from the analyses (n = 13; 6 males, 7 females). Finally, the interactions between sex and each of the early life variables were also fitted.

All continuous variables were scaled and centred prior to analysis to improve the interpretability of the models (Schielzeth, 2010). Collinearity between the explanatory variables was then assessed by constructing correlation matrices and calculating variance inflation factors (VIFs, following Zuur et al., 2009). All pairs of variables had weak correlations (r < 0.4) and VIFs were small (< 2 in all cases), so all variables were included in the analysis. For each measure of dispersal distance, the global model was subjected to the 'dredge' function in the package *MuMIn* (Barton, 2016), to fit all possible models with all combinations of the explanatory variables and their interactions (n = 97 models). These models were then compared using Akaike's Information Criterion corrected for small sample size (AICc). Plotting and model averaging was performed using the MuMIn package (Barton, 2016) to average all models within 2 AICc units of the best-fitting model. Models were validated by assessing the distribution of the residuals, the residuals plotted against fitted values, and the residuals plotted against each explanatory variable.

Results

The observed estimated mean (± SE) Euclidean dispersal distance of dippers was 4103.72 ± 304.10m for females (n = 33) and 1988.25 ± 171.52m for males (n = 52), with a range of 296.53m to 8493.55m. The estimated mean (± SE) instream dispersal distance was 7838.55 ± 749.81m for females (n = 33) and 3509.77 ± 429.15m for males (n = 52), with a range of 323.67m to 17329.12m. Dispersal distance distributions were right-skewed for each of the two measures of distance, but they both provided clear evidence of female-biased dispersal (Fig. 3).
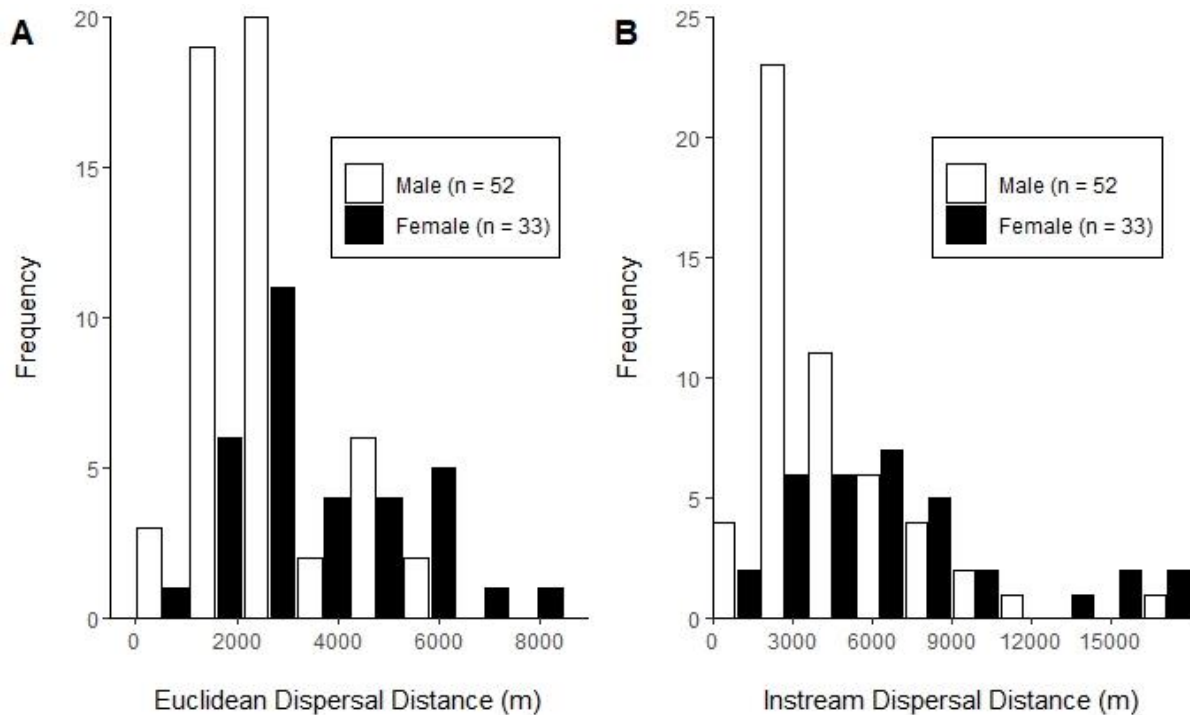
Figure 3. Dispersal distance distributions (in m) of male and female dippers in Yorkshire Dales National Park, UK, 2013-2020, based on (A) Euclidean dispersal distance; and (B) instream dispersal distance.

There was a strong positive correlation between the two measures of dispersal distance (Spearman's rank: r = 0.9, n = 85, p < 0.01); dippers which travelled greater Euclidean distances also dispersed greater instream distances, although this relationship was weaker for longer movements (Fig. 4).

Euclidean Dispersal Distance

Sex was an important predictor of the Euclidean dispersal distance of dippers, being present in all of the best-fitting models (Table 1A); females typically dispersed further than males (Fig. 5A). Julian hatch date was also contained in one of the best-fitting models with a negative coefficient suggesting that those hatching later moved shorter distances, but the effect size was negligible and unlikely to be biologically meaningful (Table 1A). No other explanatory variables were present in the best-fitting models.
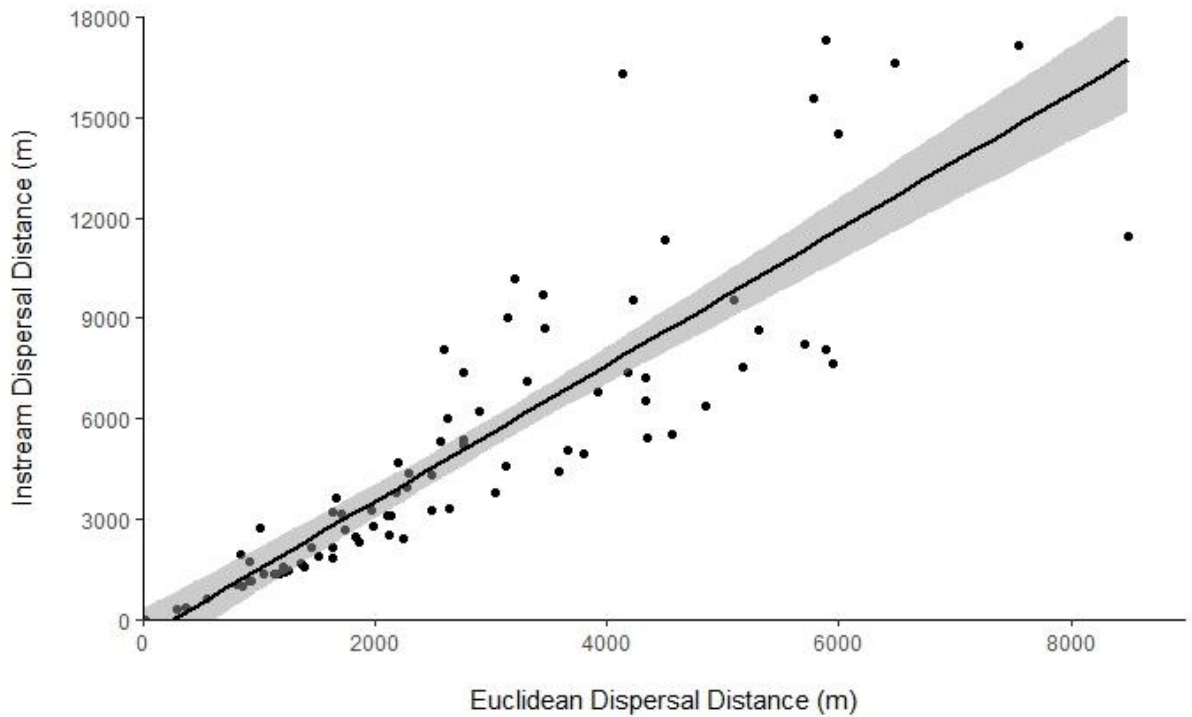
Figure 4. The relationship between Euclidean dispersal distance and instream dispersal distance of dippers in the Yorkshire Dales National Park, UK, 2013-2020 (n = 85). The line represents a simple linear regression with the 95% confidence interval shown in grey.
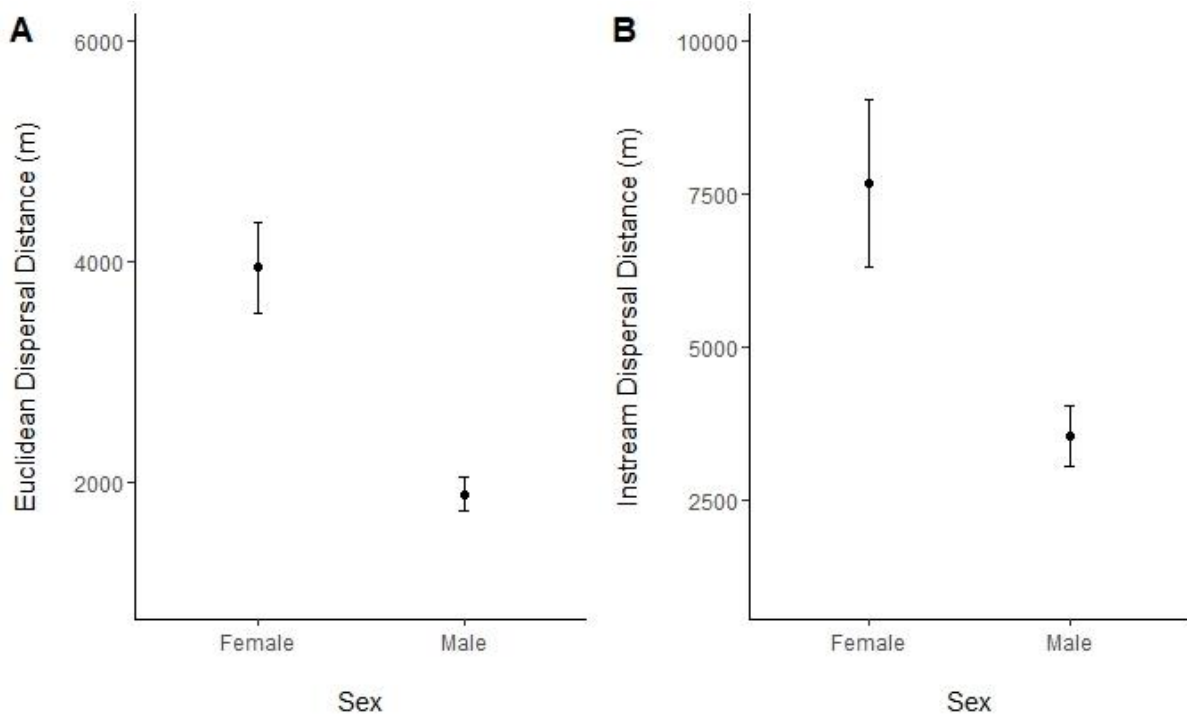
Figure 5. The Euclidean natal dispersal distance (A) and instream natal dispersal distance (B) of female and male dippers in the Yorkshire Dales National Park, UK, 2013-2020. Closed points and error bars show the fitted predictions and standard errors from an averaged generalised linear model. Model predictions were generated with hatch date set to its mean.

