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Responses to global change in a river passerine

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A thesis submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy at University College Cork

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Research Supervisors:

Prof. John O'Halloran

Prof. John L. Quinn

Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.

Darío Fernández-Bellon

Summary

Human-induced environmental change is affecting biodiversity across the world. River systems and species associated with these habtitats are particularly vulnerable to the different drivers of global change (e.g. land use, climate change, pollution). Understanding how species respond to these drivers is key for any attempts to address and minimise the effects of global change. In this thesis I focus on a river passerine, the white-throated dipper *Cinclus cinclus*, as a model to assess the effects of two of the main drivers affecting river ecosystems (land use and climate change) on different ecological traits across multiple scales and life stages. Breeding phenology (Chapter 2) was influenced by climate and land use at different scales, but the interactive effect of climate and land use was significant only at local scales. Lay dates were advanced for nests in areas dominated by farmland and under conditions of increased rainfall and warmer temperatures. Land use also affected stress hormones in developing nestlings (Chapter 3): higher forest cover in the riparian area was linked to lower nestling stress hormone levels but had no apparent effect on morphological traits traditionally associated with nestling development. This land use signal on stress hormones however, was no longer evident in later life (Chapter 4), when stress hormone variation had a strong year component, likely due to weather patterns. Climate also appeared to be associated with long-term morphological change (Chapter 5). Female and male dippers experienced a relative shortening of the wing in relation to body size, reducing dimorphism between the sexes during a period concurrent with increased magnitude and fluctuations in river flow conditions. Overall, these findings suggest that dippers are adjusting their phenology, physiology and morphology in response to global change. However, adjustments in one trait may have adverse consequences for other traits. This thesis highlights the value of using multiple approaches to understand how species respond to global change, and the importance of considering multiple drivers of environmental change.

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Thesis structure

The data chapters in this thesis are written as stand alone manuscripts and formatted for submission to peer-reviewed journals. For this reason, there is a certain amount of repetition, especially in the introduction and methods sections of some chapters. For ease of reading, tables and figures are embedded in the text. Authors and their contributions are listed at the beginning of each chapter.

Chapter 1

General introduction



Biodiversity and ecosystems across the globe are currently changing at rates unprecedented in human history (MEA 2005, Ripple et al. 2017). This period of human-driven global changes known as the Anthropocene (Steffen et al. 2007) has been linked to large-scale changes in biogeochemical cycles (CO_2 emissions, changes in water cycles, release of fertilizers and pollutants into the environment), climate (ozone layer depletion and global warming), land use (land clearing, grazing, afforestation, and urbanization), and biodiversity (species invasions, harvesting, and extinctions) (Vitousek 1994, Vitousek et al. 1997, Steffen et al. 2011). On the biodiversity front, human impacts on the environment are causing changes in the distribution of species on a global scale (Chapin III et al. 2000) and have triggered the sixth major extinction event in the history of life (Barnosky et al. 2011). As a result, ecosystem services beneficial for humans are being lost, negative repercussions for the global economy have been registered, and effects on human well-being and associated human costs are becoming more frequent (Chapin III et al. 2000, Díaz et al. 2006). In this context, understanding whether and how species respond to drivers of global change is crucial to address and minimise biodiversity loss.

Despite the existence of general patterns of response to global change drivers (Walther et al. 2002), there is considerable variability in the sensitivity and response of individual species (Tylianakis et al. 2008). For instance, although distributions of plants, invertebrates and vertebrates have shown an overall shift to higher elevations and latitudes as a response to climate change, there is a wide diversity in the direction and rates of shifts by individual species (Chen et al. 2011). Variability in responses exists not only between species, but also between populations of the same species (Charmantier et al. 2008) and between individuals of the same population (Reed et al. 2009). Within populations, responses can be specific to a wide range of factors including sex (Chin et al. 2005, Petry et al. 2016), stage within the annual cycle (e.g. dispersal, breeding, migration) (Small-Lorenz et al. 2013, Marra et al. 2015, Saunders et al. 2018), life stage (Pankhurst and Munday 2011, Radchuk et al. 2013), colour polymorphism (Roulin 2014) or behaviour (Sih 2013).

Our understanding of this broad variation in sensitivity and responses to environmental change is complicated by the difficulty of detecting these environmental effects. The signal of global change drivers is often weak or indirect

and can be confounded by other factors (Walther et al. 2002, Oliver and Morecroft 2014). Even if they exist, effects can occur at some spatial or temporal scales but not others (Rogers and Schindler 2011, Logan et al. 2013). Furthermore, variability in responses can be magnified when the effects of multiple, rather than single, drivers are taken into consideration (Oliver and Morecroft 2014). Different drivers can have non-additive or synergistic effects, modifying how we interpret a species' response to global change (Brook et al. 2008, de Sassi et al. 2012).

Climate and land use modification are two of the main drivers of global change (Parmesan and Yohe 2003, Foley et al. 2005, Feddema et al. 2005). Climate change has been identified as a major threat to ecosystems and biodiversity (Walther et al. 2002, Walther 2010), with one in six species expected to face extinction if current trends in global warming are maintained (Urban 2015). However, range contractions of many species are driven by anthropogenic land conversions rather than climate change (Jetz et al. 2007, Nilsson et al. 2008). Changes in land use can result in habitat fragmentation and loss, but also lead to increased release of pollutants into the environment (Foley et al. 2005, Haddad et al. 2015) with widespread consequences for different taxa (Flynn et al. 2009, Pekin and Pijanowski 2012). In fact, the combined effect of land use conversion and climate change can be critical for the survival of many species. For example, some species are experiencing range shifts tracking changes in climate, but these shifts may be truncated if their new optimal distributions are limited by habitat loss and land use changes (Feeley and Silman 2010). Conversely, land use can also mitigate the effects of climate change, either through increased permeability allowing for range shifts (Mawdsley et al. 2009) or through active buffering of climatic effects (Thomas et al. 2016). Despite the importance of these processes, research on the impacts of global change have centred on the effects of climate and largely neglected changes in land use, or combined effects (Titeux et al. 2016).

The combined effects of climate change and land use are particularly relevant for river systems (Carpenter et al. 2011). Climate change has direct effects on rivers through precipitation-induced alterations to flow regimes, but also through changes in temperature which affect water chemistry and biotic interactions (Kundzewicz et al. 2008, Arnell and Gosling 2016). Rivers and streams are also heavily influenced by

land use. Instream habitat structure, water chemistry and flow regimes are affected not only by processes occurring in the riparian zone but also in the wider catchment (Allan 2004), and in fact, "in every respect, the valley rules the stream" (Hynes 1975). Land use cover across the catchment and riparian areas can affect run-off rates, erosion and river flow, with important consequences for stream integrity and hydrological processes (Allan et al. 1997, DeFries and Eshleman 2004). These processes not only affect stream abiotic properties, but also have profound consequences for the biotic components of river ecosystems (Mantyka-Pringle et al. 2014, Thomas et al. 2015, Jackson et al. 2016). River species thus have the potential to be affected by environmental changes occurring, not only in their immediate home ranges within the river system, but also in the upstream stretches and in the wider catchment area. As a consequence of this sensitivity to environmental change, rivers are currently among the most altered ecosystems on the planet (Carpenter et al. 2011), with higher rates of declines in biodiversity than other habitats (Jenkins 2003, Balian et al. 2008, Vörösmarty et al. 2010).

Here I present work exploring the responses to global change in a river species using the white-throated dipper *Cinclus cinclus* as a study model. Dippers are uniquely linked to rivers on which they depend for all aspects of their life cycle. They are found along streams and rivers in upland and mountainous areas, and, along with the four other species in the dipper family (Cinclidae), they are uniquely adapted among passerines to swimming and diving in fast-flowing waters (Ormerod and Tyler 2005). Morphological adaptations to this lifestyle include short, broad and muscular wings for swimming in strong currents; long, strong legs with sharp curved claws for gripping and turning small stones; narrow nostrils which can be closed by means of nasal flaps during diving; and abundant body contour feathers for warmth and insulation (Ormerod and Tyler 2005). These distinctive characteristics allow dippers to prey on underwater macroinvertebrates (Taylor and O'Halloran 1997, Ormerod and Tyler 2005) and small fish or fish eggs where these are available (Obermeyer et al. 2006, Morrissey et al. 2012), exploiting a trophic niche inaccessible to most birds. Dippers build nests close to or over running water, in crevices or ledges on rock walls, waterfalls, or earth banks. Artificial sites such as holes or ledges in stone bridges are readily used where these are available. Birds use these sites to build a dome-like structure out of mud and moss measuring up to 30-45 cm in diameter

which provides waterproofing, insulation and concealment. Although local factors can influence time of breeding, dipper species tend to nest earlier than other passerine species (Tyler and Ormerod 1994). Location of nest sites ensures that predation is marginal, resulting in high hatching and fledging rates compared to other passerines (Tyler and Ormerod 1994). Double-brooding is hugely dependent on local factors (e.g. date of first broods, habitat quality, food availability) but is frequent in some areas (Ormerod et al. 1991, Ormerod and Tyler 2005). Once fledged, young are dependent on the adults for 1-2 weeks but often remain in their parents' territory for longer periods. Dispersal, as all other aspects of dipper ecology, is generally constrained to following river systems. Once birds establish a territory, they display high site fidelity and movements of adult birds are rare (Tyler and Ormerod 1994, O'Halloran et al. 2000).

The ecological dependence of dippers on riparian habitats makes them susceptible to changes in physical and biological processes occurring within these ecosystems. Prey abundance and accessibility are influenced by river flow, structure and water quality (Ormerod et al. 1991, Taylor and O'Halloran 2001, Chen and Wang 2010), while physical features provide nest sites and perches for foraging and roosting (Ormerod and Tyler 2005). During the breeding season, breeding pairs and nestlings are dependent on the resources available within a limited stretch of river determined by territory size, increasing their potential to reflect ecosystem conditions within a certain area (Sullivan and Vierling 2012). These conditions are determined by processes acting within the territory, but, due to the dendritic nature of rivers, they are also influenced by processes operating up river and in other parts of the watershed (Vannote et al. 1980, Campbell Grant et al. 2007). As a result, dippers can act as indicators of habitat quality within small stretches of river, but they can also serve as a tool to evaluate the environmental health of larger areas of influence.

To provide a comprehensive understanding of how a river species responds to global change this work evaluates the combined effects of the two main drivers of global change in river systems (climate change and land use); how effects vary across different life stages (breeding, nestlings, juveniles and adults); and variations in responses of different aspects of the species' ecology (phenology, physiology and morphology). The approaches used throughout this thesis are aimed at overcoming

issues associated with the detectability of effects of environmental change highlighted by previous work (Oliver and Morecroft 2014): analysis of driver effects across multiple spatial and temporal scales improve our ability to detect and understand underlying processes (Rogers and Schindler 2011, Nadeau et al. 2017) while large data sets covering broad geographical (20 – 46 rivers) and temporal scales (25 – 34 years) allow for detection of weak or confounded environmental signals (Magurran et al. 2010, Oliver and Morecroft 2014).

The specific aims of this thesis were:

- To assess how climate change, land use and their interactions influence breeding phenology across multiple spatial and temporal scales (Chapter 2).
- To compare morphological and physiological variables as measures of factors influencing early development with a particular focus on the effects of land use (Chapter 3).
- To evaluate how environmental effects important during early development affect individuals at later life stages (Chapter 4).
- To assess phenotypic variation over time in changing environments (Chapter 5).

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Chapter 2

Climate, land use, and spatio-temporal scale have interacting effects on the breeding phenology of a freshwater insectivorous bird



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Abstract

Detecting the effects of global change drivers and their interactions on species is a major challenge in ecology. Although climate change and land use have been identified as two of the main drivers of global change, most research to date has focused on the effects of these drivers in isolation. Furthermore, when interactions are studied, the possibility that effects may vary spatially and temporally is often overlooked. Inappropriate selection of predictors and spatio-temporal scales can preclude detection of effects or result in an incomplete understanding of underlying processes. Using a 34-year data set, we investigated the effect of climate, land use and their interactions on the breeding phenology of a passerine intimately linked to river systems, the white-throated dipper *Cinclus cinclus*. We evaluated effects of large and local scale climate predictors using a sliding window approach, of land use cover at catchment-wide and territory scales, and of the interactions between climate and land use at all scales. Lay dates were influenced by climate and land use factors at multiple scales. Lay dates were generally advanced under positive North Atlantic Oscillation index phases, under increased rainfall, and in areas dominated by farmland and with low forest cover. Interactions between climate and land use were only significant for

local climate (rainfall) at the catchment scale. In these interactions, rainfall was the dominating driver of lay date in all scenarios, while the effect of land use was climate-dependent and was strongest during dry periods but buffered during rainy periods. During the 34-year period, lay dates appeared relatively stable in comparison to other populations, possibly due to lower rates of climate change in Ireland and the buffering effects of land use. Overall, our results show that interactions between land use and climate influence dipper breeding phenology. These effects were scale-specific, and would therefore not be detectable by single-scale studies. Combined with the relatively homogeneous nature of our study system (i.e. relatively low variation in climate patterns, land use cover and river water quality compared to other studies), this highlights the importance of multi-scale approaches for detecting interactions between global change drivers and their effects on species.

Keywords: breeding phenology, climate change, *Cinclus cinclus*, global change, land use, lay date, sliding windows, spatial scale, temporal scale, white-throated dipper.