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Table 1. The best-fitting generalised linear models for the factors associated with (A) Euclidean dispersal distance and (B) instream dispersal distance of dippers in the Yorkshire Dales National Park, UK. All combinations of explanatory variables and their interactions were fitted. Only the best-fitting models which were those within a delta AICc of 2 of the best overall model are shown. Values are the parameter estimates for each variable. Weight represents the normalised model likelihoods. The null (intercept only) model is shown for comparison.

(A) glm(Euclidean Dispersal Distance ~ Sex + Hatch date + Brood Size + Population Density + Body Condition + Hatch Date: Sex + Brood Size: Sex + Population Density: Sex + Condition: Sex).

Intercept	Sex	Hatch Date	Brood Size	Population Density	Body Condition	Hatch Date x Sex	Brood Size x Sex	Population Density x Sex	Condition x Sex	df	logLik	AICc	delta	weight
8.28	-0.741									3	-610.99	1228.34	**0.00**	0.19
8.27	-0.723	-0.003								4	-610.68	1229.95	**1.61**	0.08
7.88										2	-625.49	1255.15	**26.81**	3E-07

(B) glm(Instream Dispersal Distance ~ Sex + Hatch date + Brood Size + Population Density + Body Condition + Hatch Date: Sex + Brood Size: Sex + Population Density: Sex + Condition: Sex).

Intercept	Sex	Hatch Date	Brood Size	Population Density	Body Condition	Hatch Date x Sex	Brood Size x Sex	Population Density x Sex	Condition x Sex	df	logLik	AICc	delta	weight
8.87	-0.718				-0.030					4	-669.08	1346.76	**0**	0.11
8.75	-0.726		0.235		-0.035					5	-668.11	1347.12	**0.36**	0.09
8.93	-0.761				0.006				-0.050	5	-668.29	1347.48	**0.73**	0.08
8.92	-0.772									3	-670.57	1347.49	**0.73**	0.08
8.81	-0.761		0.199		-0.006				-0.040	6	-667.61	1348.51	**1.76**	0.05
8.50										2	-679.82	1363.82	**17.06**	2E-05

Instream Dispersal Distance

Five models had an AICc of within 2 of the best-fitting model (Table 1B). They included sex, body condition, brood size, and the interaction between sex and body condition. As for Euclidean dispersal distance, sex was an important predictor of instream dispersal distance and was present in all five models (Table 1B), with females typically dispersing further than males (Fig. 5B). Body condition was contained in four of the models, including the best-fitting overall model (Table 1B), which suggests that both males and females that were in better condition as nestlings dispersed shorter distances (Fig. 6). While brood size and the interaction between sex and body condition each appeared in two of the best-fitting models, the effects of both were small (Table 1B).
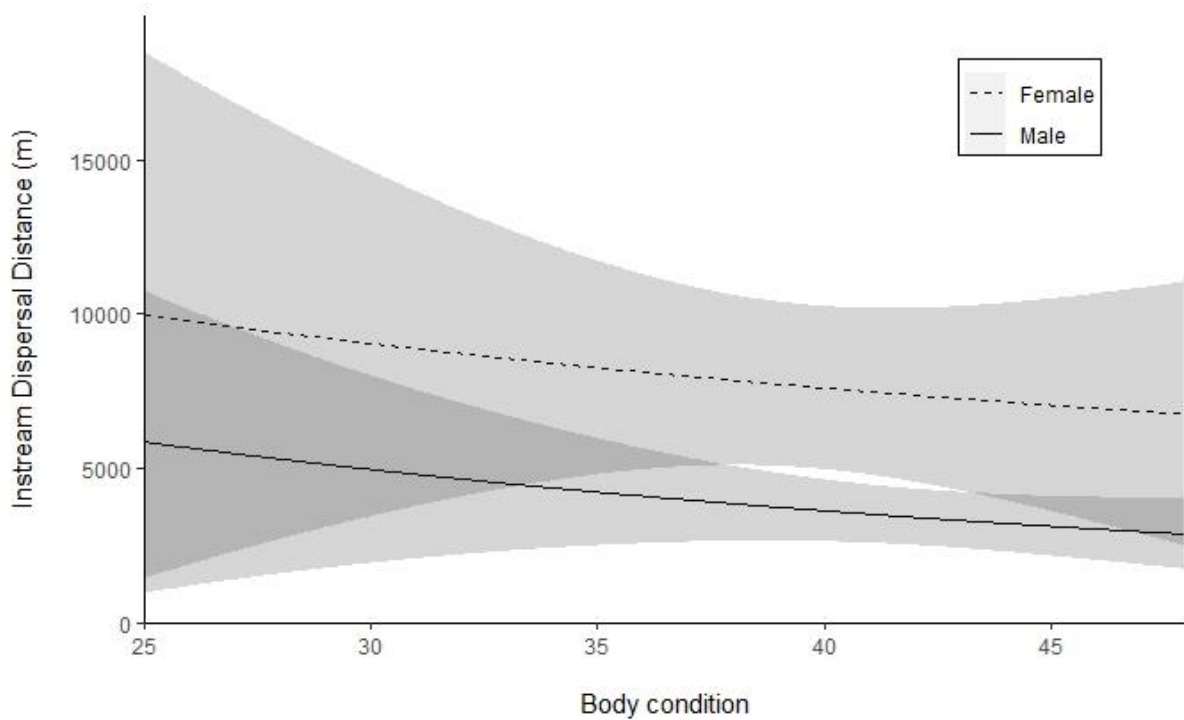
Figure 6. The relationship between instream dispersal distance and nestling body condition of male and female dippers in Yorkshire Dales National Park, UK, 2013-2020. Instream measurements are predicted values from an averaged generalised linear model. Model predictions were generated with brood size set to small. Shaded areas show the 95% confidence intervals for the predictions.

Discussion

This study used long-term data from a marked population of white-throated dippers to investigate the relationship between individual traits, early life conditions and natal dispersal distance. Dispersal distance was strongly female-biased, which conforms to the general pattern of sex-biased dispersal in birds (Greenwood, 1980; Clarke et al., 1997), and supports previous findings for this species (Tyler and Ormerod, 1994; Becker, 2014). This result was evident from both measures of dispersal distance. However, the analysis of instream dispersal distance revealed a weak negative correlation with nestling body condition, for which there was no evidence in the analysis of Euclidean dispersal distance. Brood size appeared in two of the models for instream dispersal distance, including the second-best fitting model, suggesting that birds from small broods dispersed shorter distance than those from large broods. However, the effect size was small, and a larger sample size is needed to detect potentially subtle effects. The interaction between sex and condition appeared in two of the best fitting models but the effect sizes were very small and the weight was not similar to the best fitting model, therefore further research is required.

The vast majority of studies of avian dispersal have analysed Euclidean distances (Greenwood et al., 1979; Verhulst et al., 1997; Suh et al., 2020). While this metric undoubtedly provides a useful measure of dispersal distance, and for many studies is the only feasible option, it is unlikely to represent the true distance that an individual moved. For instance, individuals might backtrack or engage in more exploratory movements before settlement (Wolfson et al., 2020; Engler and Krone, 2021). Indeed, without the use of tracking technology, it may be impossible to determine the full extent of movements between leaving the natal area and establishing a breeding site (i.e. during transience). However, in this study, the ecology of dippers allowed for a more meaningful dispersal distance to be measured; the instream distance. Similar measures have been used for other riverine organisms (Watts et al., 2006; Chaput-Bardy et al., 2008; Borges et al., 2021), and this is especially important for studies of influences such as condition because Euclidean measurements might mask the relationship between condition and the actual distance travelled. In a study of the damselfly *Coenagrion mercuriale*, there was a positive correlation between genetic differentiation and Euclidean dispersal distance, but the fit of this relationship was improved when using instream distance (Watts et al., 2006). Here, a positive correlation was shown between the two measures of distance; birds which dispersed greater instream distances generally travelled greater Euclidean distances, but the relationship was weaker for longer movements. This is at least partly because some natal and breeding sites are relatively close in absolute terms but separated by land and only connected by long, meandering stretches of river. While some

individuals, particularly those born in upland territories, are thought to cross watersheds and therefore underdo dispersal that may be better reflected by Euclidean distances, such movements are thought to be rare (Tyler et al., 1990). Future studies of any species should consider carefully the most appropriate measure of distance and acknowledge the potential limitations of using Euclidean measurements. As tracking technology continues to develop, more reliable measurements of true distances will become increasingly feasible (López-López, 2016).

Female-biased dispersal is the dominant pattern in birds, especially passerines (Greenwood, 1980; Clarke et al., 1997), and this is often attributed to inbreeding avoidance (Clobert, 2012; Dobson, 2013; Li and Kokko, 2019b). However, inbreeding avoidance as a proximate driver of sex-biased dispersal has been questioned (Pusey, 1987; Perrin and Goudet, 2001; Sharp et al., 2008a; Li and Kokko, 2019b). Some argue that in monogamous species, the cost of inbreeding should be similar in the two sexes and therefore female-biased dispersal should not be observed if inbreeding avoidance is the sole underlying determinant of dispersal propensity (Taylor et al., 2003; Li and Kokko, 2019b). Furthermore, high levels of inbreeding have been detected in a Swiss population of dippers, but female-biased dispersal was still evident (Becker, 2014). As such, female bias in this species provides support for the 'resource-defence mating system' hypothesis, whereby males defend territories and resources, and females disperse to choose a suitable breeding opportunity (Greenwood, 1980; Tyler et al., 1990; Clarke et al., 1997). Males may benefit from staying close to their natal area where they are likely to be familiar with good foraging and nesting sites which they can use to attract females. In contrast, females might benefit from covering greater distances through an increase in mate choice opportunities, whilst simultaneously avoiding the costs associated with staying in the natal territory such as kin competition (Greenwood, 1980; Clarke et al., 1997; Trochet et al., 2016; Végvári et al., 2018; Li and Kokko, 2019b).

The results of this study suggest that individuals do not simply settle in the nearest available territory. Many field observations over the years have revealed individuals being observed outside of the natal territory having passed through multiple vacant territories, and birds regularly breed at sites further from the natal area than apparently suitable vacancies (SP Sharp, pers. comm.; see also Chapter 3). As suggested by Tyler et al. (1990), there is likely a trade-off between the costs and benefits of searching for a better quality breeding opportunity, and this may be a key determinant of dispersal distance. Similarly, in line with findings from Becker (2014), individuals might engage in exploratory movements before finding a territory in which to settle, but the ability to explore and compete for the best vacancies is likely to be condition-dependent (see below). Future work should determine the fitness consequences of

dispersing different distances; this is not only important for understanding variation, but will provide insights into the potential impact of environmental change.

Early life conditions

The analyses of instream distance highlighted condition as a significant factor in four out of the five best fitting models which provides weak evidence of condition-dependent dispersal; individuals in better condition during the nestling period moved shorter distances; this was true of both sexes. The relationship between body condition and dispersal distance has been studied extensively across taxa (Barbraud et al., 2003; Edelman, 2011; Hewison et al., 2021). In some species, individuals in better condition have been found to disperse further, presumably because they are better able to bear the costs of travel. For example, heavier female roe deer (*Capreolus capreolus*) have been found to travel greater distances in search of a suitable territory (Hewison et al., 2021). In contrast, it appears that the opposite pattern occurs in dippers. These results might be explained by the social dominance hypothesis, which suggests that weaker or subordinate individuals will be forced out of the natal area by more dominant individuals (Gyllenberg et al., 2011; Suh et al., 2020). Similarly, intrasexual kin competition may play a role; if males compete for suitable breeding territories and resources, as seems to be the case in dippers (Tyler and Ormerod, 1994), those in better condition may be more successful at securing local territories and benefiting from familiarity with the area (Engler and Krone, 2021). In turn, females in better condition may be more likely to pair with higher quality males and thereby settle close to their natal area. However, the sample size for females was smaller and the confidence interval for the effect therefore large. Indeed, there appeared to be some indication of an interaction between sex and body condition and, while the effect size was small, this would be interesting to research further. A recent study of the banner-tailed kangaroo rat (*Dipodomys spectabilis*) found that size and condition are important influences on dispersal in males but not females (Edelman, 2011). Ongoing analyses of the long-term data from the dipper study may provide insights into the sex-specific costs and benefits of dispersal, in particular by quantifying the fitness consequences of dispersing different distances. Future studies might benefit from making use of alternative measurements, for example wing length and tarsus length, to better analyse influences of size and body condition independently.