1 Introduction

Global change is affecting community composition, ecosystem functioning, and the range and abundance of species across the world (Pereira et al. 2010). In recent decades, many of the drivers behind these changes have accelerated, with serious consequences for biodiversity and humanity (Ripple et al. 2017). Climate change and land use transformation in particular have been recognised as two of the main drivers of global change (Titeux et al. 2016). Climate change has led to rising sea levels, melting of polar ice caps and increased frequency of extreme weather events (McLean et al. 2001, Coumou and Rahmstorf 2012), while changes in land use have resulted in the destruction and fragmentation of natural habitats, and an increased release of chemicals and pollutants into the environment (Bu et al. 2014, Haddad et al. 2015, Smith et al. 2016). Both drivers have also been shown to influence distribution, population dynamics and phenology across a wide range of taxa (Parmesan and Yohe 2003, Jetz et al. 2007, Barbet-Massin et al. 2012).

Despite growing efforts to understand how climate change and land use affect biodiversity, the interactions between these drivers are rarely assessed and poorly understood (Oliver and Morecroft 2014). Detecting such interactions is fraught with difficulties. First, interactions may be weak, and only detectable with large data sets (Walther et al. 2002). Second, due to variable effects between species and regions, some study systems may be more sensitive to these processes than others (Sala et al. 2000). Third, appropriate experimental designs and specific analytical tools that are not easily adapted for use on natural systems are often required to allow for detection of these interactions (Oliver and Morecroft 2014). Finally, as interactions may occur only at distinct spatio-temporal scales, the choice of scale or the use of multi-scale analysis may determine our ability to detect driver effects and their interactions (Oliver and Morecroft 2014).

The importance of selecting appropriate spatio-temporal scales has long been recognised in ecology (Wiens 1989, Levin 1992). This is especially relevant when studying variables which vary strongly with scale, as is often the case for studies of climate or land use change. For example, studies of species' extinction risk have reported opposing predictions of species persistence depending on the climate scale

used (Randin et al. 2008, Early and Sax 2011). Selection of the scale of land use factors has also been shown to be critical for understanding their influence on species, for example, when comparing stream versus catchment scales in river systems (Allan 2004, Sponseller et al. 2008). Overall, the temporal and spatial scales of predictors selected need to be relevant to the specific process under study (Rogers and Schindler 2011, Oliver and Morecroft 2014, Nadeau et al. 2017).

Appropriate selection of relevant predictors is also essential for detecting biological processes. While this may seem obvious and is rarely an issue in most ecological research, it is a common problem in studies of weather or climate effects, with many relying on assumptions lacking in empirical evidence to select climate predictors (van de Pol et al. 2016). While knowledge of a study system can help narrow down the potential factors most likely to influence a process (for example drought in species of arid habitats), the choice of a specific variable for analysis (e.g. maximum temperature) over others (average rainfall, days without rain, days above a threshold temperature, etc.) is often made with little or no empirical support. Therefore, to maximise detection of global change driver effects and interactions, and in the absence of a clear mechanistic understanding, there is a need for approaches that evaluate a range of potential predictors across multiple temporal and spatial scales.

In this context, rivers present an ideal system to assess the interactions between climate and land use. River systems are highly sensitive to climatic variation and changes in land use (Jackson et al. 2016), with higher rates of declines in biodiversity reported for freshwater habitats than for many other ecosystems (Jenkins 2003, Balian et al. 2008). Variation in precipitation can lead to important changes in flow regime (e.g. floods, dry river beds), while changes in temperature can have critical effects on the ecosystem's properties (e.g. freezing, changes in pH) (Woodward et al. 2016). Furthermore, due to their dendritic nature and topography, rivers have the potential to be affected by land uses not only in the immediate areas surrounding the river bed, but also in the wider catchment (Allan 2004). As a consequence of rivers' directionality, sites along a river are not independent but instead describe a gradient with regard to factors which can accumulate or difuse along the river continuum (Vannote et al. 1980). This catchment-wide influence and river continuum effect are especially important in the context of increased nutrient run-off and pollution due to

deforestation and agricultural transformation to meet rising food demands (Foley et al. 2011).

Here we take advantage of these characteristics to study the combined effects of climate and land use at multiple scales on the breeding phenology of a vertebrate insectivore. The white-throated dipper (*Cinclus cinclus*) is one of few aquatic passerine species, with unique morphological and physiological adaptations to river life. Dippers feed on aquatic macroinvertebrates, nest along streams, disperse through river systems, and roost over running water (Tyler and Ormerod 1994). This intimate connection to freshwater systems makes the dipper an ideal model species to investigate the effects of climate and land use on river ecosystems, as they can integrate processes occurring not only in their immediate territory, but also in the surrounding areas and across the wider catchment.

Phenological variables provide a useful measure to assess interactions of global change drivers. Phenology has been shown to respond to habitat (Wilkin et al. 2007) or climate (Reed et al. 2013) in some species but not in others (Keogan et al. 2018), with important consequences for breeding rates and population dynamics (Linton and Macdonald 2018). In birds, lay date is an important trait that influences breeding success (Perrins 1970, Verhulst and Nilsson 2008). Shifts in lay date have generally been linked to seasonal fluctuations in food abundance, with climate-induced changes in these patterns resulting in a variety of responses across different bird species (Visser and Both 2005, Burgess et al. 2018, Samplonius et al. 2018). In the case of dippers, global change may affect breeding phenology through direct interactions with the river ecosystem (e.g. flow, water quality) but also through effects on macroinvertebrate prey populations which are susceptible to climate change and land use (Grove et al. 2004, Sponseller et al. 2008).

Using a 34-year data set, we addressed three questions relating to the detection of the effects of global change drivers and their interactions on dipper breeding phenology. (1) Which climatic predictors best explain lay date as a measure of dipper breeding phenology, and during what time periods are these predictors most relevant? (2) Does land use interact with climate to influence lay dates, and if so, what is the

nature of these interactions? (3) How do the scales at which climate and land use are considered affect our understanding of these processes?

2 Methods

2.1 Dipper breeding data

We used breeding data from long-term monitoring of dippers in two study areas, one in south-west Ireland (Cork) and the other in central Ireland (the Slieve Bloom mountains; Fig. 2.1). Nest sites were monitored from 1983 to 2016 in Cork and from 2012 to 2016 in the Slieve Blooms. A total of 191 nest sites were monitored across 37 rivers in Cork and 73 nest sites on 9 rivers in the Slieve Blooms (total n = 264 nest sites). Occupation of sites and monitoring effort varied across years, with a range of 12 to 118 nesting attempts (i.e. full clutch of eggs laid) recorded per year (study median = 49). This resulted in a total of 2166 nesting attempts recorded, of which 1891 were first clutches; the remaining 275 were second and replacement clutches which were excluded from the analysis.

Rivers in both study areas are fast flowing and shallow second or third order streams in landscapes dominated by cattle pasture and other agricultural land uses (>60%), intermixed with patches of plantation (>20%), and to a lesser extent, natural forestry (>5%). Water chemistry is circumneutral with a pH range of 6.8 – 8.8 (Fernández-Bellon and O'Halloran, unpublished data) and generally of low pollution status (Giller and O'Halloran 2004). Elevation ranges from 0 to 270 m above sea level with mean annual minimum and maximum air temperatures of 6 ºC and 13 ºC, and mean annual precipitation of 1207mm. Climate is characterised by mild winters with occasional heavy rainfall, leading to river spates and flooding in late winter or early spring (Steele-Dunne et al. 2008, Gleeson et al. 2013).

Nest finding effort was variable across the study areas, resulting in focal rivers with high coverage (up to one nest/km) while in others only a few nest sites were located and monitored. Dippers in our study areas nested predominantly on man-made structures (e.g. bridges, pipes, walls, nest boxes; 88% of sites) and occasionally on natural features (e.g. upturned roots, boulders; 12% of sites). Each season, sites were

visited three to five times to determine occupation, lay date of the first egg, to ring nestlings, and, after chicks fledged or a nest failed, to detect replacement and second clutches. When lay dates were not observed directly, they were calculated assuming 24-hour laying intervals and 16-day incubation periods (Smiddy et al. 1995), or chick ages based on field workers' experience. See Smiddy et al. (1995) for further details on nest monitoring.

All fieldwork was carried out under licence from the National Parks and Wildlife Service and the British Trust for Ornithology.

2.2 Climate data

To assess climate patterns at a broad geographical scale, we used daily values of the North Atlantic Oscillation (NAO), an index of the difference in atmospheric pressure at sea level between the sub-polar Icelandic low pressure zone and the sub-tropic Azores high pressure zone. In Ireland and north-west Europe, high NAO values are associated with warm and wet weather, while low values are linked to cold and dry spells. Daily values of NAO indices were obtained from the Climate Prediction Center (www.cpc.ncep.noaa.gov). To assess the influence of local climate we downloaded daily rainfall (mm) and minimum daily temperature (ºC) data from Met Éireann (www.met.ie) for three weather stations in the Cork study area (Cork Airport, Moorepark and Dungarvan), and two stations in the Slieve Blooms study area (Gurteen and Nealstown). Each nest site was assigned daily weather values from the nearest station. We used spatial interpolation (Kemp et al. 1983, DeGaetano et al. 1995) to estimate missing daily weather values (< 2% of all data). This was done by averaging data for missing values from three nearby stations (< 40km) with similar weather (mean yearly rain and temperature within ± 5% of target station values).

2.3 GIS data

All nests sites were mapped using ArcMap 10.2 (ESRI, Redlands, California) to characterise site topography and land use with data obtained from the Environmental Protection Agency (EPA) website (http://gis.epa.ie/). We used river gradient (river bed slope in m/m) to describe site topography as this variable reflects changes in

elevation and river order and is key in determining habitat characteristics important for dipper prey populations (e.g. epifaunal substrate and velocity regimes). River gradients were extracted for the location of every nest site and were scaled by log-transformation for analysis. We tested the influence of land use at different scales by measuring land use cover in the territory and in the wider catchment for each nest site (Fig. 2.1c). Territory land use cover was calculated by creating a 125m buffer on each side of the river, following a corridor 500m upstream and 500m downstream from each nest site, as 1 km is the average dipper territory size in Ireland (Hutchinson 2010). Catchment land use was calculated by creating a buffer for each nest site defined by the sub basin (from EPA river GIS files) containing the nest site and all sub basins upstream from it. We used CORINE Landcover data to extract the percentage of farmland (pasture and all other agricultural uses) and forest cover (plantation and natural forestry) for each territory and catchment buffer. CORINE Landcover datasets are available for 1990, 2000, 2006, and 2012. Dipper breeding data from each study year was linked to land use data from the temporally nearest available dataset.

2.4 Climate analysis

We used a two-step approach using generalised linear mixed models (GLMM's) to first determine the best climatic predictors of dipper lay dates and then assess the effect of the interactions between these predictors and land use cover. Climatic predictors in phenological studies are often selected arbitrarily or based on prior assumptions of the study system (van de Pol et al. 2016). To overcome these issues, we performed a sliding window analysis following van de Pol et al. (2016). For a series of climate hypotheses, this analysis implements an exploratory sliding window approach which investigates the explanatory power of all possible temporal windows (different start dates and window durations) for each hypothesis and compares the resulting models based on AIC (Bailey and van de Pol 2016). This results in an optimal window for each hypothesis which can then be compared to other competing hypotheses (Bailey and van de Pol 2016). To avoid selecting spurious climate signals (type I error), resulting models are compared to those generated by sliding window analyses of randomizations of the response data, i.e. lay date in our case (see Bailey and van de Pol (2016) for details). This approach allowed us to

identify the best climatic predictors and the time period during which they best explained the biological variables in our study system.

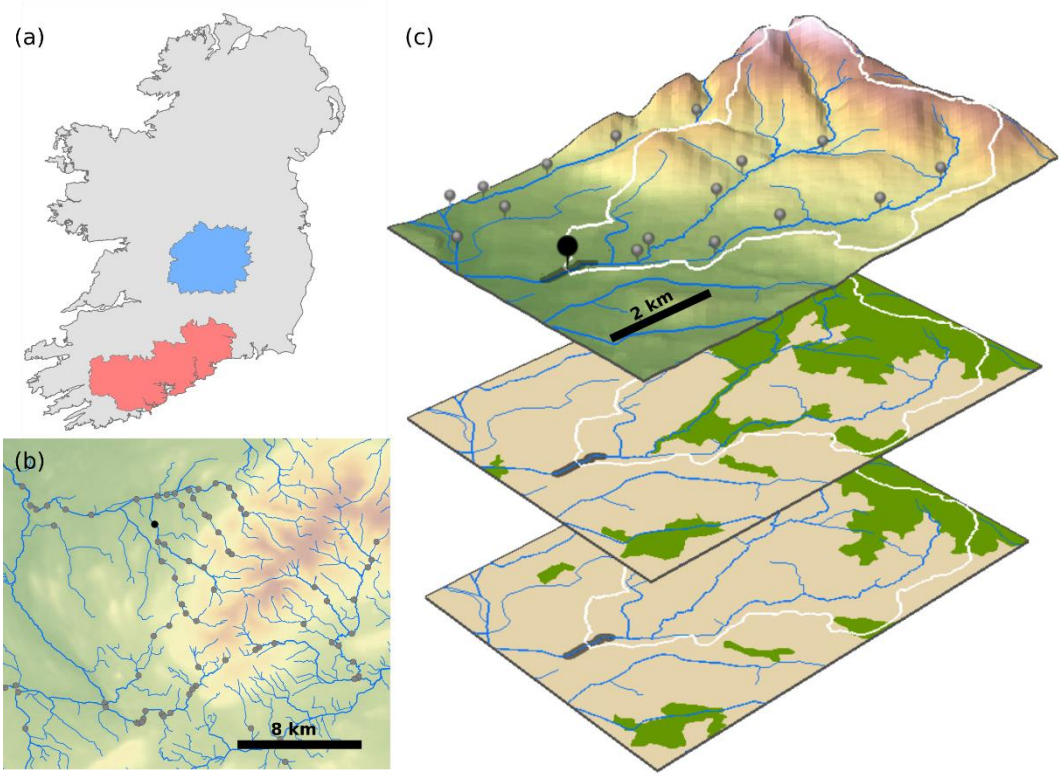


Figure 2.1. Dipper study areas monitored from 1983 to 2016: (a) map showing Slieve Blooms (blue) and Cork (red) study areas; (b) detail of Slieve Blooms study area; (c) example of a catchment in the Slieve Blooms area, showing topography (top), land use in 2012 (middle) and in 1990 (bottom) depicting areas of forest (green) and farmland cover (beige). Grey dots and pins represent dipper nests, the black pin represents a focal nest and its corresponding territory buffer (shaded area) and catchment buffer (delimited by white line).

We used sliding windows on a baseline model predicting individual nest lay dates where fixed effects were river gradient and study area (Cork or Slieve Blooms), and random effects were year and nest site nested within river (GLMM, Gaussian distribution with an identity link). The climate predictors we tested were daily values of large (NAO index) and local scale variables (rainfall and minimum temperature). For each of these predictors we generated sliding window models testing the effect of their minimum, mean and maximum value within each window. We also tested sliding window models of the effect of the number of days with temperatures below freezing. All hypotheses were tested with both linear and quadratic response curves to test for non-linear effects. We set sliding windows to test all possible windows in the 100 days leading up to lay date (window size from one to 100 days; starting date range from 100 days prior up until lay date; total of >5000 windows tested for each

of 20 hypotheses). We selected a time frame of 100 days as this covers relevant alterations in dipper physiology such as blood chemistry changes in breeding adults in the month prior to laying (Ormerod et al. 1991); weather windows which have been shown to influence lay dates in other passerines (Williams et al. 2015); and rainfall patterns characteristic of our study system in late winter (Steele-Dunne et al. 2008) which can impact river hydrology and potentially dipper phenology. The sliding window analysis thus generated a best model for each combination of climate predictor (NAO, rainfall, temperature, days below freezing), statistic (mean, maximum, minimum; sum in the case of days below freezing) and linear/quadratic function. We performed 50 randomizations on each model to test whether they represented spurious effects (type I error). We used AIC to select the climate predictor models that best explained lay date in our study system.

2.5 Land use and interactions with climate

We selected the best models from the sliding window analysis at each climate scale to evaluate interactions with land use and their effects on lay date. Building on the selected sliding window models, we incorporated land use factors in interaction with the climate predictor (see Table 2.1). We thus generated four models to assess the interaction of each climate predictor with land use: farmland and forest cover at the territory scale, and farmland and forest cover at the catchment scale. We calculated marginal R^2 values for all models and used p-values to evaluate the significance of different factors and interaction terms.

2.6 Temporal trends

To assess temporal trends in lay dates during our study, we built a univariate model to predict lay date as a function of year, with nest site nested within river as a random effect. We evaluated climatic trends by building generalised linear models for selected large scale and local climate predictors where the average of the climate value during the selected window was the response variable and year was a fixed effect. We also calculated changes in percentage land cover throughout the study areas during the study period.

Alternative models obtained by step-wise selection and retaining only significant variables produced similar results (same significant variables) to those presented here. All statistical analyses were performed in R 3.4.3 (www.r-project.org). We used *climwin* package for sliding window analysis, *lmer* package for generalised linear mixed models and *MuMIn* package to calculate model R^2 values.

3 Results

3.1 Climate predictors

Our climate analysis revealed advanced dippers lay dates in years when conditions prior to laying were wetter and warmer (see Appendix S2.1 for summary statistics). Specifically, of the 20 climate signal hypotheses tested, lay dates showed a negative non-linear relationship with minimum NAO values at the broad scale and with mean rainfall at the local scale (Fig. 2.2, Appendices S2.2 and S2.3). The temporal window during which these climate predictors influenced lay date differed considerably. Values of NAO in the final 33 days before laying were the best predictor of lay dates. Thus, higher minimum NAO values during this period (associated with increased rainfall and temperature) led to earlier lay dates in our study (Fig. 2.3a). At the local climate scale, mean rainfall between 83 to 11 days prior to laying was the best predictor of lay date, with higher mean rainfall values resulting in earlier lay dates (Fig. 2.3b). Validation of our analysis by randomization showed that type I error was unlikely for the selected climate windows (all $p < 0.001$, Appendix S2.4).

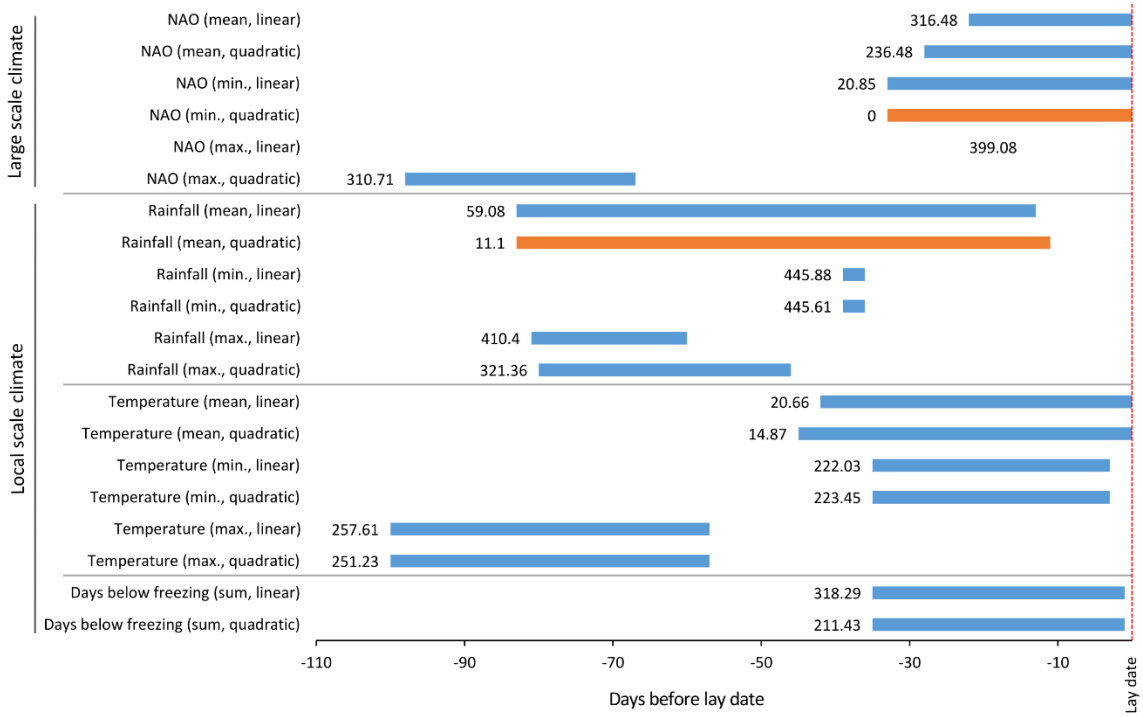


Figure 2.2. Results of sliding window analysis to identify best climate predictors for dipper lay dates. The y-axis shows the different climate signal hypotheses tested for each climate predictor (NAO, rainfall, minimum temperature and number of days below freezing). For each climate signal hypothesis, bars represent the temporal window that best explained lay date of all windows tested (>5000) according to AIC. Numbers next to bars indicate ΔAIC values with respect to the best performing model. The best models for large and local scale climate predictors are highlighted in orange. See Appendix S2.2 for details.

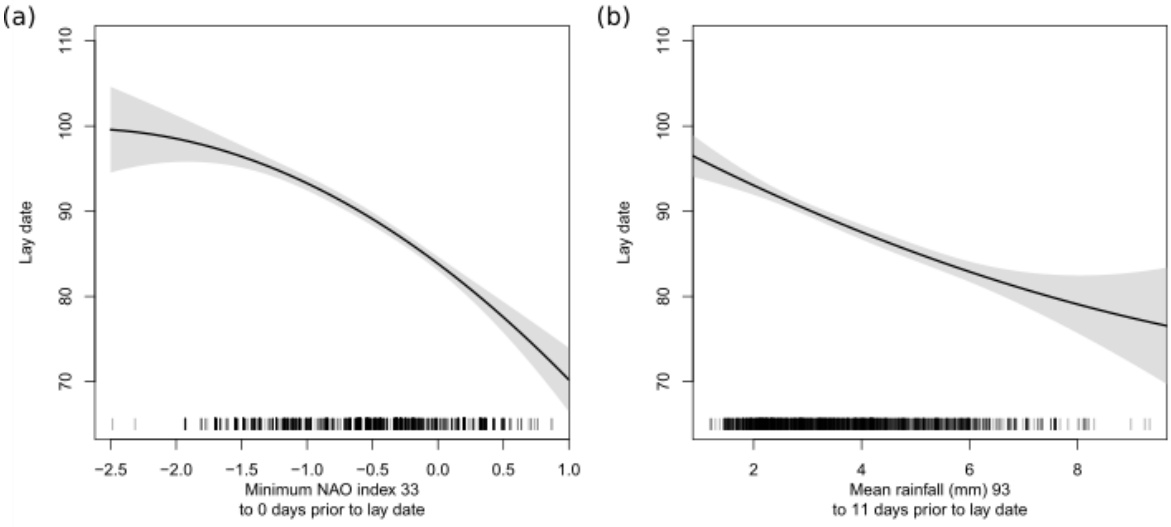


Figure 2.3. Effect of (a) large scale and (b) local scale climate predictors on dipper lay dates. Based on the best models from the sliding window analysis, the solid line represents the quadratic effect of NAO index and rainfall on dipper lay dates (in Julian days); the shaded area represents the 95% confidence interval; tick marks above the x-axis represent values of data collected during the study and used to develop the model.

3.2 Land use and interactions with climate

Analysis including land use variables revealed that lower forest cover and higher farmland cover were associated with earlier lay dates across the different land use and climate scales considered (Table 2.1, Appendices S2.5 and S2.6).

Table 2.1. Models testing the effects of climate, land use cover, and their interactions at different scales on dipper lay dates. Region was fixed to Cork in the models and compared to Slieve Blooms (SB), significant factors are highlighted in bold, '+' and '–' signs indicate the value of the estimate. See Tables S2.5 and S2.6 for full model outputs.

Climate scale	Land use scale	Fixed effects				
Large scale (NAO)	Territory	**+ Gradient**	Region (SB)	**– NAO**	**+ Terr. forest**	NAO*Terr. forest
		+ Gradient	Region (SB)	**– NAO**	**– Terr. farmland**	NAO*Terr. farmland
	Catchment	**+ Gradient**	Region (SB)	**– NAO**	**+ Catch. forest**	NAO*Catch. forest
		+ Gradient	Region (SB)	**– NAO**	**– Catch. farmland**	NAO*Catch. farmland
Local scale (rainfall)	Territory	**+ Gradient**	**– Region (SB)**	**– Rain**	**+ Terr. forest**	Rain*Terr. forest
		+ Gradient	**– Region (SB)**	**– Rain**	**– Terr. farmland**	Rain*Terr. farmland
	Catchment	**+ Gradient**	**– Region (SB)**	**– Rain**	**+ Catch. forest**	**– Rain*Catch. forest**
		+ Gradient	**– Region (SB)**	**– Rain**	**– Catch. farmland**	**+ Rain*Catch. farmland**

Interactions between climate and land use factors were only significant for local climate (rainfall) models at the catchment scale and non-significant in all other models. The interaction between rainfall and forest cover in the catchment was negative. This means that in catchments with more forest cover, lay date was delayed under dry conditions, but advanced in periods of heavier rain. On the other hand, the interaction between rainfall and farmland cover was positive: catchments with high farmland cover recorded earlier lay dates under dry conditions, while wet conditions resulted in later lay dates (Fig. 2.4).

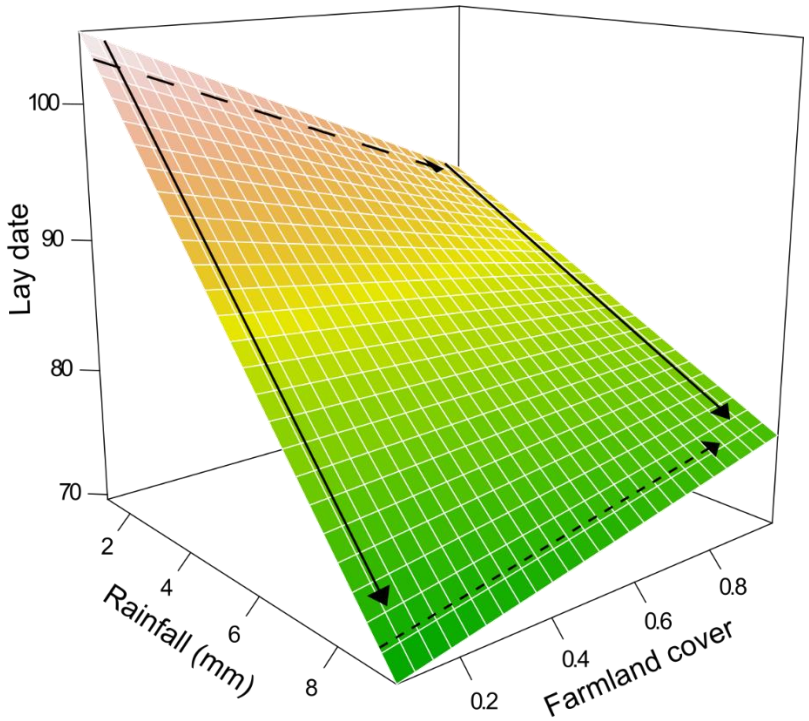


Figure 2.4. Graphical representation of the interaction effect between local climate (rainfall) and proportion of farmland cover at the catchment scale on dipper lay dates (in Julian days). Lines highlight how the effect of rainfall on lay date (continuous lines) was stronger than the effect of land use on lay date (dashed lines) in all scenarios (i.e. increases in rainfall correspond to larger changes in lay date); but how increased farmland cover had a stronger and opposite effect on lay date under dry (long dashed line) than under wet conditions (short dashed line).