There was no clear effect of hatch date on either measure of dispersal distance. This is surprising, especially given that in some species, birds which hatch earlier in the season have been argued to be in better condition (Saino et al., 2012; Suh et al., 2020), and this in turn influences dispersal as seen here in dippers. Furthermore, individuals which hatch earlier may secure closer territories and therefore force later hatching birds to disperse greater distances

as vacancies are filled (Dhondt and Hublé, 1968). One explanation might be that seasonal declines in food availability are less marked in dippers than in those species for which an effect of hatch date has been observed. For example, many woodland species rely on seasonal peaks in caterpillar abundance to raise their offspring (Visser et al., 1998; Cresswell and Mccleery, 2003). However, more research on the relationship between the timing of breeding, food availability and condition-dependent dispersal is needed. Studies of behaviour and movements during the transience stage of dispersal may be particularly insightful, as any effects of seasonality may be mitigated during this time.

There was an indication of brood size effects in two of the models for instream distance which suggests that birds from smaller broods dispersed shorter distances than birds from larger broods. This might be expected given the predictions of the literature, but effects sizes were small, and further investigations are needed. Brood size was included in the analysis as an index of the level of sibling competition, which has been shown to impact dispersal distance in other species (e.g. Sharp et al., 2008a). Indeed, kin competition is often argued to be a major driver of sex biases in dispersal distance (Cote and Clobert, 2010; Dobson, 2013), although others have highlighted that if competition between kin is equally distributed between the sexes, female-biased dispersal is not expected to occur (Matthysen, 2012). Dippers typically only lay four to five eggs, and so brood size does not vary much across the population; a larger sample size is needed in order to model brood size as a continuous variable and thereby investigate potentially subtle effects of sibling competition. Furthermore, analyses that include brood sex ratio would be useful because individuals may disperse different distances according to sex-specific kin competition (Sharp et al., 2008a; Li and Kokko, 2019a).

There was no evidence of a relationship between population size and dispersal distance. Although density-dependence has been used to describe different dispersal strategies throughout the animal kingdom (Matthysen, 2005; Baines et al., 2020), there is conflicting evidence regarding the influence of population density, and some research suggests that interactions between population density and habitat quality might prove more useful explanations of variation in dispersal (Enfjäll and Leimar, 2009; Pärn et al., 2012). It may be that individuals only disperse from a densely populated area if overcrowding increases competition for food. For example, in island populations of house sparrows (*Passer domesticus*) with limited food resources, dispersal rates increased with natal population size (Pärn et al., 2012). In the dipper study population, juveniles from different natal broods have regularly been observed feeding together, suggesting that competition for food may be relatively low in the post-fledging period, at least in certain areas (Chapter 3). Measuring population density at a more local scale, rather than across the entire site, may be more useful before density-dependence can be ruled out.

In this study, only birds which have successfully dispersed (i.e. dispersed and recruited into the breeding population) are represented. As such, mortality rather than dispersal might explain some of the results, and it is important that future work investigates the factors affecting recruitment probability rather than simply dispersal distance (Sharp et al., 2008a). Additional measures of body size for example wing length, and additional measures relevant to dispersal such as flight efficiency (Claramunt, 2021), should be used to better assess dispersal to investigate if individuals are better able to disperse, or if increased body mass and condition only means that birds are better able to survive and therefore are more likely to be re-sighted the following year. Furthermore, like most avian dispersal studies, the results here fail to account for the inherent bias of finite site boundaries, not least because the most widely used methods for doing so are unsuitable for movement in a linear landscape (Baker et al., 1995). However, for riverine species like the dipper, the effects of bias are potentially smaller because of greater detection probabilities and the reduced amount of the landscape in which the birds can feasibly move and settle. Indeed, a concerted effort is made each year to survey the rivers and streams in the immediate area surrounding the study site, and few colour-ringed birds are ever found; almost all are observed less than 1km from the study site boundary. In addition, only seven birds of the many hundreds to have fledged during the study have ever been found observed on a different catchment, despite dippers being a well-watched and photographed species throughout the wider region.

Conclusion

This study found strong support for female biased dispersal in this population of white-throated dippers. There appeared to be a weak effect of body condition influencing dispersal distance in both males and females when using measures of instream distance, which was not apparent with Euclidean dispersal measurements. Brood size and the interaction between sex and condition were highlighted in the analysis of instream distance, but larger sample sizes are needed to detect potentially subtle effects. Further work is needed to understand the fitness consequences of dispersal and the potential role of early life conditions. In particular, critical aspects of dispersal such as the timing of departure from the natal site and behaviour during transience are often overlooked. Riverine systems provide ideal models for studying spatial processes such as these due to their linear nature and, for some species at least, the relative ease of observing and following individuals, and tracking technology is likely to be crucial for future research. Rivers are also among the most threatened of the earth's ecosystems, and it is therefore particularly important to understand dispersal in rivers if the effects of pollution, urbanisation and changing flow regimes are to be mitigated (Vörösmarty et al., 2010; Reid et al., 2019).

Chapter 3 – Post-fledging care and juvenile movements in white-throated dippers

Introduction

In avian ecology, the post-fledging period is a poorly understood life history stage, largely due to the methodological difficulties which field studies face when following wide-ranging individuals once they have left the nest (Cox et al., 2014; Naef-Daenzer and Grüebler, 2016). In passerines, fledglings usually continue to receive parental care, including provisioning, after leaving the nest and up to the onset of dispersal, when they depart from the natal territory (Tarwater and Brawn, 2010). Parental and juvenile behaviour during this period can have important consequences for individual fitness, population growth and demography (Anders et al., 1998; Cox et al., 2014; Naef-Daenzer and Grüebler, 2016), but for many species, even basic information about these processes is lacking.

The post-fledging period of passerines can be broadly split into two stages according to the reliance of fledglings on parental care (Cox et al., 2014; Goguen, 2019). Generally, the first two weeks or more after fledging are known as the 'dependent' stage, in which the altricial young are not fully developed and often almost immobile unless disturbed (Goguen, 2019). During this time, juvenile mortality is typically high, mainly as a result of predation, until individuals have learnt to fly, forage independently and evade predators (Kershner et al., 2004; King et al., 2006; Naef-Daenzer and Grüebler, 2016). The remainder of the post-fledging period is known as the 'independent' stage, by which time juveniles are no longer dependent on parental provisioning and start to engage in exploratory, prospecting behaviour before leaving the natal territory (Anders et al., 1998; Goguen, 2019).

Parental provisioning strategies can help to overcome environmental stressors and are known to have a profound influence on offspring survival (Naef-Daenzer and Grüebler, 2016). For example, extended parental care can help to reduce the risk of predation and increase the condition of juveniles before they depart from the natal territory, thereby increasing the value of offspring to parents (Tarwater and Brawn, 2008; Naef-Daenzer and Grüebler, 2016). However, the duration and extent of parental care can vary considerably between species, and this variation depends on complex interactions between adult survival, the potential for raising multiple broods in a season, and extra-pair copulation opportunities (Tarwater and Brawn, 2010; Naef-Daenzer and Grüebler, 2016; Darrah and van Riper III, 2021).

In many biparental species, brood division provides a flexible strategy for breeders to deal with the challenges and trade-offs associated with caring for fledglings. This strategy involves parents dividing the brood, and each then allocating parental care to their own half. In doing so, foraging efficiency of the adults may increase (Anthonisen et al., 1997), and by spatially separating the brood, the risk of predation may be reduced (Rivera et al., 2000; Russell, 2000). Brood division has been demonstrated in a range of species (see Smith, 1978; Harper, 1985; Tarwater and Brawn, 2008), and it has long been hypothesised that adults may allocate division randomly, or based on sex and size (Harper, 1985; Vega et al., 2007). In most passerines, the sharing of reproductive effort evenly between the parents results in rapid development of the young, and often enables the parents to raise multiple broods within the season (Naef-Daenzer and Grüebler, 2016; Nomi et al., 2018).

In multi-brooded species, the dynamics of the post-fledging period are likely to be particularly important, because individuals should rear the number of broods that maximises fitness in the long-term (Grüebler and Naef-Daenzer, 2008b). Increasing parental effort might enhance the survival of fledglings, but it may also delay future breeding opportunities; terminating parental care for the current brood can lead to earlier laying of a second clutch and increase the number of offspring (Stodola et al., 2009). As such, parents often face a trade-off between continuing care for the first brood and starting a second brood early (Grüebler, 2007; Naef-Daenzer et al., 2011).

Parents often expend more energy providing nutritional provisioning during the initial stages after fledging, and then gradually reduce effort as the young become more independent (Ogden and Stutchbury, 1997; Darrah and van Riper III, 2021). Species which attempt multiple broods are often limited by food resources and the length of the breeding season (Stodola et al., 2009). As such, attempting a second brood may mean limiting the amount of parental care issued to the first brood to optimise reproductive output. For example, research on barn swallows (*Hirundo rustica*) has demonstrated steeper declines in feeding rates for first broods than for single or second broods (Grüebler and Naef-Daenzer, 2008b). Similarly, males might provide extended parental care and take on more provisioning duties if this increases the probability of a second brood by allowing females to better prepare and conserve energy (Stodola et al., 2009; Nomi et al., 2018; Darrah and van Riper III, 2021). However, few studies have investigated the importance of the male role in multi-brooded species (Nomi et al., 2018).

The age at which juveniles depart from the natal territory is another poorly studied aspect of the post-fledging period, but again can have important fitness consequences. Individuals which leave the natal territory sooner might have greater success in finding a nearby vacant territory, whereas those which depart later might incur costs from sibling rivalry and so must

disperse further to avoid competition for breeding vacancies in an already saturated environment (Matthysen, 2005; Suh et al., 2020). However, if the costs of staying in the natal area are outweighed by the benefits, such as familiarity and access to good foraging grounds, then individuals might opt for delayed dispersal strategies (Ekman et al., 2004; Hatchwell, 2009). Moreover, differing levels of parental care can lead to variation in fledging condition and the timing of departure, within and between species, and this in turn can impact post-fledging movements and survival (Middleton and Green, 2008; Ausprey and Rodewald, 2013; Naef-Daenzer and Grüebler, 2016).