Models assessing large scale climate predictors (NAO) had lower AIC values than those evaluating local predictors (rainfall). Similarly, models assessing catchment scale land use performed better than those assessing territory scale land use. Despite these differences, all models explained a similar proportion of lay date variance (marginal R^2 values ranging from 0.37 to 0.44).

3.3 Temporal trends

There was a significant ($p = 0.03$) increase in lay date during our study period. The increase amounted to a delay of 0.08 days per year, suggesting that by the end of our 34-year study, dipper lay dates were 2.6 days later than at the start of the study (see Fig. 2.5 for comparison with other studies). We found no trends in minimum NAO or mean rainfall values for the relevant windows during the study period (all $p > 0.2$, Appendix S2.7). During the same period, forest cover in our study area increased by 3.33%, while farmland cover decreased by 0.52%.

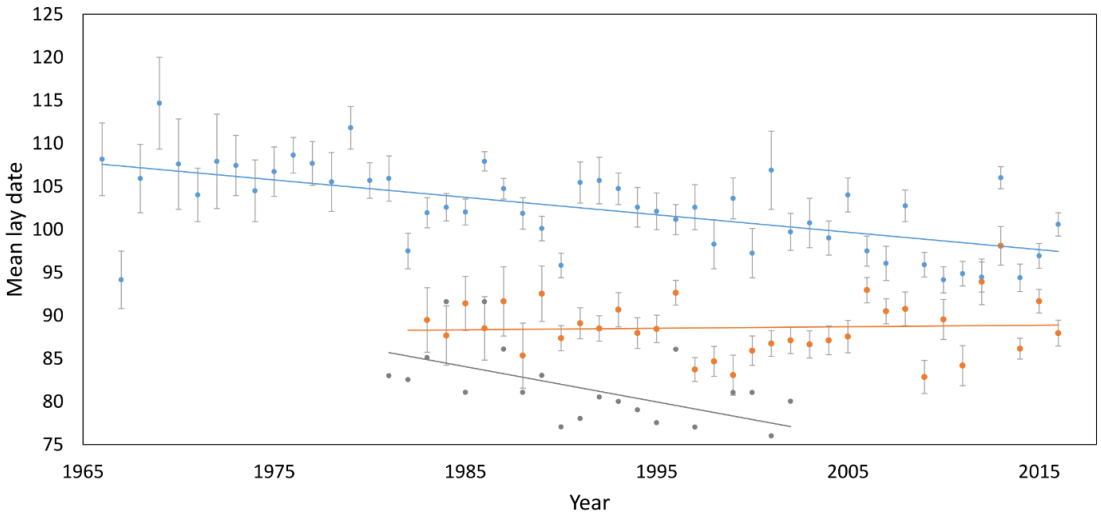


Figure 2. 5. Mean yearly dipper lay date and linear regression trends during the study period (orange) compared to data from other long term studies in France (grey; Marzolin and D'Amico 2017) and the UK (blue, includes second and replacement clutches; Massimino et al. 2017). Standard errors are shown where available.

4 Discussion

4.1 Dipper lay dates, climate and land use effects and interactions

We found that both climate and land use influenced dipper lay dates, and that these drivers interacted at some, but not all, of the spatial scales considered. Large scale climate factors (minimum daily NAO) in the month prior to breeding were the best predictors of dipper lay dates. However, models including local weather patterns (mean rainfall) in the months before laying performed almost as well. Land use factors were also significant in explaining dipper lay dates and interacted significantly with local climate (mean rainfall) at the catchment, but not the territory, scale. In these interactions, high percentage cover of farmland buffered the effects of rainfall on lay date.

The effects of climate on lay dates reflect the close ecological link of dippers with rivers. Higher minimum values of daily NAO indices (associated with wetter and warmer conditions) in the month before breeding and heavier rainfall in the three months prior to breeding resulted in earlier lay dates. These conditions would result in higher water temperatures and increased flow rates. Dipper foraging is heavily

influenced by river conditions. Although extreme flooding compromises foraging (O'Halloran et al. 1990, Taylor and O'Halloran 2001, Chiu et al. 2008), intermediate flow conditions combined with warming temperatures in early spring trigger stream macroinvertebrate population growth, accelerating nymph growth and advancing adult emergence (Vannote and Sweeney 1980, Grove et al. 2004). It is likely that river conditions act as a cue for breeding, either through improved adult body condition or as an indicator of food availability for provisioning of nestlings. Therefore, weather patterns, and their effects on river systems, are a key factor in determining time of breeding in dippers.

Lay dates were also influenced by forest and farmland cover, at both the territory and catchment scale in all our models. Higher forest cover was associated with later lay dates, while higher farmland cover was linked to earlier lay dates. Increased forest cover along rivers buffers water temperature oscillations (Durance and Ormerod 2007) and reduces run-off due to rainfall (Johnson 1998) and thus nutrient contribution to stream waters. These effects could slow macroinvertebrate population growth (Grove et al. 2004), with knock-on effects for dipper foraging, lay dates, and breeding output (O'Halloran et al. 1990). Although plantation forestry has also been associated with stream acidification and negative consequences for macroinvertebrates and dipper populations (Tyler and Ormerod 1992), conifer forest cover and acidity in our system are well below the levels which result in acidification (Clenaghan et al. 2002, Fernández-Bellon and O'Halloran, unpublished data). On the other hand, increased farmland cover was related to earlier lay dates. Although the main source of river pollution in Ireland is organic and of agricultural origin, river water quality is generally considered good (Bradley et al. 2013, Fanning et al. 2017). In our study areas, organic pollution of agricultural origin feeds into river systems via run-off but is generally below eutrophication levels (Fernández-Bellon and O'Halloran, unpublished data), effectively providing increased nutrient loads. Combined with faster water temperature increases in spring due to lack of forest cover, macroinvertebrate communities in catchments with high farmland cover are likely to register earlier spring population growth and exist at higher densities. Ultimately, these effects of farmland cover on river systems translate into earlier lay dates for dippers.

Interactions between climate predictors and land use were only significant for local climate variables (mean rainfall) at the catchment scale. Rainfall had a stronger effect on lay date than land use in all scenarios (see Fig. 2.4). On the other hand, the effect of land use on lay date depended on rainfall: whether conditions were dry or rainy affected the strength (larger or smaller change in lay date) and the nature (increase or decrease in lay date) of land use effects. It is possible that under dry conditions which are generally unfavourable for macroinvertebrates and dippers, marginal changes such as temperature increases and low levels of nutrient run-off in rivers in farmland areas can have an important effect on advancing lay dates. However, increasing rainfall and flow effectively buffer these land use effects and minimise differences between catchments with different land cover. Climate change has been linked to changes in stream nutrient concentrations due to increased run-off in agricultural areas, with consequences for macroinvertebrate populations (Bussi et al. 2018). This appears to be the case in our study where rainfall (and thus river flow) showed strong effects on dipper phenology.

Lay dates for most bird species are advancing in response to climate change (Dunn and Winkler 2010). Work on dippers in the UK (Crick and Sparks 1999, Massimino et al. 2017) and France (Marzolin and D'Amico 2017) has found similar trends, with substantial advances in lay dates for those populations. However, we found lay dates to be slightly delayed during our 34-year study (0.08 days per year), a trend that appears to approach stability when compared to other populations (see Fig. 2.5). This is possibly a consequence of the rate of climate change in Ireland and the buffering effect of land use. Climate records show that changes in temperature and precipitation during the second half of the 20th century have been less pronounced in Ireland than in the UK or France (Stainforth et al. 2013). Our analysis of climate data support this, with no temporal trends detected in NAO or precipitation values within the windows selected by our models. Despite this, long-term average comparisons in Ireland between 1961-1990 and 1981-2010 indicate that temperatures and precipitation have indeed increased by 0.5ºC and 5% respectively (Walsh 2012). While these changes may be responsible for yearly variations in lay dates (Fig. S2.7), they may be insufficient to result in clear trends in dipper lay dates. Furthermore, land use may play a role in buffering the effects of climate change. Land use change trends in our study areas mirror those reported for the rest of Ireland, where forestry

cover has increased by 2.05% and farmland has decreased by 0.11% (Wall et al. 2016). Although our models indicate increasing rainfall and temperature due to climate change should advance dipper lay dates, increasing forest cover and reductions in farmland should have the opposite effect. Therefore, it is possible that land use trends may be buffering the effects of climate change on long-term dipper phenology patterns.

4.2 Spatio-temporal scales and detection of interaction effects

Our analysis revealed that large scale climate patterns to be better predictors of lay date than local climate predictors. The utility of large-scale predictors to predict phenology has been questioned (Haest et al. 2018) and it has been suggested that if they outperform small-scale predictors, this is due to the lack of analytical tools to accurately identify optimal predictors and temporal windows at local scales (Hallett et al. 2004). However, sliding window analysis, which trials all possible temporal windows within a certain period for different statistical descriptors of multiple climate predictors optimises detection of such patterns. Furthermore, large-scale predictors are often linked to multiple local predictors and thus provide an integrated measure of weather patterns (Mauck et al. 2017). In our case, the NAO index is associated with patterns in rainfall as well as temperature. It is likely that this relationship with different local weather measures makes the NAO an overall better predictor of the conditions which regulate lay dates in dippers.

Despite the importance of large-scale predictors, interactions between climate and land use were only significant for local climate predictors. The interactions detected in our study occur through specific, complex mechanisms. Detection of such interactions requires local scale, high resolution climatic predictors. Although land use was important across multiple scales (forest and farmland cover influenced lay dates at the catchment and territory scale), interactions between local climate and land use were only significant at the catchment scale. These interactions were related to rainfall and run-off and their effects on river flow, processes which are magnified by area (e.g. run-off over a larger area has a greater impact on nutrient leaching). Thus, the territory scale would appear to be insufficient to detect any effects on lay dates of climate interactions with land use.

Temporal scales also played a key role in detecting global change driver effects on lay dates. Sliding window analysis allowed us to test multiple temporal scales to accurately identify the best climatic predictors and the time frame during which they exerted a strongest influence on lay dates. Overall, our approach considered predictors from multiple geographical scales for climate (NAO index and local weather variables) and land use (territory and catchment scales), and multiple temporal scales for climate (sliding windows) over long temporal scales of land use and phenological data. Despite the homogenous nature of our study system (relatively low variability in climate patterns, land use cover and river water quality compared to other studies (Ormerod et al. 1991, Marzolin and D'amico 2017)), this multi-scale approach allowed us to detect global change driver effects, interactions, and temporal trends in phenology.

4.3 Conclusions

Breeding phenology in dippers was influenced by both climate and land use factors at multiple scales. Lay dates were explained by large-scale and local climate patterns, but interactions between climate and land use occurred only for local climatic predictors. Contrary to other dipper populations, we found lay dates to remain relatively stable with a slight delay during the study period. Under current predictions of changes in climate (increased temperature and rainfall (Gleeson et al. 2013)) and land use (agricultural intensification and afforestation (Teagasc 2014)) in Ireland, it is likely that these phenological trends will persist.

Our results highlight the importance of multi-scale assessments for the study of global change effects on phenology, and in particular to allow for detection of interactions between different global change drivers. Ecological processes can operate at a single spatial or temporal scale, consistently across multiple scales, or at several scales but in different ways. Therefore, to study these processes, correct scale selection is essential. It is rare in ecological studies to have the precise prior knowledge necessary to correctly select the appropriate scales. However, existing knowledge of a study system can guide scale selection, and, in combination with multi-scale assessments, can greatly increase the likelihood of detecting these

ecological processes. In some instances, analytical tools are available to optimise selection of scale. Sliding window analysis, for example, allow assessment of all potential temporal scales within a certain time frame. In other cases, it is necessary to rely on the availability of data and existing knowledge of the study system to select multiple scales likely to be important (e.g. territory and catchment scales in our study). Future studies on global change effects on biodiversity should routinely incorporate multi-scale analysis and consider multiple drivers as well as their potential interactions.

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Supporting information

Summary statistics of dipper phenology, climate predictors and land use cover (Appendix S2.1), output from sliding window analysis (Appendix S2.2), output of selected climate models (Appendix S2.3) and their validation (Appendix S2.4), output of models testing land use interactions with large scale (Appendix S2.5) and local scale climate predictors (Appendix S2.6), and climate and dipper phenology patterns during the study period (Appendix S2.7) are available at the end of this chapter.

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Supporting information

Appendix S2.1. Summary statistics of dipper phenology, climate predictors and land use cover during the study.

Variable	Mean	SD	Minimum	Maximum
Dipper lay date (Julian days)	88.64	13.57	41	139
NAO (all values)	0.06	0.83	-3.25	2.75
NAO (within selected window)	-0.53	0.60	-2.49	0.87
Rainfall (mm; all values)	3.11	5.61	0.00	91.80
Rainfall (mm; within selected window)	3.66	1.48	1.20	9.34
Minimum temperature (ºC)	6.37	4.42	-13.40	19.10
Forest cover (% territory)	20.72	25.80	0.00	98.73
Farmland cover (% territory)	72.10	29.70	0.00	100
Forest cover (% catchment)	11.23	8.81	0.00	47.15
Farmland cover (% catchment)	77.02	18.30	7.28	98.24

Appendix S2.2. Output from sliding window analysis showing all climate signal hypotheses tested, models selected in our study are highlighted in bold (note that ΔAIC values shown here are calculated with respect to the null model and therefore differ from ΔAIC values in Fig. 2.2). See Bailey and van de Pol (2016)* for details on interpretation.

Model	Climate predictor	Statistic	Function	ΔAIC	Window open	Window close	betaL	betaQ	upper	lower	binary
1	Rainfall	Mean	Linear	-426.59	83	13	-9.62	NA	NA	NA	NA
2	Rainfall	Min.	Linear	-39.79	39	36	-1.63	NA	NA	NA	NA
3	Rainfall	Max.	Linear	-75.27	81	60	-0.37	NA	NA	NA	NA
4	**Rainfall**	**Mean**	**Quadratic**	**-474.57**	**83**	**11**	**-18.97**	**0.95**	**NA**	**NA**	**NA**
5	Rainfall	Min.	Quadratic	-40.06	39	36	-2.32	0.11	NA	NA	NA
6	Rainfall	Max.	Quadratic	-164.31	80	46	-1.87	0.03	NA	NA	NA
7	Min. temperature	Mean	Linear	-465.01	42	0	10.86	NA	NA	NA	NA
8	Min. temperature	Min.	Linear	-263.64	35	3	4.45	NA	NA	NA	NA
9	Min. temperature	Max.	Linear	-228.06	100	57	-4.79	NA	NA	NA	NA
10	Min. temperature	Mean	Quadratic	-470.8	45	0	8.27	0.53	NA	NA	NA
11	Min. temperature	Min.	Quadratic	-262.22	35	3	4.18	-0.07	NA	NA	NA
12	Min. temperature	Max.	Quadratic	-234.44	100	57	-12.89	0.45	NA	NA	NA
19	NAO	Mean	Linear	-169.19	22	0	-12.67	NA	NA	NA	NA
20	NAO	Min.	Linear	-464.82	33	0	-16.89	NA	NA	NA	NA
21	NAO	Max.	Linear	-86.59	14	14	-4.84	NA	NA	NA	NA
22	NAO	Mean	Quadratic	-249.19	28	0	-7.99	-13.99	NA	NA	NA
23	**NAO**	**Min.**	**Quadratic**	**-485.67**	**33**	**0**	**-21.93**	**-4.11**	**NA**	**NA**	**NA**
24	NAO	Max.	Quadratic	-174.96	98	67	20.74	-11.47	NA	NA	NA
25	Days below 0ºC	Sum	Linear	-167.38	35	1	0.71	NA	NA	0	FALSE
26	Days below 0ºC	Sum	Quadratic	-274.24	35	1	1.63	0.02	NA	0	FALSE

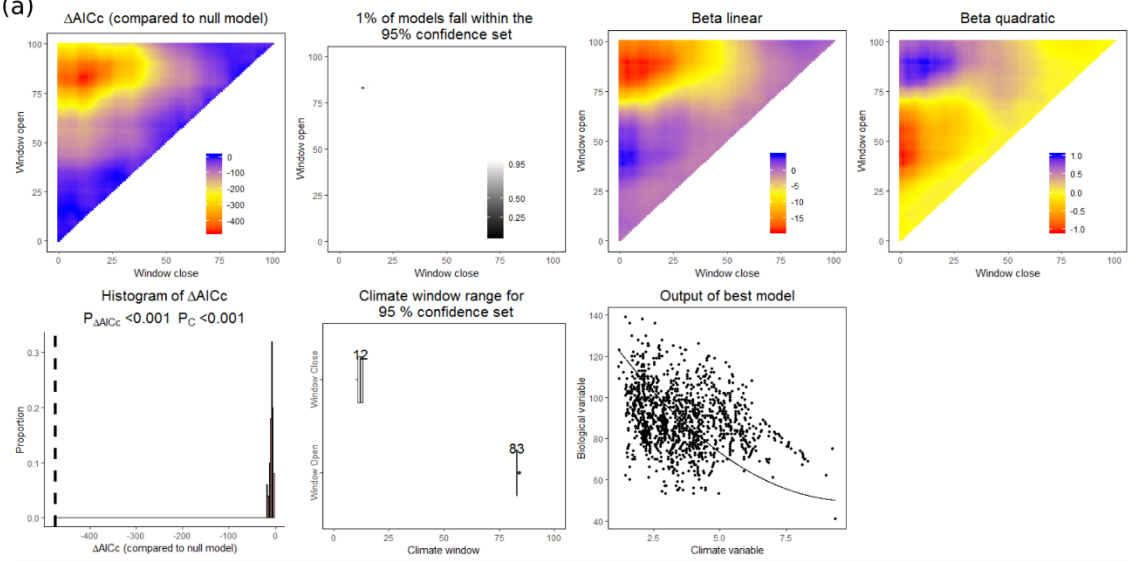
* Bailey, L. D., and M. van de Pol. 2016. climwin: An R Toolbox for Climate Window Analysis. PLOS ONE 11:e0167980.

Appendix S2.3. Output of models selected from sliding window analysis for large scale (minimum NAO quadratic function) and local scale climate predictors (mean rainfall quadratic function).

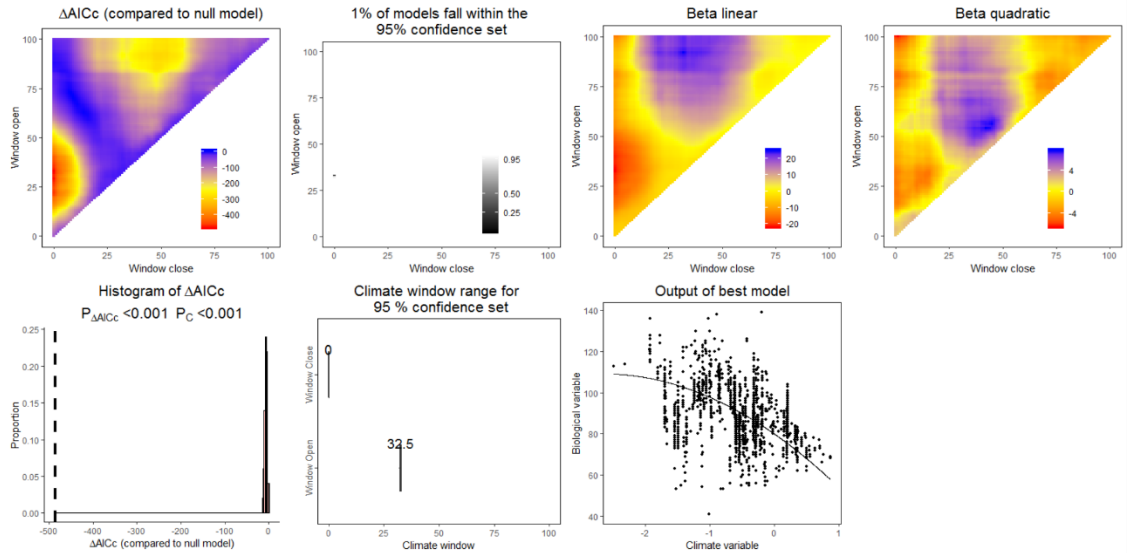
Climate Predictor	Factor	Estimate	SE	Variance	SD	t-value	p-value
NAO (min. quadratic)	Intercept	85.43	2.31	-	-	36.97	0.000
	Gradient	1.40	0.38	-	-	3.66	0.000
	Region (Slieve Blooms)	-0.46	1.48	-	-	-0.31	0.756
	Climate	-21.92	1.26	-	-	-17.47	0.000
	Climate^2	-4.11	0.86	-	-	-4.80	0.000
	Territory : River (random effect)	-	-	8.08	2.84	-	-
	River (random effect)	-	-	2.64	1.62	-	-
	Year (random effect)	-	-	50.05	7.08	-	-
Rainfall (mean quadratic)	Intercept	151.15	4.16	-	-	36.32	0.000
	Gradient	1.35	-0.38	-	-	3.58	0.000
	Region (Slieve Blooms)	-12.45	1.92	-	-	-6.49	0.000
	Climate	-18.97	1.30	-	-	-14.64	0.000
	Climate^2	0.95	0.13	-	-	7.26	0.000
	Territory : River (random effect)	-	-	6.29	2.51	-	-
	River (random effect)	-	-	7.90	2.81	-	-
	Year (random effect)	-	-	196.52	14.02	-	-

Appendix S2.4. Validation of models selected from sliding window analysis for (a) large scale (minimum NAO quadratic function) and (b) local scale climate predictors (mean rainfall quadratic function). See Bailey and van de Pol (2016)* for details on interpretation.

(a)



(b)



* Bailey, L. D., and M. van de Pol. 2016. *climwin*: An R Toolbox for Climate Window Analysis. PLOS ONE 11:e0167980.

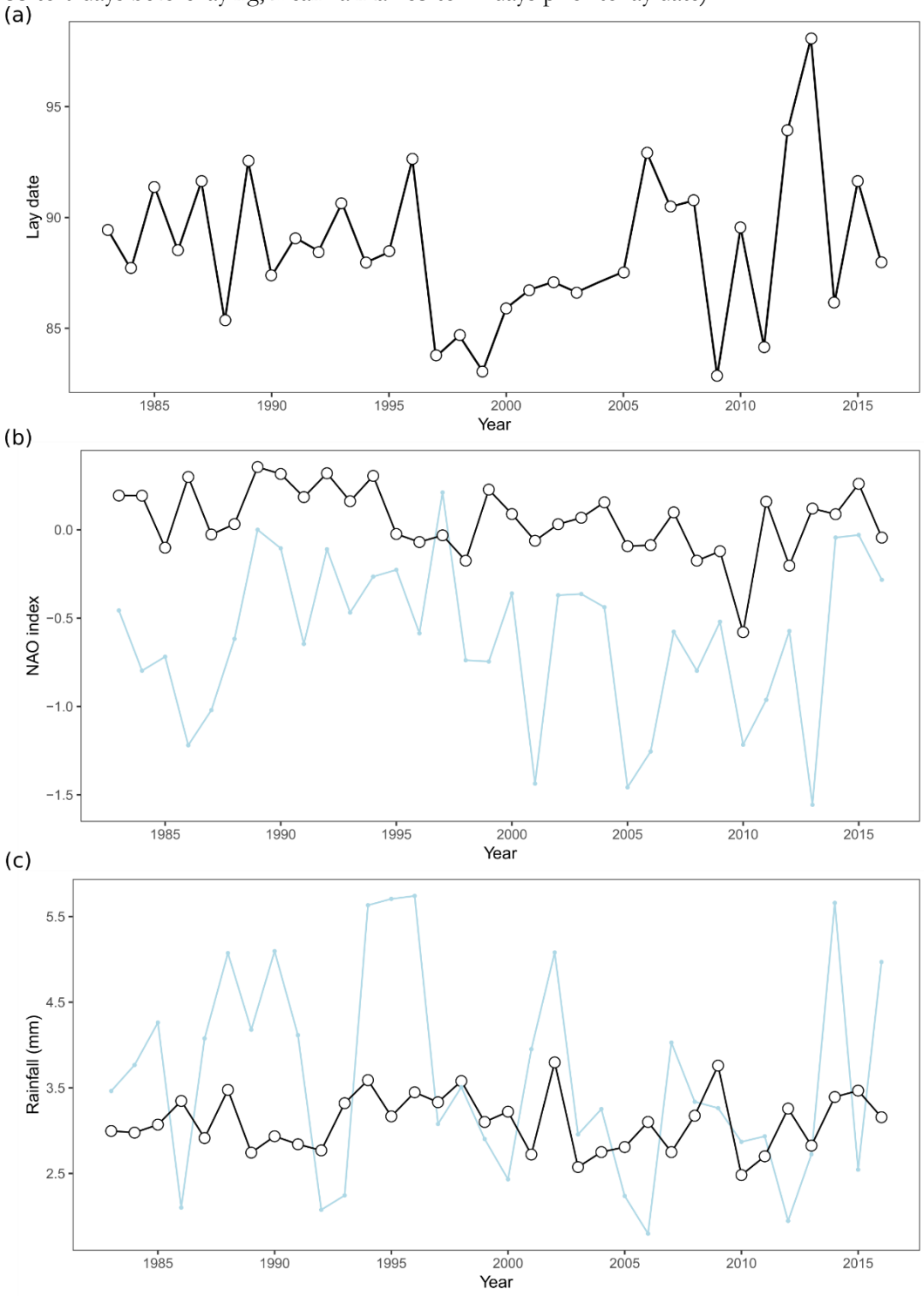
Appendix S2.5. Output of dipper lay date models evaluating interactions between large scale climate predictors (minimum NAO quadratic function) and land use cover.

Land use scale	Factor	Estimate	SE	t-value	p-value
Territory	Intercept	83.52	2.34	35.72	0.000
	Gradient	1.23	0.37	3.29	0.001
	Region (Slieve Blooms)	-0.06	1.50	-0.04	0.966
	NAO	-16.58	0.79	-20.99	0.000
	Forest cover	5.61	1.74	3.23	0.001
	NAO * Forest cover	-0.90	1.82	-0.49	0.622
Territory	Intercept	88.78	2.59	34.34	0.000
	Gradient	1.46	0.38	3.84	0.000
	Region (Slieve Blooms)	-0.40	1.51	-0.27	0.789
	NAO	-16.95	1.31	-12.95	0.000
	Forest cover	-3.95	1.51	-2.62	0.009
	NAO * Farmland cover	0.28	1.54	0.18	0.857
Catchment	Intercept	82.51	2.39	34.51	0.000
	Gradient	1.19	0.37	3.17	0.002
	Region (Slieve Blooms)	-2.85	1.47	-1.94	0.053
	NAO	-16.78	0.92	-18.25	0.000
	Forest cover	19.39	5.21	3.72	0.000
	NAO * Forest cover	-0.09	4.96	-0.02	0.985
Catchment	Intercept	92.85	2.92	31.78	0.000
	Gradient	1.18	0.38	3.12	0.002
	Region (Slieve Blooms)	-2.72	1.52	-1.79	0.073
	NAO	-16.64	2.03	-8.21	0.000
	Forest cover	-10.76	2.68	-4.01	0.000
	NAO * Farmland cover	-0.23	2.53	-0.09	0.928

Appendix S2.6. Output of dipper lay date models evaluating interactions between local scale climate predictors (mean rainfall quadratic function) and land use cover.