The timing and distance of movements during the 'independent' stage and after departure from the natal area are likely to be key determinants of juvenile survival, settlement decisions and recruitment (Vitz and Rodewald, 2010; Ausprey and Rodewald, 2013; Darrah and van Riper III, 2021; Şahin-Arslan and Martin, 2021). After fledging, the young of most passerines initially stay close to the nest site and move further away as they get older (Vitz and Rodewald, 2010; Goguen, 2019). The distances moved vary greatly among species, but juveniles are often highly mobile and able to travel long distances within just a few weeks of fledging (Vitz and Rodewald, 2010; Jenkins et al., 2017). In some species, juveniles are known to temporarily leave the natal area for short periods before being truly independent (Guo et al., 2010; Engler and Krone, 2021). Juvenile movements may be influenced by early life conditions such as body condition and population density (Pärn et al., 2012; Ausprey and Rodewald, 2013). For instance, birds in better condition may be better able to travel greater distances or compete for high quality territories, both of which might be more important when local population density is high (Ausprey and Rodewald, 2013; Jenkins et al., 2017). Similarly, the time of year and current weather conditions are also likely to be influential (Naef-Daenzer et al., 2001; Vitz and Rodewald, 2010; Jenkins et al., 2017). However, as with the age of departure from the natal territory, the factors affecting variation in juvenile movements require further study.

Here, I use field observations to describe parental provisioning behaviour and movements of juvenile white-throated dippers (hereafter 'dippers') during the post-fledging period. Dippers provide a useful model system for following juveniles once they have left the nest because individuals invariably move along watercourses rather than crossing between them, and fledglings are relatively easy to locate due to their loud and distinctive begging call (Tyler and Ormerod, 1994; Crowther et al., 2018). Fledglings remain on the natal territory and are reliant on parental provisioning for approximately two weeks until they reach independence (Tyler and Ormerod, 1994), although this may vary with individual and ecological conditions (SP Sharp, pers. comm.). Becker (2014) showed that the distance juvenile dippers travel increases rapidly only a few weeks after fledging, and that long but temporary periods away from the

natal territory can occur following independence. However, this study was carried out on a series of small, fragmented rivers, rather than areas of a larger, more complex catchment, and it is not clear whether similar patterns occur where more continuous stretches of suitable habitat are present.

There is anecdotal evidence of brood division from previous studies of dippers, with parents 'splitting' the brood and each caring for their share of the fledglings (Tyler and Ormerod, 1994). However, it is not known whether having a second brood impacts the amount of parental provisioning received by offspring from the first brood, or if multi-brooding influences the likelihood of brood division. In most dipper populations, only a small proportion go on to have a second brood; approximately 70 to 80% of pairs will produce only one, in part because of temporal constraints (Tyler and Ormerod, 1994). Brood division can take different forms and is often considered to be the division of labour among the parents, each allocating parental care to separate members of the brood. Similarly, brood division can refer to spatial separation of the brood. Here, brood division is defined as the division of labour, and was considered apparent if parents allocated resources to separate fledglings. This was determined by feeding events; if only one parent was seen feeding a fledgling for the entire focal watch, the brood was considered divided.

The specific objectives of this study were to: (1) quantify the provisioning rates of fledglings by male and female parents; (2) investigate whether brood division occurs; (3) estimate variation in the age of independence and departure from the natal territory, together with potential correlates; and (4) investigate the pattern of juvenile movements during the early stages of natal dispersal.

Methods

Study population

Data were collected from observations of colour-ringed juvenile dippers from mid-April through to mid-July during the 2021 breeding season as part of a long-term study in the River Lune catchment near Sedbergh, Cumbria, UK (54.323°N, 2.528°W). The site consists of four main rivers and their associated tributaries: the Lune, Rawthey, Clough, and Dee (see Fig. 2, Chapter 2). Since 2013, almost all birds within the study site have been individually marked with a combination of three plastic colour rings and a British Trust for Ornithology metal ring. Each year, all unmarked adults that have immigrated into the population are caught and ringed using mist nets placed across the river channels, or with a hand net placed directly over the

nest. Adult birds are sexed according to wing length measurements, taken with a wing rule (± 0.5mm; Demongin, 2016). A total of 50 breeding attempts (nests which reached the laying stage), by 40 different breeding pairs, took place between February and July 2021 and were closely monitored through to fledging or failure following established protocols. This allows key life history, behavioural and population data to be collected, including the timing and outcome of each nest attempt, territory borders and nestling provisioning rates (for further detail, see Crowther et al., 2018 and Magoolagan et al., 2019). Nest sites are recorded to within 10m using a Garmin eTrex H GPS unit (Garmin Ltd., Switzerland). All nestlings are ringed using the same system as for adults, and most are measured when nine days old ('day 9'); measurements include tarsus length, measured with dial callipers (± 0.1mm), and body mass, measured with digital scales (± 0.1g). A small proportion of nestlings are ringed and measured when older than this, for example if the nest is not safe to access on day 9.

Post-fledging provisioning rates

Breeding attempts were considered successful if at least one young fledged from the nest. The territories of all successful attempts along the four rivers and their major tributaries were visited at least twice per week during the first two weeks after fledging (n = 18). Territories were searched systematically until a fledgling was located, but if no fledglings were found within 30 – 60 minutes of arriving at a territory, efforts were abandoned. If this happened on two consecutive visits, it was presumed that the young had either not survived or moved beyond the territory limit (see Crowther et al., 2018). Once a fledgling was located, a site was found from which a focal watch could be conducted without causing disturbance. This was usually at least 15m away from the bird; watches were only started once all fledglings present had remained settled for 5 minutes, although disturbance was rare. If more than one fledgling was present, one bird was selected randomly for the focal watch, although repeat sampling of the same individual on subsequent visits was avoided. Focal watches were conducted for up to 60 minutes but were terminated if the focal bird moved out of sight or dense foliage made it too difficult to continue. Watches lasting less than 30 minutes were excluded from the analyses; the mean (± SD) duration of all remaining watches was 31.6 ± 4.0 minutes. All watches were carried out before 12pm and after 2pm to avoid midday inactivity, but if both parents were absent and provisioning did not take place, the watch was excluded.

The focal bird was observed through binoculars (10x magnification) and all feeds by each parent were recorded. The identity of all adults and fledglings present during the watch was recorded. Offspring provisioning rates were then calculated as hourly feeding rates by each parent. To compare post-fledging provisioning rates with nestling provisioning rates, all nestling provisioning rate data from 2021 were obtained from the wider study (SP Sharp,

unpublished data). Nest watches are carried out for 1 hour in each of the three weeks of the nestling period (see Magoolagan et al., 2018), so nestling provisioning rates were summarised by week.

Age of departure from the natal territory and post-fledging movements

As noted above, 18 successful territories along the four main rivers were visited at least twice weekly for the first two weeks after fledging. This 'core' area includes territories where the nest itself was located on a tributary, but the birds spent much of their time on the river. However, it excludes a small number of territories located further upstream along tributaries (n = 6), where regular access was not feasible. In addition to these visits, unsuccessful territories were also visited such that the entire core area was surveyed at least once every five days throughout the post-fledging period up to 15th July, 16 days after the penultimate nest fledged. The final successful nest of the year fledged on 7th July, so the age of departure from the natal territory and post-fledging movements of these birds were not recorded. Of the 23 fledglings produced in successful territories outside of the core area, only one was ever seen anywhere in the study site after fledging; this bird was also excluded from the results. The location of all juveniles observed outside of their natal territory was recorded with a GPS unit, and the 'instream distance' between the natal nest and this location was obtained using the 'measure' tool in ArcGIS Pro 2.5.1 (Esri, 2020; for further details, see Chapter 2). 'Age of departure' from the natal territory was calculated as the number of days between fledging and the date of the first observation of an individual outside of its natal territory.

Statistical analysis

In order to investigate the potential causes of variation in age of departure, correlational analyses were carried out for the relationship between age of departure and each of three variables: (1) hatch date, as a proxy for seasonal effects; (2) brood size, as a proxy for sibling competition; and (3) nestling condition, in order to test for condition-dependence. In addition, the correlation between age of departure and instream distance was analysed to test whether the age at which birds first left their natal territory influenced the distance they travelled. In all cases, Spearman's rank correlations were used to account for non-normal data distributions. Hatch date was converted to a Julian date where 1st January = 1. Brood size was taken as the number of nestlings recorded in the natal nest when ringing at day 9. This varied from one to six and was fitted as a continuous variable as the sample size was small (n = 16). Nestling condition was estimated using a scaled mass index (Peig and Green, 2009; for further details, see Chapter 2).

Results

The 18 successful territories in the core monitoring area produced a total of 82 fledglings from 22 breeding attempts (four pairs raised two broods successfully). One brood of two chicks fledged too late in the season to be monitored beyond fledging (see Methods). Of the remaining 80 fledglings, 32 individuals (40%) from 13 different broods were identified at least once between fledging and the end of the field season in mid-July. Twenty-one (26%) were seen in the first week after fledging, all within their natal territory, and of these, five (16%) were subsequently observed outside of their natal territory. However, a further 11 individuals (14%) which were not recorded anywhere during the first week after fledging were later seen outside of their natal territory.

Post-fledging provisioning rates

A total of 30 focal watches which lasted at least 30 minutes, and during which at least one parent was present, were conducted. Of these, there were 17 watches during which only the male fed the fledglings (57%), and 11 watches consisting only of feeds by the female (37%). Only during two focal watches did both parents feed the same fledgling at least once. Of the 18 successful territories visited, at least one focal watch was conducted in nine of them during the first week after fledging and three of them during the second week. No post-fledging provisioning was observed in any territory later than the 13th day after fledging.

Overall, post-fledging provisioning rates by males appeared to be higher than those of females. Males fed at a mean (± SE) rate of 16.4 ± 2.8 (n = 19) feeds per hour, and females at 11.9 ± 2.2 (n = 13) feeds per hour. During the first week after fledging, observations suggest that males fed at a mean rate of 17.6 ± 3.4 (n = 15) feeds per hour and females averaged 11.3 ± 2.3 (n = 12) feeds per hour. For first broods, males in pairs that later attempted a second brood fed at a lower rate than those in single-brooded and second-brood pairs (15.6 ± 4.6, n = 8; vs 17.1 ± 3.7, n = 11), but sample sizes were small.

Provisioning rates appeared to be higher for second broods than first broods, with males averaging 14.4 ± 3.2 (n = 15) feeds per hour for first broods and 26.3 ± 6.5 (n = 4) feeds per hour for second broods; and females averaging 10.7 ± 2.5 (n = 11) feeds per hour for first broods and 14.0 ± 6.0 (n = 2) feeds per hour for second broods (all calculated for the week after fledging only). Feeding rates appeared lower during the second week after fledging for males (12.2 ± 3.7, n = 4) but not females (20.0 ± 0.0, n = 1), but again sample sizes were very small. Post-fledgling provisioning rates were consistently higher than nestling provisioning rates, which averaged 4.0 ± 0.6 (n = 27) feeds per hour for males and 2.4 ± 0.5 (n = 27) feeds

per hour for females in week 1 of the nestling period; 6.2 ± 0.8 (n = 22) for males and 5.4 ± 0.8 (n = 22) for females in week 2; and 5.2 ± 0.9 (n = 19) for males and 7.2 ± 1.0 (n = 19) for females in week 3.

Age of departure

The mean age of departure for the 16 birds observed outside of their natal territory was 29.7 ± 11.5 days. The youngest of these was only 9 days old. There was a significant positive correlation between the age of departure and the instream distance travelled (Spearman's rank: r = 0.59, n = 16, p = 0.02; Fig. 7). There was also a slight positive correlation between the age of departure and nestling condition at day 9, although marginally non-significant (Spearman's rank: r = 0.48, n = 16, p = 0.06; Fig. 8). There was no significant correlation between age of departure and hatch date (Spearman's rank: r = -0.34, n = 16, p = 0.20), or between age of departure and brood size (Spearman's rank: r = -0.05, n = 16, p = 0.84).
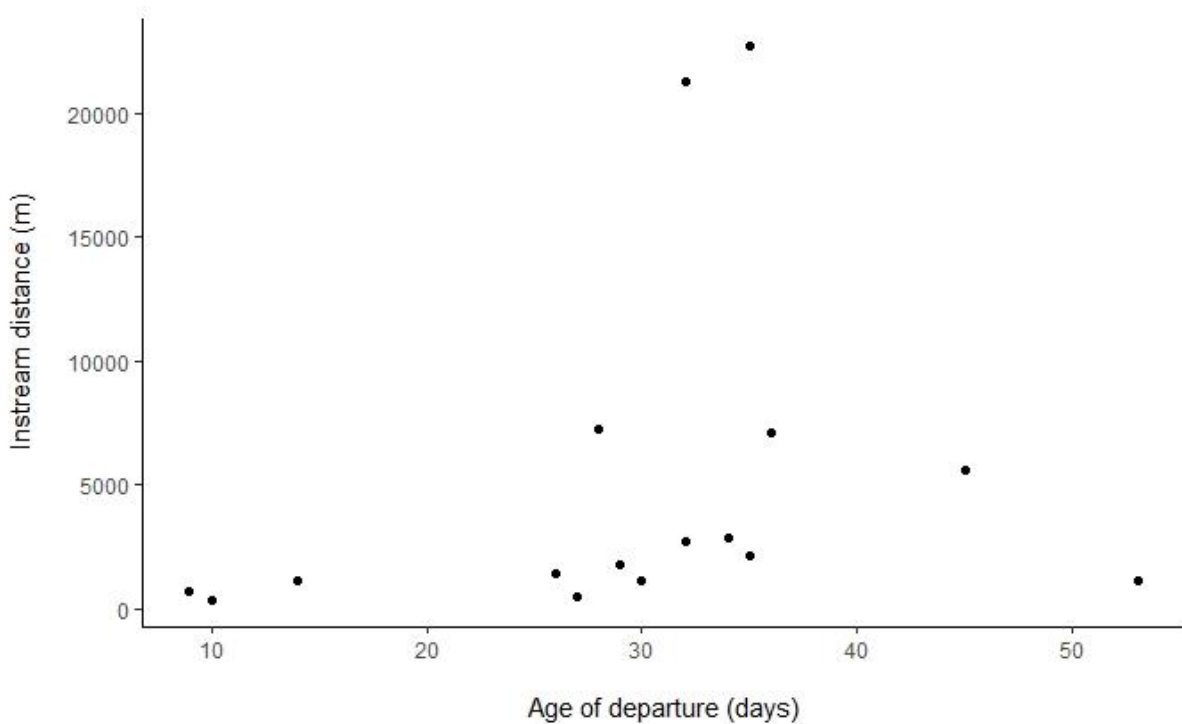
Figure 7. The relationship between age of departure from the natal territory and instream distance travelled in juvenile dippers (n = 16) in Yorkshire Dales National Park, UK, 2021.
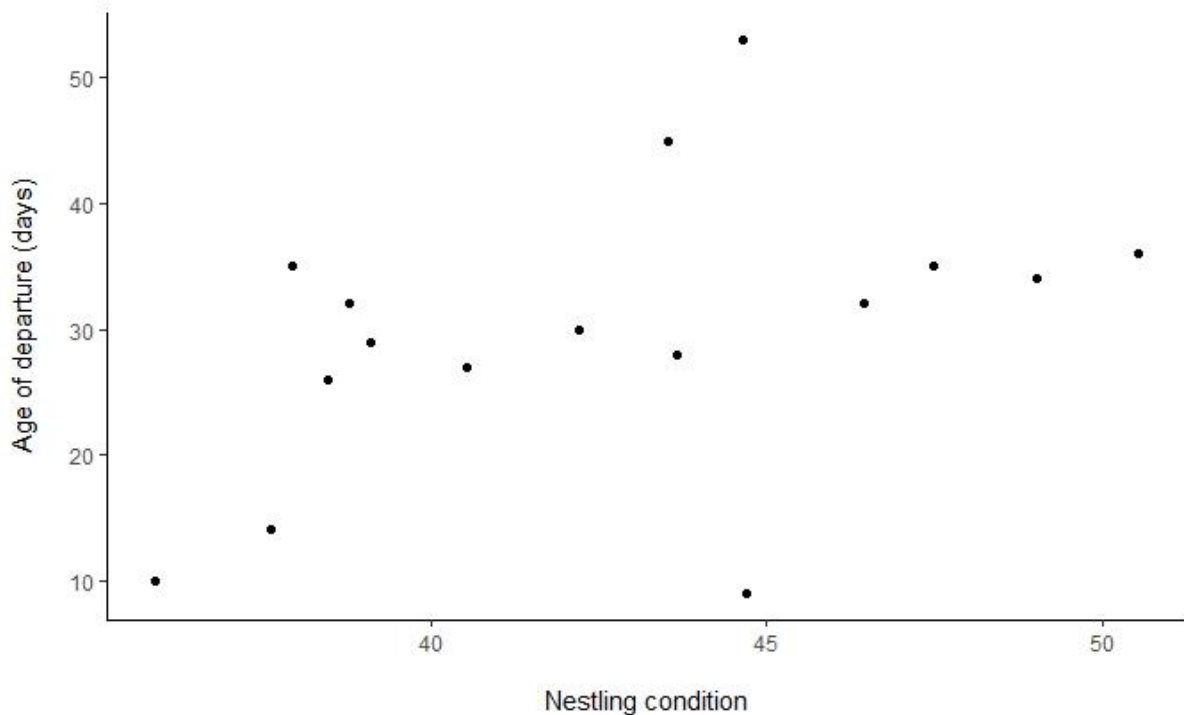
Figure 8. The relationship between nestling condition on day 9 and age of departure from the natal territory in dippers (n = 16) in Yorkshire Dales National Park, UK, 2021.

Post-fledging movements

Five individuals were sighted on multiple occasions (at least three times) outside of their natal territories, between 26 and 54 days after fledging. Four of these birds were over 1000m from their natal territory but only moved between 100 and 800m between the first and last sighting thereafter (Fig. 9); the fifth bird was first seen 485m from its natal territory and then moved 2027m in 11 days (Fig. 9).

On five occasions, individuals from different broods were observed within 1-10m of each other, with no apparent signs of aggression. At one territory, on three separate occasions over a six-day period, more than five different juveniles from at least four broods were recorded in close proximity. The maximum number of juveniles identified here at any one time was seven, including five colour-ringed birds from four different broods, and two un-ringed birds that had moved in from outside of the study area.
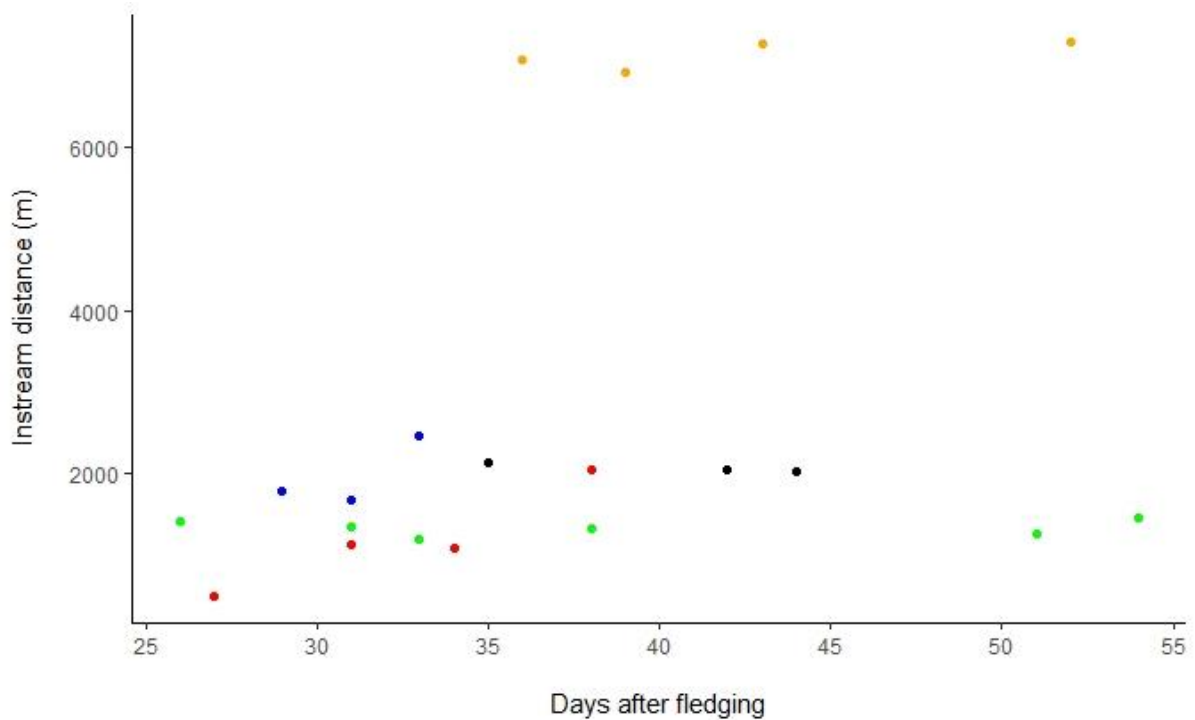
Figure 9. The relationship between the number of days since fledging and the instream distance travelled by five juvenile dippers outside of their natal territories in Yorkshire Dales National Park, UK, 2021. Different colours represent different individuals.

Discussion

Studies of the post-fledging period in birds are rare, mainly due to the difficulties of tracking and monitoring juveniles, but also because survival is low in many altricial species during the first few weeks after leaving the nest (Kershner et al., 2004; King et al., 2006; Grüebler and Naef-Daenzer, 2008a). Long-term studies of individually marked populations offer an opportunity to gain novel insights into behaviour and movement patterns which occur during this poorly understood life history stage. Owing to the ecology of white-throated dippers and their linear territories, as well as the fact that juveniles are relatively simple to locate by their loud and distinctive begging calls, this species provides an ideal model system for researching the post-fledging period.

In this study, results suggest that survival during the first week after fledging is low, as has been reported in other passerines (Naef-Daenzer et al., 2001; Tarwater and Brawn, 2010; Cox et al., 2014). Assuming that birds do not disappear from the study site within the first seven days of fledging, when they have not yet reached independence and are still relatively poor fliers, the absence of fledglings during visits to successful territories is likely to indicate mortality. Only 26% of fledglings from these territories were seen in the first week, and similarly low survival during this period has been reported in other passerines (Cox et al., 2014).

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However, eleven individuals appeared later in the season which were not detected during the week after fledging, bringing the estimate of survival during this period to 40%. This highlights the fact that, even in a species for which the detection probability of juveniles is relatively high (D'Amico and Hemery, 2003), individuals can be missed. Here, five of the eleven birds were from nests on tributaries, and so they may have initially ventured upstream before returning to the main river. Alternatively, some of these fledglings may have moved temporarily to very small streams within their territory which are often harder to survey. Nevertheless, it seems likely that less than half of all fledglings survived the first week. One explanation for the low post-fledging survival rate in this population is that juveniles are relatively weak and unable to sustain efficient flight to avoid predation from the main predators including corvids, mustelids such as stoats (*Mustela erminea*), weasels (*Mustela* nivalis) and American Mink (*Neovison vison*), as well as various raptor species (Tyler and Ormerod, 1994). As with most studies, it is impossible to distinguish between departure from the natal territory, or indeed from the study site, and mortality, but as advanced tracking technology becomes available for small birds, future research on this and other species offers huge potential for assessing the discrepancy between apparent survival and true survival (López-López, 2016). By combining the use of technology with long-term studies of marked individuals, researchers will be better able to understand how post-fledging survival varies with environmental conditions.