Land use scale	Factor	Estimate	SE	t-value	p-value
Territory	Intercept	129.83	3.28	39.54	0.000
	Gradient	1.21	0.37	3.25	0.001
	Region (Slieve Blooms)	-12.47	1.86	-6.70	0.000
	Rainfall	-9.66	0.43	-22.44	0.000
	Forest cover	7.80	2.93	2.66	0.008
	Rainfall * Forest cover	-0.66	0.73	-0.90	0.368
Territory	Intercept	137.29	3.65	37.59	0.000
	Gradient	1.41	0.38	3.74	0.000
	Region (Slieve Blooms)	-12.84	1.88	-6.83	0.000
	Rainfall	-10.29	0.62	-16.47	0.000
	Forest cover	-6.40	2.53	-2.53	0.011
	Rainfall * Farmland cover	0.65	0.63	1.04	0.300
Catchment	Intercept	126.02	3.37	37.36	0.000
	Gradient	1.05	0.37	2.87	0.004
	Region (Slieve Blooms)	-15.76	1.87	-8.43	0.000
	Rainfall	-9.00	0.43	-20.71	0.000
	Forest cover	65.07	9.09	7.16	0.000
	Rainfall * Forest cover	-13.05	2.34	-5.58	0.000
Catchment	Intercept	156.27	4.75	32.91	0.000
	Gradient	1.06	0.37	2.86	0.004
	Region (Slieve Blooms)	-15.63	1.91	-8.17	0.000
	Rainfall	-14.88	1.05	-14.23	0.000
	Forest cover	-30.25	4.55	-6.66	0.000
	Rainfall * Farmland cover	5.84	1.12	5.19	0.000

Appendix S2.7. Trends in (a) lay date, (b) large scale (NAO) and (c) local scale climate (rainfall) during the study. Black lines represent mean climate predictor yearly values, blue lines represent mean yearly values for all nests during the selected windows (minimum NAO 33 to 0 days before laying, mean rainfall 83 to 11 days prior to lay date).



Stress hormones, but not long-term biometrics, reflect land use signal in nestlings of a river passerine



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Abstract

Early life conditions in vertebrates can have important consequences for fitness in later life. In some species, such as altricial birds, inital life stages occur in a different environment to that of free-roaming adults. Nestlings can be affected by factors that are intrinsic or extrinsic to the nest. How these factors affect developing nestlings is especially relevant in the context of global change. Here we evaluate how intrinsic (nestling age, brood size and nest structure) and extrinsic factors (land use and lay date) influence nestling biometrics (n = 523 nests, 27 years) and feather corticosterone concentrations (n = 39 nests, one year) in an altricial passerine closely linked to river systems. Biometrics were mostly explained by intrinsic factors (nestling age, brood size and nest structure, but also lay date) while nestling corticosterone was linked to brood size and land use. Brood size effects were likely mediated by sibling competition while land use effects were mediated by system stability and predictability. Physiological measures proved a useful indicator of land

use effects and were more sensitive to this factor than biometrics. This approach can be especially relevant for studies assessing environmental or disturbance effects on endangered or rare species.

Keywords: biometrics, *Cinclus cinclus*, feather corticosterone, global change, glucocorticoids, land use, mass, nestling, stress hormones, white-throated dipper.

1 Introduction

Conditions during early life and development in vertebrates can have important consequences for later life stages (Lindström 1999), with effects on fecundity and survival described in most taxa, including reptiles, birds and mammals (Cam et al. 2003, Warner and Shine 2007, Hamel et al. 2009). For instance, stressful conditions during early life influence telomere length, which is linked to longevity in birds and mammals (Cam et al. 2003, Heidinger et al. 2012, Fairlie et al. 2016). Considering conditions during early development is of particular relevance for species that undergo these life stages in distinct environments from those experienced in later life. In these species, exposure and response to environmental factors may change considerably between life stages. The magnitude of this variation is related to each species' life history. For example, amphibians with aquatic larvae and land-based adult forms occupy drastically different habitats at each stage (Becker et al. 2007), while altricial birds often occupy the same habitats throughout their life but may be buffered or protected from certain environmental factors during the nestling period (Gebhardt-Henrich and Richner 1998, Monaghan 2008).

A variety of factors can influence early life conditions. In altricial birds these can be intrinsic or extrinsic to the nest (Traylor and Alisauskas 2006, Jetz et al. 2008). Intrinsic factors are largely influenced by species' life history (although they can be affected by geographic variation or parental behaviour and fitness), while extrinsic factors are largely dependent on the environment and are of particular interest in the context of global change (Jetz et al. 2008). For example, intrinsic factors such as nest structure and microclimate can influence the development and growth of nestlings (Dawson et al. 2005). In species where brood size is variable, intensity of sibling competition can also vary and affect nestling condition (Vitousek et al. 2017). Nestling development, however, is most directly linked to food availability and its nutritional value (Saino et al. 2003, Honarmand et al. 2010) which are largely dependent on extrinsic factors. Parental quality and environmental variation can affect different aspects of nestling food intake. Foraging ability of breeding birds can influence the nutritional value of food items and provisioning rates at the nest (Wright et al. 1998). Habitat quality and climatic factors can influence the abundance and quality of food available (Wilkin et al. 2009, Burger et al. 2012) which can also

follow seasonal variations, affecting breeding phenology and nestling development (Reed et al. 2013). In the current context of human driven environmental change, how extrinsic factors (e.g. climate change, pollution, land use) combine with intrinsic factors to influence early development is key to understand how species are affected by global change.

The increase in anthropogenic land uses has long been recognised as one of the main drivers of global change (Haddad et al. 2015), affecting species' abundance, distribution and phenology (Hansen et al. 2001, Kremen et al. 2007, Morisette et al. 2008). Despite the far-reaching consequences of land use and habitat modification on wild populations, detecting a signal of these effects remains problematic as it is often weak and confounded by other factors. Long-term studies provide an opportunity to overcome some of these difficulties, as large data sets can enhance the detection of weak environmental signals (Magurran et al. 2010). Data covering large temporal scales can also help us disentangle strong year-specific effects such as weather, while analysis of relevant geographical scales allows us to observe and compare patterns across different land use types (Levin 1992, Rogers and Schindler 2011, Nadeau et al. 2017).

In recent years, the field of conservation physiology has been used to improve our ability to detect and quantify effects of global change on wild populations (Wikelski and Cooke 2006, Cooke 2014). Conservation physiology has the potential to provide more direct and finer scale measures of how an organism responds to environmental factors than traditional measures (e.g. biometrics, breeding success). Glucocorticoids (stress hormones) in particular, have been one of the main tools used to assess environmental effects and stress exposure in vertebrate species (Lennox and Cooke 2014). When vertebrates are exposed to stressful stimuli, the hypothalamo-pituitary-adrenal (HPA) axis releases glucocorticoids into the blood stream. This in turn elicits physiological and behavioural modifications aimed at returning the organism to a state of homeostasis. While circulating in the blood stream, glucocorticoids are deposited in highly vascularized tissues, such as growing hair or feathers (Sheriff et al. 2011). While glucocorticoids deposited in these tissues do not reflect short-term stressful events which generate a brief peak in circulating stress hormones (e.g. exposure to a predator, territorial dispute with a conspecific), they have the potential

to reflect long-term or repeated stressful stimuli, which raise blood stream glucocorticoid concentrations for a sufficiently prolonged period of time to be registered in the hair or feather of animals (Sheriff et al. 2011, Jenni-Eiermann et al. 2015, Barrett et al. 2015). Feather corticosterone, the main glucocorticoid molecule in birds (Romero and Fairhurst 2016), thus has the potential to provide a useful measure of intrinsic and extrinsic stressors during early development in altricial birds.

Here we compare the effects of intrinsic and extrinsic factors on nestling biometrics and physiology in an altricial passerine exclusive to riverine habitats, the white-throated dipper *Cinclus cinclus*. Dippers are intimately linked to freshwater systems: they have unique morphological and physiological adaptations to river life, and roost, nest and disperse along rivers (Tyler and Ormerod 1994). They also feed on aquatic macroinvertebrates, whose populations are highly sensitive to water quality and flow regimes and are thus heavily influenced by land use in the surrounding areas (Ormerod et al. 1991). We evaluated the influence of (i) intrinsic (nestling age, brood size and nest structure) and (ii) extrinsic factors (phenology and riparian land use) on dipper nestlings using long-term data on biometrics spanning 27 years and on feather corticosterone concentrations collected in a single year and (iii) compared how these two approaches performed in detecting effects of land use and other factors.

2 Methods

2.1 Dipper monitoring

Dipper nestling data were collected as part of long-term monitoring of 183 nest sites on 33 rivers in south-west Ireland. All monitored rivers are fast flowing, shallow, second or third order streams in landscapes dominated by cattle pasture and agricultural lands (>60%) intermixed with commercial (>20%), and to a lesser extent, natural forestry (>5%). Water chemistry is circumneutral with a pH range of 6.8-8.8 (Fernández-Bellon and O'Halloran, unpublished data) and generally of low pollution status (Giller and O'Halloran 2004).

Long-term breeding data were collected from 1984 to 2012. Dippers build or use an enclosed structure to nest in, the nature of which can vary considerably. We

therefore distinguished three types of nest structures (see Appendix S3.1): (i) domed nests where the outer protective structure was the dome built by dippers out of moss and other vegetation; (ii) encased nests built in holes in man-made structures (e.g. bridges) where the outer protective structure was stone or concrete lined to a lesser or greater extent by moss depending on the space available; (iii) nest boxes where the outer protective structure was the wooden nest box, lined on the inside by a moss dome. Each season, nests were visited three to five times to determine lay dates and to ring, weigh, measure and age nestlings, and, after chicks fledged or a nest failed, to detect replacement and second clutches. Lay dates (in Julian days) and nestling ages (in days) were calculated based on direct observation of hatching or egg-laying and assuming 24-hour laying intervals and 16-day incubation periods. Field workers' experience on nestling development was used to estimate nestling ages when necessary. Nestlings were weighed using spring pesolas until 2002 (± 0.2 g) and electronic scales thereafter (± 0.1 g). Tarsus length was measured using callipers (± 0.1 mm). See Smiddy et al. (1995) for further details on nest monitoring.

Corticosterone data were collected in 2014. Nests were monitored following the same protocols to determine nest structure, ring, weigh, measure and age nestlings. Additionally, feather samples were taken from every nestling in the brood. Feathers were sampled from the nestling's rump, as this minimised discomfort to the birds (feathers from this area are easier to remove) and they were generally more developed than those in other parts of the body. Samples were obtained by pinching feathers between the thumb and index finger and pulling sharply, repeating the procedure two to three times and storing the sampled feathers from each nestling in individual paper envelopes (see below for quantities).

To maximise our ability to detect environmental effects, we subset data from nestlings between 10 and 17 days of age. This also allowed for optimisation of feather sampling, which requires sufficient nestling development and feather growth for corticosterone analysis. During the long-term part of the study (1984-2012), we monitored 1661 nesting attempts, with data on nestlings in this age bracket collected from 523 nesting attempts. In 2014, we monitored 77 nesting attempts and collected feathers and nestling biometric data from 39 nesting attempts.

All fieldwork was carried out under licence from the National Parks and Wildlife Service and the British Trust for Ornithology. Feather sampling was carried out under licence from the National Parks and Wildlife Service and the Health Products Regulatory Authority in accordance with EU legislation.

2.2 Feather corticosterone analysis

In order to obtain sufficient sample size for corticosterone analysis, nestling feathers were pooled by nest (range of 2-5 nestlings per nest). This resulted in samples of a minimum of 30 mg (see Lattin et al. 2011) and approximate total feather length of 100 cm per pool (weight and length were recorded for each sample). We used an optimized protocol for extracting corticosterone from feathers following Monclús et al. (2018). Feathers from each pooled sample were ground with a ball-mill (MM2 type, Retsch, Germany) for 2 min at 25 Hz. Then, 1.5 mL of methanol was added and samples were placed in a vortex for 30 min at room temperature. Samples were then incubated overnight at 32ºC for steroid extraction (G24 Environmental Incubator Shaker, New Brunswick Scientific, Edison, NJ) after which they were centrifuged at 6000 rpm for 20 min at 23ºC (Hermle Z300K, Hermle Labortechnik, Wehingen, Germany), and 1 mL of supernatant was transferred to a new aliquot and placed in an oven at 37ºC until totally dry. Dried extracts were reconstituted with 0.25 mL of enzyme immunoassay (EIA) buffer provided by the EIA kit (Neogen Corporation, Ayr, UK), shaken for 1 min and immediately frozen at –20 ºC.

Feather corticosterone concentrations were quantified using a competitive EIA (Neogen Corporation, Ayr, UK). Corticosterone concentrations were expressed as a function of feather length (pg / mm feather) following Bortolotti et al. (2008). Results were validated following Lattin et al. (2011) by comparing them with corticosterone concentrations calculated by mass (pg / mg). Both values were significantly and positively correlated ($r = 0.82$, $p < 0.01$). The intra-assay coefficient of variation of the EIA kit was 5.16%. For assay validation, precision, linearity and accuracy assessment, see Chapter 4.