Post-fledging provisioning

In this study, brood division was defined as the division of labour among the parents. This was determined by feeding events, if only one parent was observed feeding a fledgling for the entirety of the focal watch it was assumed that parents were allocating resources to separate individuals, and brood division was considered apparent. Overall, results from this study provide some evidence, albeit weak, that brood division is likely common in this population of dippers. Of the 30 feeding watches conducted during which provisioning was observed, only two involved both parents feeding the same fledgling. Indeed, in the vast majority of cases, only one parent was present in the part of the territory where the watch took place. Brood division has been previously demonstrated in a number of other biparental passerines, including European robins (*Erithacus rubecula;* Harper, 1985), slaty antshrikes (*Thamnophilus atrinucha;* Tarwater and Brawn, 2008), bluethroats (*Luscinia svecica;* Anthonisen et al., 1997) and white-throated sparrows (*Zonotrichia albicollis;* Kopachena and Falls, 1991), and it is often thought to be a strategy to help reduce predation pressure and increase offspring survival through better allocation of resources (Kopachena and Falls, 1991; Rivera et al., 2000; Darrah and van Riper III, 2021). Given that fledgling mortality is apparently high in dippers, spatially separating the brood and allocating resources to a set number of individuals might increase

offspring survival (Şahin-Arslan and Martin, 2021). Alternatively, in some of the cases where only the male fed the young, a more frequent occurrence than the converse, it may be that the male was the sole carer for all surviving fledglings while the female was preparing to re-lay. It is worth noting that brood division can still occur if young are not spatially dispersed (Vega et al., 2007), which was accounted for in this study. Here, brood division was only considered as the division of labour among the parents. Further work is needed to investigate spatial dispersion of the young to better analyse brood division in this population.

During the first week after fledging, there was modest evidence suggesting that males fed young at a higher rate than females. One explanation for this is that females incur higher breeding costs than males, including during laying and incubation (Verhulst, 1998), and therefore invest lower effort in provisioning to conserve energy for survival and future reproduction, either later in the season or in subsequent years (Naef-Daenzer et al., 2011). Indeed, by increasing investment in care, males increase the probability of females having a second clutch in several species (Nomi et al., 2018; Darrah and van Riper III, 2021). In this study, male provisioning rates of first broods which went on to have a second brood were lower than those of single-brooded and second brood pairs, but sample sizes were small. One explanation for this might be that males reduce parental care for the first brood in order to focus on preparing for a second brood. Whereas, in single-brooded and second-brood pairs which are not going to attempt another clutch, males maintain similar levels of care to increase offspring survival.

While sample sizes were small, provisioning rates appeared to be lower in the second week after fledging. This may be because juveniles are already approaching independence at this stage and are able to feed themselves. Yet, juveniles from a few territories were observed still within the natal site after having reached full independence. This suggests that some individuals might choose to hold on to the benefits of the natal territory, possibly to make use of familiar foraging waters. In other species, individuals have been known to postpone emigration when resources are plentiful within the parental territory (Suh et al., 2020; Engler and Krone, 2021). Similarly, during a few watches, individuals were seen begging near to their parents but not being fed. After having provided extensive parental care immediately after fledging, parents might reduce their effort in subsequent weeks to encourage juvenile foraging behaviour and independence, and to conserve energy for further breeding opportunities (Grüebler and Naef-Daenzer, 2008b). It has been shown in some species that provisioning rates show steeper declines for first broods compared to second broods (Grüebler and Naef-Daenzer, 2008b), which was shown here but sample sizes were small. Further research with larger sample sizes is now needed to gain a better understanding of the causes and consequences of variation in post-fledging provisioning rates.

Finally, it is worth noting that fledgling provisioning rates were found to be much higher than nestling provisioning rates, especially given that the latter are measured for the whole brood rather than a single individual. This might be expected as not all the young in the nest will survive and therefore parents expend more energy caring for the ones who have reached the fledgling stage. However, this also suggests that parental behaviour during this time is likely to be a key determinant of offspring survival. An increase in provisioning after fledging has been documented in other species (Kopachena and Falls, 1991; Ogden and Stutchbury, 1997; Darrah and van Riper III, 2021). As such, higher rates for fledglings might be due to the energetic demands as flight muscles develop, but also because food load might be much lower for nestlings if single, larger, food items are being delivered to the nest to feed multiple chicks. Further study could research provisioning rates alongside food load to investigate this link.

Age of departure

Dippers are thought to reach independence between two and three weeks after fledging (Tyler and Ormerod, 1994), and here, the mean age of individuals when first recorded outside of their natal territory was 29.7 days. This is likely an overestimate because many stretches of river were only surveyed every five days. However, two individuals were observed outside of their natal area when less than two weeks old, and one individual was only 9 days old. This highlights the variation in the age of independence and indicates how mobile some very young birds are; as noted above, this may lead to underestimates of juvenile survival.

There was a positive correlation between age of departure and instream distance travelled. This was expected, as younger birds of many species generally stay closer to the natal nest and are more reliant on parental provisioning, with movements increasing as birds become older and more independent (Vitz and Rodewald, 2010; Darrah and van Riper III, 2021). There was also a weak positive correlation between age of departure and nestling condition at day 9, although marginally non-significant. This suggests that the age of departure, and therefore the age at which independence is reached, might be condition-dependent, with birds in better condition remaining in their natal territory for longer. This may be because these individuals are more competitive and therefore better able to secure the benefits of remaining in the natal area for longer, which has been demonstrated in many cooperatively breeding species (Nelson-Flower et al., 2018; Suh et al., 2020). A similar pattern was observed for the relationship between condition and natal dispersal distance in Chapter 2.

There was no correlation between age of departure and hatch date. This is perhaps surprising, because previous studies have shown that birds which hatch later in the season are often in poorer condition (Grüebler and Naef-Daenzer, 2008a; Saino et al., 2012) and therefore

expected to depart soon. However, sample sizes were small, and a larger sample might detect potentially subtle effects. Similarly, kin competition might be expected to influence condition or perhaps favour earlier departure from the natal area (Suh et al., 2020), but there was no correlation between the age of departure and brood size. Again, further research with larger sample sizes is required.

Post-fledging movements

Juveniles are highly mobile, and distances travelled from the natal territory apparently increase rapidly a few weeks after fledging. For example, two individuals were found to have travelled over 20km within only 35 days of fledging. Similar results have been shown in another population of dippers, and these movements are thought to represent the first stage of natal dispersal (emigration) and the start of the second stage (transience; Becker, 2014). While it is possible that some of these birds may have crossed watersheds rather than following the watercourse, and hence instream distance may be an overestimate, such movements are thought to be uncommon (Tyler et al., 1990). However, without the use of tracking technology, it is not possible to be sure exactly how far birds have travelled.

Observations from this study support previous findings that individuals did not settle in the first available territory (Tyler et al., 1990). On multiple occasions, individuals were observed in the next available territory along from their natal site only to be recorded at more distant locations on subsequent surveys. There may be a trade-off between settling in the first available territory and searching for better opportunities elsewhere (Stamps et al., 2005). However, it is also possible that individuals which have moved far from their natal territories may subsequently return, as reported by Becker (2014). Long-term studies over multiple seasons offer the best opportunities for exploring the costs and benefits of movements during transience and subsequent patterns of settlement.

Regardless of where birds ultimately settle to breed, juveniles must engage in at least some exploratory movements in order to find suitable habitat for feeding during the post-fledging period, a time when survival rates appear to be low (Vitz and Rodewald, 2010; Ausprey and Rodewald, 2011). In fact, selection for foraging success during transience may be so high that individuals will tolerate conspecifics at sites where food is plentiful. In this study, there were multiple observations of several individuals from different broods being present at the same site, presumably areas with high food availability. This is supported by the fact that movements were much shorter once birds had reached these sites. Individuals might use the presence of conspecifics as a cue for food availability, and therefore settle together in suitable areas (Clobert et al., 2009; Forsman et al., 2009; Ausprey and Rodewald, 2013). Given that the transience stage is considered to be costly (Maag et al., 2018), these areas might be essential

during the post-fledging period. Furthermore, individuals may also benefit from lower predation risk by feeding in close proximity at such a critical time.

Conclusion

Together, the results from this study have provided novel insights into behaviour during the post-fledging period and the early stages of dispersal, which is a poorly understood aspect of avian life histories. The relationship between behaviour after leaving the nest and how it influences dispersal requires further study, ideally using a combination of long-term studies of individually marked populations and advanced tracking technologies.

Chapter 4 – General discussion

Dispersal is one of the most important behavioural and life history traits, with far-reaching consequences for ecology, evolution and conservation (Clobert et al., 2009; Clobert, 2012). However, despite a wealth of research across many taxa, key knowledge gaps remain. In particular, the early life determinants of variation in natal dispersal, and the behavioural and spatiotemporal dynamics of the post-fledging period remain poorly understood. Capitalising on the dipper's linear habitat and ecology, this thesis used a combination of long-term data analysis and field observations of a marked population to obtain novel insights into these processes.

In Chapter 2, I investigated how a number of measures relating to early life conditions influence dispersal distance, using both Euclidean distance, which most dispersal studies rely on (Verhulst et al., 1997; Suh et al., 2020), and instream distance, which is likely a more reliable representation of the true distance travelled. For both measures, I found that females dispersed further than males, which was expected as this is the most common pattern in passerine species (Dhondt and Hublé, 1968; Greenwood et al., 1979; Clarke et al., 1997). Furthermore, I also found potential evidence, albeit weak, for condition-dependent dispersal, with individuals that were in better conditions as nestlings dispersing shorter distances. However, this effect was only detected in the analysis of instream distance. While condition-dependent dispersal has been demonstrated in a number of species (Barbraud et al., 2003; Debeffe et al., 2012; Hewison et al., 2021), this is one of relatively few studies to link dispersal distance with body condition in the early part of life. This adds to our knowledge that nutrition and growth during early life have long-term consequences, including through the impact on dispersal. Here, the negative correlation suggests that staying local is advantageous, but studies of the fitness consequences are now needed to analyse this trend.

The discrepancy between the analyses of Euclidean and instream distances highlights the importance of measuring dispersal distances in a biologically meaningful way. Here, potentially critical effects would have been missed if relying on Euclidean distance alone, as most studies do. While similar measures of instream distance have been used for other riverine organisms (Watts et al., 2006; Chaput-Bardy et al., 2008), it is extremely challenging to make more reliable measures in most terrestrial and marine species based on observations alone. Radio-tracking has been useful (Anders et al., 1998; Grüebler and Naef-Daenzer, 2008a; Ausprey and Rodewald, 2013), but is labour intensive and tends to produce a series of intermittent fixes rather than continuous data; however, GPS trackers and similar devices have revolutionised the options (López-López, 2016).

In Chapter 3, observations of the post-fledging period provided some of the first descriptions of fledgling provisioning and juvenile movements in this species. The results suggest that there is a division of labour among the parents, and therefore it appears that brood division is a common strategy used by parents, and that males provide greater provisioning to young, possibly to maximise the chances of having a second brood sooner or because females have incurred greater reproductive costs (Stodola et al., 2009; Nomi et al., 2018; Darrah and van Riper III, 2021). In addition, the findings demonstrate variation in the age of departure from the natal territory, and that juveniles are highly mobile shortly after leaving the nest, engaging in large movements within only a few weeks of fledging. Age of departure from the natal site is often considered to be the first stage of natal dispersal, yet remains one of the least studied aspects of the process (Ausprey and Rodewald, 2013). Variation in age of departure has been previously linked to condition (Grüebler and Naef-Daenzer, 2008a; Saino et al., 2012), and a non-significant trend for a positive correlation in this study may be worthy of further study. Indeed, such a link may be part of the mechanism that underpins the condition-dependence in dispersal distance. Further studies of the post-fledging period in birds, and in particular the links between parental behaviour, condition, and early juvenile movements, is essential for a better understanding of not only natal dispersal but also offspring survival. This is arguably the most significant gap in our knowledge of avian life histories, with major implications for ecological and conservation initiatives (Engler and Krone, 2021; Şahin-Arslan and Martin, 2021). This is especially important for understanding how wildlife responds to environmental change.

This study is hindered by small sample sizes and requires further work to detect potentially subtle underlying determinants of dispersal distance. A larger sample and additional measures of body size might help strengthen the statistical analysis of a condition effect in Chapter 2. On top of this, a larger sample would allow for more robust statistical analyses in Chapter 3, which would allow for more confident conclusions of provisioning rates, and of the likelihood of brood division, to be drawn. While this study made use of measures of instream distance, which provides a much more accurate approximation of the true dispersal distance an individual travels, measures are still prone to study site biases and dispersal distances are likely to be underestimated.

The future of dispersal research is unquestionably dependent on the fast-growing development of tracking technology. Recent advancements in the use of GPS devices and other bio-loggers is bringing the study of animal movements into the realm of big data (Kays et al., 2015; López-López, 2016). These technologies are able to generate precise information on animal movements including dispersal (Morales et al., 2010), and are being increasingly used in wildlife studies (Wolfson et al., 2020; Engler and Krone, 2021; Hewison et al., 2021).

This opens up the best opportunity to eliminate spatial biases and dispersal underestimates (Koenig et al., 1996; Sharp et al., 2008a). As both the size and the cost of these devices comes down, it is becoming possible to gather data remotely on movements in real time, even for relatively small animals such as passerines (Brown and Taylor, 2015; Bernath-Plaisted et al., 2021; Feldman et al., 2021). However, while this technology is revolutionising the study of animal movements, to really develop our understanding of dispersal, we will still need long-term studies of marked populations. Combining both methods would allow precise measures of movements during transience, and dispersal distance distributions with little or no bias, to be obtained. Moreover, with these more accurate metrics, further analyses of the underlying causes such as early life conditions and age of departure could be conducted, and, importantly, this would allow consequences for individual fitness and population dynamics to be investigated.

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Appendix

Table 1. The best-fitting generalised linear models for the factors associated with (A) Euclidean dispersal distance and (B) instream dispersal distance of dippers in the Yorkshire Dales National Park, UK. All combinations of explanatory variables and their interactions were fitted. Only the best-fitting models which were those within a delta AICc of 2 of the best overall model are shown. Values are the parameter estimates for each variable. Weight represents the normalised model likelihoods, and the null (intercept only) model is shown for comparison.

(A) glm(Euclidean Dispersal Distance ~ Sex + Hatch date + Brood Size + Population Density + Body Condition + Hatch Date: Sex + Brood Size: Sex + Population Density: Sex + Condition: Sex).

Intercept	Sex	Hatch Date	Brood Size	Population Density	Body Condition	Hatch Date x Sex	Brood Size x Sex	Population Density x Sex	Condition x Sex	df	logLik	AICc	delta	weight
8.28	-0.741									3	-610.99	1228.34	**0.00**	0.19
8.27	-0.723	-0.003								4	-610.68	1229.95	**1.61**	0.08
8.28	+				-0.004					4	-610.95	1230.49	2.15	0.06
8.28	+			-0.004						4	-610.96	1230.53	2.19	0.06
8.28	+		+							4	-610.99	1230.58	2.24	0.06
8.29	+			-0.034				+		5	-609.97	1230.85	2.51	0.05
8.32	+				0.022				+	5	-610.17	1231.24	2.91	0.04
8.25	+	-0.007				+				5	-610.30	1231.50	3.17	0.04
8.27	+	-0.003		-0.006						5	-610.59	1232.09	3.75	0.03
8.26	+	-0.003			-0.003					5	-610.65	1232.21	3.87	0.02
8.26	+	-0.003	+							5	-610.67	1232.25	3.91	0.02
8.27	+	-0.003		-0.037				+		6	-609.55	1232.39	4.05	0.02
8.28	+			-0.005	-0.005					5	-610.90	1232.71	4.37	0.02
8.31	+		+				+			5	-610.93	1232.78	4.44	0.02
8.27	+		+		-0.004					5	-610.94	1232.80	4.46	0.02
8.28	+		+	-0.004						5	-610.96	1232.84	4.50	0.02
8.28	+			-0.036	-0.006			+		6	-609.87	1233.03	4.69	0.02
8.29	+		+	-0.034				+		6	-609.96	1233.22	4.88	0.01
8.30	+	-0.002			0.020				+	6	-609.96	1233.22	4.88	0.01
8.24	+	-0.009		-0.042		+		+		7	-608.83	1233.41	5.07	0.01

8.33	+		+		0.023				+	6	-610.15	1233.59	5.25	0.01
8.32	+			-0.003	0.021				+	6	-610.15	1233.60	5.26	0.01
8.25	+	-0.007		-0.006		+				6	-610.21	1233.72	5.38	0.01
8.25	+	-0.007			-0.004	+				6	-610.24	1233.77	5.43	0.01
8.24	+	-0.007	+			+				6	-610.28	1233.86	5.52	0.01
8.26	+	-0.003		-0.007	-0.004					6	-610.54	1234.37	6.03	0.01
8.26	+	-0.003	+	-0.006						6	-610.58	1234.46	6.12	0.01
8.29	+	-0.003	+				+			6	-610.63	1234.55	6.21	0.01
8.25	+	-0.003	+		-0.004					6	-610.63	1234.56	6.22	0.01
8.26	+	-0.003		-0.039	-0.005			+		7	-609.46	1234.67	6.33	0.01
8.31	+			-0.029	0.013			+	+	7	-609.49	1234.73	6.39	0.01
8.28	+	-0.006			0.019	+			+	7	-609.53	1234.82	6.48	0.01
8.27	+	-0.003	+	-0.037				+		7	-609.55	1234.85	6.51	0.01
8.27	+		+	-0.005	-0.005					6	-610.90	1235.08	6.75	0.01
8.31	+		+	-0.004			+			6	-610.90	1235.09	6.75	0.01
8.30	+		+		-0.003		+			6	-610.90	1235.09	6.75	0.01
8.43	+		+		0.032		+		+	7	-609.79	1235.34	7.00	0.01
8.33	+		+	-0.035			+	+		7	-609.86	1235.48	7.14	0.00
8.28	+		+	-0.036	-0.006			+		7	-609.87	1235.48	7.14	0.00
8.30	+	-0.003		-0.005	0.019				+	7	-609.91	1235.57	7.23	0.00
8.23	+	-0.009		-0.045	-0.008	+		+		8	-608.65	1235.58	7.24	0.00
8.31	+	-0.002	+		0.021				+	7	-609.96	1235.67	7.33	0.00
8.24	+	-0.009	+	-0.042		+		+		8	-608.83	1235.95	7.61	0.00
8.24	+	-0.007		-0.007	-0.006	+				7	-610.12	1236.00	7.66	0.00
8.33	+		+	-0.003	0.022				+	7	-610.14	1236.02	7.69	0.00
8.24	+	-0.007	+	-0.006		+				7	-610.20	1236.14	7.81	0.00
8.23	+	-0.007	+		-0.005	+				7	-610.21	1236.17	7.83	0.00
8.25	+	-0.007	+			+	+			7	-610.27	1236.30	7.96	0.00
8.29	+	-0.003		-0.033	0.010			+	+	8	-609.18	1236.65	8.32	0.00
8.24	+	-0.003	+	-0.008	-0.005					7	-610.51	1236.78	8.44	0.00
8.28	+	-0.003	+	-0.007			+			7	-610.53	1236.81	8.47	0.00
8.27	+	-0.003	+		-0.003		+			7	-610.60	1236.95	8.62	0.00

8.25	+	-0.003	+	-0.039	-0.006				+	8	-609.46	1237.20	8.86	0.00
8.32	+		+	-0.029	0.014			+	+	8	-609.46	1237.21	8.88	0.00
8.30	+	-0.003	+	-0.038			+	+		8	-609.47	1237.23	8.89	0.00
8.28	+	-0.007		-0.005	0.017	+			+	8	-609.48	1237.24	8.91	0.00
8.28	+	-0.006	+		0.019	+			+	8	-609.53	1237.36	9.02	0.00
8.30	+		+	-0.005	-0.004		+			7	-610.84	1237.44	9.10	0.00
8.40	+	-0.002	+		0.030		+		+	8	-609.66	1237.61	9.27	0.00
8.25	+	-0.008		-0.039	0.006	+		+	+	9	-608.41	1237.73	9.39	0.00
8.43	+		+	-0.003	0.031		+		+	8	-609.78	1237.84	9.50	0.00
8.31	+		+	-0.037	-0.005		+	+		8	-609.79	1237.87	9.53	0.00
8.30	+	-0.003	+	-0.005	0.019				+	8	-609.91	1238.11	9.77	0.00
8.22	+	-0.009	+	-0.045	-0.008	+		+		9	-608.63	1238.17	9.83	0.00
8.22	+	-0.008	+	-0.008	-0.007	+				8	-610.08	1238.44	10.10	0.00
8.26	+	-0.009	+	-0.042		+	+	+		9	-608.81	1238.52	10.18	0.00
8.25	+	-0.007	+	-0.007		+	+			8	-610.18	1238.65	10.31	0.00
8.23	+	-0.007	+		-0.005	+	+			8	-610.21	1238.70	10.36	0.00
8.41	+		+	-0.029	0.023		+	+	+	9	-609.15	1239.20	10.86	0.00
8.27	+	-0.003	+	-0.008	-0.005		+			8	-610.47	1239.23	10.89	0.00
8.29	+	-0.003	+	-0.033	0.011			+	+	9	-609.18	1239.27	10.93	0.00
8.36	+	-0.006	+		0.026	+	+		+	9	-609.37	1239.64	11.30	0.00
8.28	+	-0.003	+	-0.040	-0.005		+	+		9	-609.40	1239.69	11.36	0.00
8.28	+	-0.007	+	-0.005	0.017	+			+	9	-609.48	1239.86	11.52	0.00
8.39	+	-0.002	+	-0.005	0.028		+		+	9	-609.61	1240.12	11.78	0.00
8.25	+	-0.008	+	-0.039	0.006	+		+	+	10	-608.41	1240.43	12.09	0.00
8.23	+	-0.009	+	-0.045	-0.008	+	+	+		10	-608.63	1240.86	12.52	0.00
8.23	+	-0.007	+	-0.008	-0.006	+	+			9	-610.07	1241.05	12.71	0.00
8.38	+	-0.003	+	-0.032	0.019		+	+	+	10	-608.93	1241.47	13.13	0.00
8.35	+	-0.006	+	-0.005	0.024	+	+		+	10	-609.31	1242.23	13.89	0.00
8.31	+	-0.008	+	-0.038	0.011	+	+	+	+	11	-608.33	1243.05	14.71	0.00
7.86		-0.007								13	-624.32	1255.00	26.66	0.00