2.3 Land use

All nesting sites were mapped using ArcMap 10.2 (ESRI, Redlands, California). Similar to other studies (Miserendino et al. 2011, Sheldon et al. 2012, Bodinof Jachowski and Hopkins 2018), preliminary comparison of different land cover buffers (immediate territory, upstream riparian corridor and catchment-wide) indicated that in our system, upstream riparian corridor land use had the strongest influence on nestlings. We therefore selected this as our measure of land cover. Upstream riparian corridor land use (hereafter 'riparian land use') was calculated by creating a 125m buffer on each side of the river, following a corridor from each nest site, upstream through all tributaries. We used CORINE Landcover data obtained from the Environmental Protection Agency (EPA) geoportal (http://gis.epa.ie/) to characterise land use by extracting the percentage of farmland (pasture and all other agricultural uses) and forest (plantation and natural forestry) cover in the upstream riparian buffer for each nest site. Riparian farmland and forest cover were strongly correlated across all rivers in the study ($r = -0.91$). Riparian forest cover is a good predictor of dipper distribution (Buckton and Ormerod 1997) and has a stabilising effect on river systems, playing a key role in macroinvertebrate population dynamics (Grove et al. 2004, Durance and Ormerod 2007). We therefore selected upstream riparian forest cover as a measure of land use for our analyses. CORINE Landcover datasets are available for 1990, 2000, 2006, and 2012. Nestling dipper data from each year was thus linked to land use data from the temporally nearest available dataset.

2.4 Response variables and statistical analysis

In passerines, body mass is considered a good reflection of an individual's condition and overall body size, while tarsus length is widely used to measure skeletal size (Labocha and Hayes 2012, Andrew et al. 2017). This provided us with two separate biometric measurements which might respond differently to nest and environmental factors. As corticosterone values were pooled by nest (see above) and to allow for comparison of effects, we calculated mean nestling mass and mean tarsus length for each nest. Our response variables were thus: mean nestling mass per nest (g; data from 1984-2012), mean nestling tarsus length per nest (mm; data from 1984-2012) and nestling feather corticosterone pooled by nest (pg / mm; data from 2014). These

are hereafter referred to as 'mass', 'tarsus length' and 'corticosterone' respectively. We used generalised linear mixed models (GLMM's) to test the effect of intrinsic and extrinsic factors on each response variable (Gaussian distribution with an identity link). Intrinsic factors tested in the long-term biometric models (mass and tarsus length) were nestling age, brood size and nest structure. Extrinsic factors were lay date and riparian forest cover. Both intrinsic and extrinsic factors were included in the models as fixed effects. Year and nest site nested within river were used as random effects. The model for nestling corticosterone included the same fixed effects (nestling age, brood size, nest structure, lay date and riparian forest cover) and also nestling mass, as this has been found to relate to corticosterone concentrations in some species (Tilgar et al. 2017). River was the only random effect for the corticosterone model, as all feather samples were collected from different nest sites in the same year. We calculated marginal R^2 values for all models and, as sample size varied between models, we used significance of fixed effects ($p < 0.05$) to determine which factors influenced our response variables. Analysis including and excluding second and replacement clutches ($n = 56$ for 1984-2012, $n = 3$ for 2014) yielded similar results, so we present results using all data. We tested all models for collinearity using variance inflation factor (all VIF < 2). To confirm that corticosterone results did not reflect processes occurring solely during the year we sampled feathers, we also built biometrics models with data from 2014, which yielded similar results to long-term analyses (see Appendix S3.2). Alternative models obtained by step-wise selection and retaining only significant variables produced similar results (same significant variables) to those presented here. All statistical analyses were performed in R 3.4.3 (www.r-project.org). We used *lmer* package for generalised linear mixed models and *MuMIn* package to calculate R^2 values.

3 Results

GLMM results indicated that factors intrinsic and extrinsic to the nest had varying effects on nestling biometrics and corticosterone (Table 3.1). Nestling age was related to mass and tarsus length (older nestlings were heavier and had longer tarsus) but not to corticosterone concentrations. Nestlings from larger broods were lighter and had higher corticosterone values. We used post-hoc Bonferroni analysis to determine the thresholds of significance for changes in mass and corticosterone in relation to brood

size (Fig. 3.1). Mass dropped significantly for nests with four or more nestlings ($p < 0.02$), while corticosterone increased significantly for nests with three or more nestlings (all $p < 0.001$). Nest structure type influenced biometrics but not corticosterone values: nestlings raised in nest boxes were lighter than those from all other nest types (domed or encased) and had shorter tarsus than those from domed nests.

Table 3.1. Generalised linear mixed models testing the effect of factors on dipper nestling mass and tarsus length (1984-2012; n = 523) and feather corticosterone (2014, n = 39). Random effects were 'year' and 'nest site' nested within 'river' for mass and tarsus models and 'river' for the corticosterone model. Nest structure categories are compared to the fixed category 'nest box'.

Model (marginal R^2)	Factor		Estimate	SE	t-value	p-value
Mean nestling mass per nest (g) (0.35)	Intercept		23.29	2.35	9.92	0.000
	Nestling age		1.81	0.11	16.29	0.000
	Brood size		-0.83	0.20	-4.22	0.000
	Nest structure	domed	3.10	1.04	2.98	0.003
		encased	3.14	1.06	2.97	0.003
	Lay date		0.03	0.01	2.38	0.017
	Forest cover		-0.70	5.45	-0.13	0.898
Mean nestling tarsus length per nest (mm) (0.34)	Intercept		20.68	0.91	22.81	0.000
	Nestling age		0.71	0.04	17.09	0.000
	Brood size		-0.03	0.07	-0.34	0.734
	Nest structure	domed	0.92	0.42	2.20	0.028
		encased	0.59	0.43	1.36	0.173
	Lay date		0.01	0.00	1.80	0.072
	Forest cover		-2.80	2.73	-1.03	0.305
Nestling feather corticosterone pooled by nest (pg / mm) (0.30)	Intercept		-0.70	0.46	-1.54	0.124
	Nestling mass		0.01	0.01	1.41	0.159
	Nestling age		0.01	0.02	0.55	0.581
	Brood size		0.05	0.02	2.15	0.031
	Nest structure	domed	0.02	0.10	0.23	0.821
		encased	0.10	0.10	1.05	0.296
	Lay date		0.00	0.00	1.84	0.066
	Forest cover		-1.23	0.57	-2.17	0.030

Factors extrinsic to the nest also influenced nestling biometrics and corticosterone. Riparian forest cover had no significant effect on mass or tarsus, but was negatively related to corticosterone values: high cover of forest upstream from nest sites was related to lower nestling corticosterone concentrations (see Fig. 3.2). Lay date was

related to mass (nestlings hatched later in the season were heavier) but was not significant in the models for nestling tarsus or corticosterone.

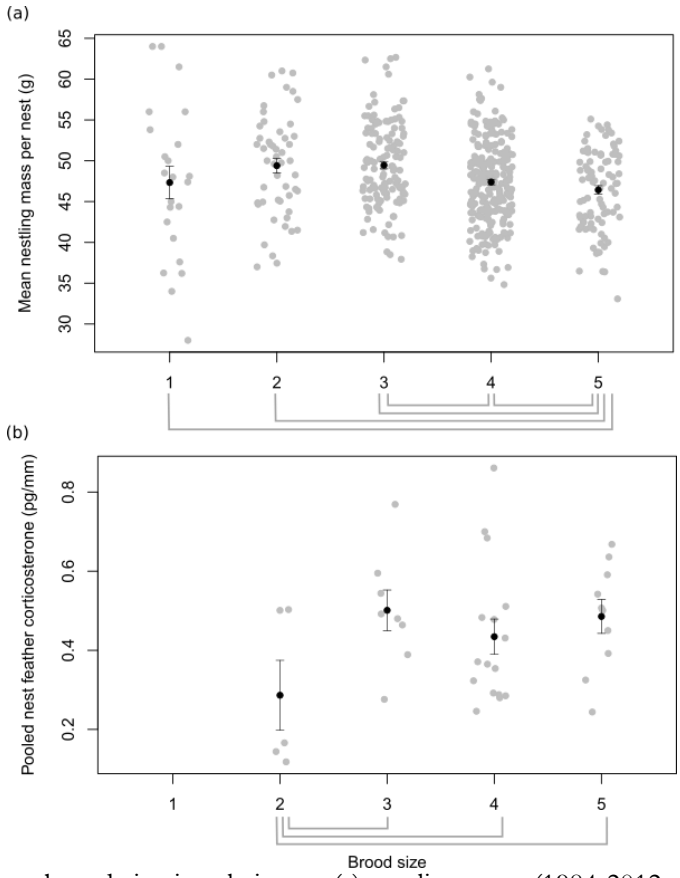


Figure 3.1. Dipper brood size in relation to (a) nestling mass (1984-2012; n = 523) and (b) nestling feather corticosterone concentrations (2014, n = 39), showing mean values, standard errors and significant differences between brood sizes (grey lines under the x-axis).

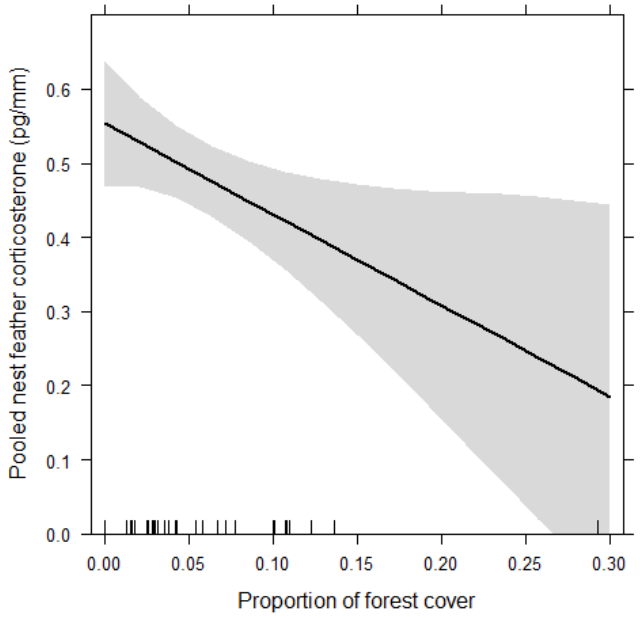


Figure 3.2. Effect of upstream riparian forest cover (and 95% confidence interval) on dipper nestling feather corticosterone concentrations (n = 39). Tick marks above the x-axis represent values of data collected during the study and used to develop the model.

4 Discussion

4.1 Intrinsic and extrinsic factors

Dipper nestling biometrics and corticosterone were affected by different factors. Mass and tarsus were mainly related to factors intrinsic to the nest (although mass was also influenced by lay date), while feather corticosterone was affected by brood size and land use. Following normal passerine growth patterns, nestling mass and tarsus length increased with age. Corticosterone values, however, did not vary with age or with mass. Previous studies on altricial nestlings have measured stress hormones in blood and appear to suggest a species-specific relationship between corticosterone, mass and age: it has been linked to mass in nestling Barn Swallows *Hirundo rustica*, Florida Scrub Jays *Aphelocoma coerulescens* and Barn Owls *Tyto alba* (Jenni-Eiermann et al. 2008, Rensel et al. 2011, Almasi et al. 2015), but not in Alpine Swifts *Apus melba* (Bize et al. 2010), and to nestling age in American Kestrels *Falco sparverius* and White Storks *Ciconia ciconia* (Sockman and Schwabl 2001, Blas et al. 2005) but not in Barn Swallows or Alpine Swifts (Jenni-Eiermann et al. 2008, Bize et al. 2010). Although feather and blood corticosterone measures are not directly comparable, our samples covered a third of the nestling development period (10 to 17 days old), suggesting that, at least during this phase, corticosterone may be independent of age and mass. Corticosterone measures (other than feather corticosterone) from earlier age ranges will be necessary to confirm whether this is the case or whether variation occurs outside of this age bracket.

Nestlings from larger broods had lower mass and higher corticosterone concentrations. This is suggestive of sibling 'scramble competition', where nestling behaviour determines food allocation to each individual (Roulin and Dreiss 2012). Dipper nests are characterised by a circular nest entrance, approximately 50 mm in diameter. This limits the number of nestlings that can comfortably access the entrance from the inside. As nestlings grow or in larger broods, this limitation becomes stronger. Although nestlings positioned behind the front line can reach out and provisioning adults can reach in, two nestlings generally occupy the optimal position at the front of the nest (own obs., see for example Appendix S3.1b and f). Therefore, a brood of two will be continuously fed with no need for turnover at the

nest entrance. A brood of three will require some, albeit limited turnover at the nest entrance, as provisioning adults can still feed a third chick behind the first two (own obs.). In the case of broods of four or five chicks, at least one of the nestlings is likely out of reach of food deliveries. This configuration suggests that as brood size increases, the need for nestlings to move in the nest to access the best feeding spots will lead to a gradual increase in sibling competition: low levels for broods of two, medium levels for broods of three, and a progressive increase thereafter. Corticosterone concentrations increased for broods of more than two (Fig. 3.1b) but this change only translated into differences in mass for broods of three or more (Fig. 3.1a). Previous work has found both evidence for (Quirici et al. 2016, Greggor et al. 2017, Vitousek et al. 2017) and against (Lobato et al. 2008, Rensel et al. 2010, Bize et al. 2010, Musgrove et al. 2017) the existence of a brood size effect on corticosterone across a range of species. The specificity of these patterns may be related to the reproductive strategy of each species, food availability, or, as seems likely in the case of dippers, nest configuration.

Nest boxes produced smaller nestlings (lower mass and shorter tarsus) than those raised in domed nests. Nestlings from nest boxes were also significantly lighter than nestlings from nests encased in holes. Different factors could contribute to these patterns. First, nest domes and encased nests are likely to provide more stable microclimates: domes have a thick insulating moss wall, while encased nests have solid structures (cement or stonework) surrounding the moss wall. Nest boxes on the other hand are often designed to host only a partial dome (i.e. reduced thickness of the moss wall) and only provide a layer of plywood beyond this. Variation in nest structure may affect insulation and nest microclimate (Fairhurst et al. 2012). Second, nest chamber size may influence nestling development and growth. Nest domes generally have a more spacious chamber than nest boxes, while that of encased nests is variable. In line with studies of experimental manipulation of nest sizes in other species (Slagsvold 1982, Soler et al. 2001), it would seem likely that dipper nestlings in more cramped conditions (nest boxes) had slower development and growth (i.e. lower mass and shorter tarsus) than those in more spacious nest chambers (domed nests). Despite these effects on nestling biometrics, corticosterone did not differ between nest structures. This is possibly due to a reduced sample size, with only three of 39 nests in 2014 located in nest boxes. Furthermore, models of biometric

data from 2014 (see Appendix S3.2) indicated no significant differences between nest structures, confirming that limited sample size may explain the observed lack of effect in 2014.