Intercept	Hatch Date	Brood Size	Population Density	Body Condition	df	logLik	AICc	delta	weight
7.88					2	-625.49	1255.15	26.81	0.00
7.87				-0.022	3	-624.55	1255.45	27.11	0.00
7.86	-0.006			-0.019	4	-623.54	1255.68	27.34	0.00
7.86	-0.007		-0.015		4	-623.97	1256.53	28.19	0.00
7.86	-0.007		-0.021	-0.023	5	-622.89	1256.69	28.36	0.00
7.87			-0.015	-0.025	4	-624.20	1256.99	28.65	0.00
7.88			-0.009		3	-625.35	1257.06	28.72	0.00
7.90		+			3	-625.44	1257.22	28.89	0.00
7.87	-0.007	+			4	-624.32	1257.24	28.90	0.00
7.87		+		-0.022	4	-624.54	1257.68	29.35	0.00
7.83	-0.006	+		-0.021	5	-623.49	1257.89	29.55	0.00
7.87	-0.007	+	-0.015		5	-623.97	1258.84	30.50	0.00
7.82	-0.008	+	-0.022	-0.025	6	-622.79	1258.87	30.53	0.00
7.90		+	-0.010		4	-625.30	1259.19	30.86	0.00
7.86		+	-0.015	-0.025	5	-624.19	1259.28	30.95	0.00

(B) glm(Instream Dispersal Distance ~ Sex + Hatch date + Brood Size + Population Density + Body Condition + Hatch Date: Sex + Brood Size: Sex + Population Density: Sex + Condition: Sex).

Intercept	Sex	Hatch Date	Brood Size	Population Density	Body Condition	Hatch Date x Sex	Brood Size x Sex	Population Density x Sex	Condition x Sex	df	logLik	AICc	delta	weight
8.87	-0.718				-0.030					4	-669.08	1346.76	**0.00**	0.11
8.75	-0.726		0.235		-0.035					5	-668.11	1347.12	**0.36**	0.09
8.93	-0.761				0.006				-0.050	5	-668.29	1347.48	**0.73**	0.08
8.92	-0.772									3	-670.57	1347.49	**0.73**	0.08
8.81	-0.761		0.199		-0.006				-0.040	6	-667.61	1348.51	**1.76**	0.05
8.84	+		+							4	-670.11	1348.81	2.05	0.03
8.87	+			-0.008	-0.031					5	-669.00	1348.92	2.16	0.03
8.87	+	0.000			-0.030					5	-669.08	1349.07	2.31	0.03
8.74	+		+	-0.012	-0.038					6	-667.94	1349.18	2.42	0.03
8.79	+		+		-0.034		+			6	-668.02	1349.34	2.58	0.03
8.74	+	-0.001	+		-0.035					6	-668.09	1349.48	2.72	0.02
8.83	+	-0.007			-0.034	+				6	-668.18	1349.65	2.89	0.02
8.91	+	-0.001								4	-670.55	1349.70	2.94	0.02
8.68	+	-0.009	+		-0.039	+				7	-666.99	1349.73	2.97	0.02

8.92	+			-0.001						4	-670.57	1349.73	2.97	0.02
8.92	+			-0.006	0.004				+	6	-668.24	1349.78	3.02	0.02
8.93	+	0.001			0.006				+	6	-668.28	1349.84	3.08	0.02
8.89	+	-0.007			0.004	+			+	7	-667.23	1350.20	3.44	0.02
8.94	+		+		0.007		+		+	7	-667.25	1350.25	3.50	0.02
8.87	+			-0.037	-0.032			+		6	-668.48	1350.26	3.50	0.02
8.91	+		+				+			5	-669.87	1350.65	3.90	0.01
8.80	+		+	-0.010	-0.009				+	7	-667.50	1350.75	3.99	0.01
8.88	+	-0.007				+				5	-669.99	1350.88	4.13	0.01
8.75	+		+	-0.036	-0.038			+		7	-667.57	1350.89	4.14	0.01
8.81	+	0.000	+		-0.006				+	7	-667.61	1350.97	4.21	0.01
8.83	+	-0.001	+							5	-670.07	1351.04	4.28	0.01
8.84	+		+	-0.003						5	-670.10	1351.11	4.35	0.01
8.75	+	-0.009	+		-0.008	+			+	8	-666.43	1351.14	4.38	0.01
8.92	+			-0.028				+		5	-670.13	1351.17	4.41	0.01
8.86	+	-0.001		-0.009	-0.031					6	-668.99	1351.28	4.52	0.01
8.79	+		+	-0.013	-0.037		+			7	-667.84	1351.42	4.66	0.01
8.72	+	-0.002	+	-0.015	-0.038					7	-667.87	1351.49	4.73	0.01
8.92	+			-0.029	-0.002			+	+	7	-667.95	1351.65	4.90	0.01
8.66	+	-0.011	+	-0.015	-0.041	+				8	-666.74	1351.77	5.01	0.01
8.79	+	-0.001	+		-0.034		+			7	-668.01	1351.78	5.02	0.01
8.80	+	-0.012		-0.058	-0.038	+		+		8	-666.76	1351.80	5.04	0.01
8.82	+	-0.008		-0.010	-0.035	+				7	-668.08	1351.91	5.15	0.01
8.91	+	-0.001		-0.003						5	-670.54	1351.99	5.23	0.01
8.78	+	-0.009	+			+				6	-669.37	1352.04	5.28	0.01
8.65	+	-0.014	+	-0.059	-0.043	+		+		9	-665.61	1352.12	5.36	0.01
8.93	+	0.000		-0.006	0.004				+	7	-668.24	1352.23	5.47	0.01
8.70	+	-0.009	+		-0.038	+	+			8	-666.98	1352.25	5.50	0.01
8.93	+		+	-0.011	0.004		+		+	8	-667.11	1352.50	5.74	0.01
8.88	+	-0.008		-0.006	0.002	+			+	8	-667.19	1352.66	5.90	0.00
8.86	+	-0.001		-0.039	-0.032			+		7	-668.46	1352.67	5.92	0.00
8.94	+	0.000	+		0.007		+		+	8	-667.25	1352.78	6.03	0.00
8.85	+		+	-0.026				+		6	-669.76	1352.81	6.05	0.00
8.80	+		+	-0.029	-0.014			+	+	8	-667.27	1352.83	6.07	0.00
8.90	+	-0.001	+				+			6	-669.85	1352.99	6.24	0.00
8.91	+		+	-0.004			+			6	-669.85	1352.99	6.24	0.00
8.80	+		+	-0.037	-0.037		+	+		8	-667.46	1353.21	6.45	0.00
8.78	+	-0.001	+	-0.012	-0.010				+	8	-667.48	1353.24	6.48	0.00
8.88	+	-0.008		-0.003		+				6	-669.98	1353.24	6.49	0.00

8.73	+	-0.002	+	-0.039	-0.038			+		8	-667.49	1353.26	6.50	0.00
8.82	+	-0.002	+	-0.005						6	-670.04	1353.37	6.61	0.00
8.85	+	-0.011		-0.049	-0.010	+		+	+	9	-666.26	1353.42	6.66	0.00
8.73	+	-0.010	+	-0.012	-0.013	+			+	9	-666.28	1353.46	6.70	0.00
8.91	+	-0.002		-0.031				+		6	-670.09	1353.47	6.71	0.00
8.84	+	-0.008	+		-0.001	+	+		+	9	-666.29	1353.48	6.72	0.00
8.87	+	-0.011		-0.045		+		+		7	-669.01	1353.78	7.02	0.00
8.77	+	-0.002	+	-0.016	-0.037		+			8	-667.76	1353.81	7.06	0.00
8.92	+	0.000		-0.029	-0.002			+	+	8	-667.95	1354.19	7.43	0.00
8.84	+	-0.008	+			+	+			7	-669.25	1354.25	7.50	0.00
8.68	+	-0.010	+	-0.015	-0.041	+	+			9	-666.73	1354.36	7.60	0.00
8.70	+	-0.013	+	-0.052	-0.024	+		+	+	10	-665.40	1354.40	7.64	0.00
8.78	+	-0.009	+	-0.005		+				7	-669.34	1354.43	7.67	0.00
8.93	+		+	-0.029			+	+		7	-669.50	1354.74	7.98	0.00
8.92	+		+	-0.029	-0.001		+	+	+	9	-666.92	1354.75	7.99	0.00
8.66	+	-0.014	+	-0.059	-0.043	+	+	+		10	-665.61	1354.82	8.06	0.00
8.92	+	-0.001	+	-0.012	0.003		+		+	9	-667.10	1355.10	8.34	0.00
8.83	+	-0.002	+	-0.029				+		7	-669.69	1355.12	8.36	0.00
8.78	+	-0.012	+	-0.044		+		+		8	-668.50	1355.28	8.52	0.00
8.90	+	-0.002	+	-0.007			+			7	-669.81	1355.36	8.61	0.00
8.78	+	-0.002	+	-0.032	-0.016			+	+	9	-667.23	1355.37	8.62	0.00
8.78	+	-0.002	+	-0.040	-0.037		+	+		9	-667.38	1355.66	8.90	0.00
8.82	+	-0.009	+	-0.012	-0.005	+	+		+	10	-666.13	1355.87	9.11	0.00
8.84	+	-0.008	+	-0.006		+	+			8	-669.21	1356.70	9.95	0.00
8.76	+	-0.012	+	-0.051	-0.018	+	+	+	+	11	-665.34	1357.09	10.33	0.00
8.91	+	-0.002	+	-0.031			+	+		8	-669.44	1357.17	10.41	0.00
8.91	+	-0.001	+	-0.031	-0.003		+	+	+	10	-666.90	1357.41	10.66	0.00
8.83	+	-0.011	+	-0.045		+	+	+		9	-668.38	1357.65	10.90	0.00
8.47					-0.047					3	-677.10	1360.55	13.79	0.00
8.35			+		-0.054					4	-676.36	1361.31	14.56	0.00
8.47		-0.004			-0.045					4	-676.80	1362.20	15.44	0.00
8.47				-0.017	-0.050					4	-676.81	1362.22	15.46	0.00
8.32		-0.005	+		-0.052					5	-675.89	1362.69	15.93	0.00
8.34			+	-0.021	-0.059					5	-675.95	1362.81	16.05	0.00
8.29		-0.008	+	-0.032	-0.058					6	-675.02	1363.33	16.57	0.00

8.46	-0.006		-0.025	-0.048		5	-676.25	1363.40	16.64	0.00
8.50						2	-679.82	1363.82	17.06	0.00
8.49	-0.005					3	-679.31	1364.97	18.21	0.00
8.45		+				3	-679.72	1365.80	19.04	0.00
8.50			-0.007			3	-679.78	1365.91	19.15	0.00
8.48	-0.007		-0.016			4	-679.10	1366.79	20.03	0.00
8.42	-0.006	+				4	-679.13	1366.85	20.09	0.00
8.45		+	-0.007			4	-679.68	1367.95	21.20	0.00
8.42	-0.007	+	-0.017			5	-678.89	1368.68	21.92	0.00