Land use in the riparian buffer upstream from the nest site had an effect on dipper nestlings. This land use signal was significant in nestling corticosterone measured from 39 sites in one season. Surprisingly, biometric data revealed no such effect, despite using data from 523 nests spanning 27 years (nor did biometric data collected the same year as corticosterone samples, Appendix S3.2). This suggests that while land use had an effect on dipper physiology, this did not translate into a measureable change in biometrics, even when using large data sets which should allow for detection of subtle environmental signals (Magurran et al. 2010). Previous work has shown that adverse conditions in early life that do not affect nestling growth rates can still have important consequences in later life. For example, conditions which affect telomere attrition are not necessarily linked to changes in nestling growth rates (Nettle et al. 2015). However, research focused on land use effects on nestling biometrics or corticosterone concentrations is limited, and studies combining both approaches are rare. Smith and Bruun (2002) found that starling *Sturnus vulgaris* nestling wing lengths, but not mass or tarsus length were related to land use surrounding the nest. Urbanization gradient effects are the focus of most research in this field, with mixed results on the existence of a relationship between nestling mass and urbanization (see review in Chamberlain et al. 2008). It is likely that this diversity of results may reflect differences in the intensity of land use and magnitude of its effects, some of which may be sufficient to have physiological, but not biometric consequences for nestlings. In our study we found no influence of land use on nestling biometrics, but work on dippers in Wales revealed that stream acidity caused by extensive commercial afforestation explained changes in several traits, including nestling growth (Ormerod et al. 1991). However, conditions in our study system are less extreme, with both forest cover and acidity below the levels reported in Wales (Fernández-Bellon and O'Halloran, unpublished data), suggesting that different processes are operating in our study system.

Dipper nestling corticosterone concentrations were lower at nest sites with higher cover of riparian forest in upstream areas. Forest cover has a stabilising effect on

rivers, buffering physical and chemical fluctuations. By reducing run-off and shading riparian areas, forest cover contributes to moderating changes in water temperature (Durance and Ormerod 2007) and buffering changes to water chemistry which may occur due to increased nutrient loads or erosion (Johnson 1998). Riparian forests are also an important source of organic material, and combined with the described buffering effects, they are a key requirement for macroinvertebrate populations which dippers rely on (Logie et al. 1996, Grove et al. 2004, Thomas et al. 2015). Riparian forest cover thus results in more stable river systems, with benefits for prey availability and nestling diet, which in turn can be reflected in corticosterone concentrations (Suorsa et al. 2004, Honarmand et al. 2010, Lodjak et al. 2015).

These results appear to contrast with previous work which indicated that farmland is associated with earlier lay dates in dippers, while forest cover is linked to later lay dates (Chapter 2). Although earlier lay dates are generally considered to improve productivity (Ormerod and Tyler 1993, Smiddy et al. 1995), the stability and predictability of rivers with higher forest cover could ultimately have positive effects for nestling condition. In fact, our results show that nestlings from later nests were heavier, matching seasonal dynamics of freshwater macroinvertebrates (i.e. food availability) as well as improving weather conditions (Vannote and Sweeney 1980, Grove et al. 2004). Although lay date had no significant effect on feather corticosterone concentration, this relationship was marginally non-significant (Table 3.1), possibly due to the limited sample size and reduced range of lay dates in the corticosterone model. Overall, these results suggest that although a higher farmland to forest cover ratio can advance dipper lay dates, it can ultimately result in negative effects for nestling development.

4.3 Conclusions

Conditions during early development can have important consequences for fitness in later life. Early life glucocorticoid concentrations in birds have been linked to telomere shortening, reduced breeding output and lower survival in later life (Blas et al. 2007, Quirici et al. 2016). Although we did not find any relationship between land use and nestling biometrics, physiological effects of land use could have consequences for individual dippers in later life. Further work monitoring individual

life-time fitness and physiological measures would provide insights into consequences of early life conditions.

Our results highlight the value of combined approaches to assess how environmental changes affect wild species. Feather corticosterone in particular proved to be a useful measure of environmental variation compared to other types of data which may be more labour intensive and require larger resources or sample sizes. This can be particularly relevant when evaluating impacts on rare or endangered species where generating large, long-term data sets is not feasible. Nestling feather corticosterone concentrations can provide optimal opportunities to evaluate such effects, as they reflect a precise period of time and minimise confounding factors which may mask environmental signals in other life stages. Furthermore, physiological measures provide a more direct and finer scale measure of an organism's response to environmental factors, enhancing the possibility of detecting such effects.

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Supporting information

Details on the categories of dipper nest structure types (Appendix S3.1) and models testing the effects of land use and other factors on nestling biometrics during 2014 (Appendix S3.2) are available at the end of this chapter.

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Supporting information

Appendix S3.1. Dipper nests structure categories used in the study: (a-c) domed nests with an outer protective structure built by dippers out of moss and other vegetation; (d-f) encased nests built in holes in man-made structures (e.g. bridges); (g) nest boxes where the outer protective structure was the wooden nest box. Note that in (d) nest is under construction and in (e) the front of the nest was torn away by a predator, exposing the nest cup.



Appendix S3.2. Output of generalised linear mixed models testing the effect of dipper nest characteristics and land use cover on mean nestling mass per nest and mean nestling tarsus length per nest (2014, n = 39). River was a random effect in both models. Nest structure categories are compared to the fixed category 'nest box'.

Model (R^2)	Factor		Estimate	SE	t-value	p-value
Nestling mass (g) (0.20)	Intercept		42.21	8.60	4.91	0.000
	Nestling age		1.01	0.48	2.09	0.036
	Brood size		-1.02	0.58	-1.76	0.078
	Nest structure	domed	-0.20	2.24	-0.09	0.929
		encased	0.58	2.25	0.26	0.795
	Lay date		0.03	-0.01	0.05	-0.20
	Forest cover		-0.70	6.85	12.56	0.55
Nestling tarsus length (mm) (0.39)	Intercept		27.14	2.59	10.47	0.000
	Nestling age		0.54	0.14	3.78	0.000
	Brood size		-0.24	0.18	-1.34	0.180
	Nest structure	domed	0.67	-1.50	0.133	0.028
		encased	0.66	-1.06	0.291	0.173
	Lay date		0.00	0.01	0.17	0.867
	Forest cover		1.84	3.64	0.51	0.613

Feather corticosterone as a measure of environmental conditions in a river passerine



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Abstract

Many phenotypic characteristics including behaviour, morphology or physiology can change throughout an individual's life and this variation can affect individuals' senstivity and responses to environmental change. Stress physiology is an important component of response to environmental factors, as glucocorticoids (stress hormones) play a key role in regulating this response. However, variation in glucocorticoid levels at different life stages is poorly understood. Here we assess the effects of land use on feather corticosterone concentrations of a songbird closely linked to river systems. Expanding on previous work on nestling feather corticosterone in the same study system, we evaluated feather corticosterone in juvenile (n = 63) and adult (n = 115) birds. There were no significant differences in feather corticosterone between juveniles and adults or between females and males. Although feather corticosterone reflected differences in land use in nestlings, juvenile and adult values showed no effect of land use. Instead, a strong year effect, attributed to weather patterns, was observed in both juveniles and adults. These results indicate

that a species' sensitivity and response to global change drivers such as land use and climate patterns can vary across different life stages. Analysis of a subset of data suggests that early life conditions, specifically brood size in the nest during development, may have consequences for corticosterone levels later in life.

Keywords: *Cinclus cinclus*, climate, feather corticosterone, global change, glucocorticoids, land use, life stage, stress hormones, white-throated dipper.

1 Introduction

Phenotypic traits such as morphology (see chapter 5), foraging ecology (Marchetti and Price 1989, Thiemann et al. 2008) or behaviour (Coltman et al. 1999, Gil et al. 2001) can change across different stages of an individual's life (van de Pol and Verhulst 2006). As a consequence of these changes, sensitivity and responses to environmental factors can also vary throughout an individual's life. In the current scenario of rapid environmental change, understanding this variation is key for a comprehensive understanding of how species are affected by global change (English et al. 2014). Different drivers of global change such as invasive species (Caut et al. 2008, Santicchia et al. 2018), pollution (Greulich and Pflugmacher 2003), or climate change (Radchuk et al. 2013, Levy et al. 2015) have been shown to have contrasting effects on distinct life stages of both invertebrates and vertebrates. These variations in age-specific responses and sensitivities to environmental change have consequences for individual life histories (Lindström 1999, Heidinger et al. 2012), but also at a population level (Fay et al. 2017).

Stress physiology has become an increasingly popular approach to understand how organisms respond to environmental factors due to its key role in this process (Romero 2004, Wikelski and Cooke 2006, Cooke 2014). The stress response is a physiological mechanism common to all vertebrates mediated by the hypothalamic-pituitary-adrenal (HPA) axis involving the production of glucocorticoids (stress hormones) in response to stressful stimuli. These hormones then elicit physiological and behavioural changes aimed at returning the organism to a state of homeostasis (Romero 2004). Glucocorticoid concentrations have been linked to an array of direct (e.g. human disturbance, food availability, weather (Creel et al. 2002, Bonier et al. 2009a, Strasser and Heath 2013, Jessop et al. 2016)) and indirect (e.g. land use, climate change (Cockrem 2007, Hopkins and DuRant 2011, Bechshøft et al. 2013, Almasi et al. 2015)) environmental factors in amphibians, reptiles, birds, and mammals. Although physiology is an integral part of animal ageing (Finkel and Holbrook 2000, Selman et al. 2012), and different physiological parameters vary throughout an individual's lifetime (Ricklefs and Wikelski 2002, Martin et al. 2008), glucocorticoid variations and their responses to environmental factors across different life stages are poorly understood (Crespi et al. 2013) with conflicting

evidence for the existence of patterns in glucocorticoid levels throughout an individuals' life or between sexes. Glucocorticoid levels have been found to both increase (Hämäläinen et al. 2015) and decrease with age (Wilcoxen et al. 2011, Lendvai et al. 2015) in birds and mammals. In some long-lived birds, glucocorticoid levels are highest in young and old individuals (Elliott et al. 2014, López-Jiménez et al. 2017), but this pattern appears to be inverted in short-lived species (Treen et al. 2015). Similarly, glucocorticoid concentrations can be sex-specific (Lendvai et al. 2009, Hopkins and DuRant 2011) or independent of sex (Chávez-Zichinelli et al. 2010, López-Jiménez et al. 2017). In this context, there is a need for studies assessing variations in stress hormones across different life stages in multiple environmental contexts (Bonier et al. 2009b, Crespi et al. 2013, Madliger and Love 2015).

Here we investigate the relationship between land use and glucocorticoid levels across two distinct age classes (pre-breeding juveniles and adults) of a songbird uniquely adapted to river life, the white-throated dipper *Cinclus cinclus*. Dippers require clean, fast-flowing waters with sufficient levels of organic matter and low sedimentation that support the aquatic macroinvertebrate communities on which they depend. These factors are influenced by weather and riparian habitats and land uses (Ormerod and Tyler 2005). Riparian forests in particular, are a good predictor of dipper distribution (Buckton and Ormerod 1997) because they are an important source of organic matter necessary for sustaining macroinvertebrate populations (Logie et al. 1996) and also provide stability to freshwater systems by buffering temperature, chemistry, sediment runoff and flow fluctuations during periods of heavy precipitation (Broadmeadow and Nisbet 2004). To assess how land use affects individual physiology, we measured dipper feather corticosterone (the main glucocorticoid in birds) over two years, as corticosterone deposited during feather growth provides a longer-term measure of individual hormone levels than blood concentrations of this hormone (Bortolotti et al. 2008). Therefore, feather corticosterone is more likely to reflect consistent environmental differences such as differences in land use cover between catchments.

Previous work in the same study system has shown that feather corticosterone concentrations of dipper nestlings were lower at sites with high forest cover in the riparian corridor upstream from the nest (see Fig. 3.1 in Chapter 3). Here, we expand

on this work by measuring feather corticosterone concentrations of first winter juvenile dippers that have undergone a post-fledging moult but have not yet bred (n = 63) and of adult birds that have undergone one or more breeding seasons (n =115). Free-roaming juvenile and adult birds are not spatially restricted and are exposed to more unknown stressors than nestlings which may confound interpretation, so we expect that (i) any signal of land use in stress hormones of juvenile and adult dippers will be weaker than that previously observed in nestlings from our study system. As reproduction imposes strong physiological demands on birds, particularly on egg-laying females, we also expect that (ii) corticosterone levels and effects of land use will differ between juvenile and adult dippers and that these variations will be stronger in female birds. Finally, for a small subset of individuals that had been ringed as nestlings (n = 18), it was possible to evaluate the influence of early development conditions on later life feather corticosterone levels. Despite sample size limitations, we expect that for these birds, (iii) early life environmental conditions may be more relevant to later life feather corticosterone concentrations than conditions at the time of sampling.

2 Methods

2.1 Dipper monitoring and feather sampling

Dipper roosts were monitored during the winters of 2014/15 and 2015/16 as part of long-term monitoring of populations in south-west and central Ireland. Rivers in the study area are fast flowing and with shallow waters, running in landscapes dominated by pasture interspersed with a mosaic of commercial and natural forests. Riparian habitats range from broadleaf or commercial plantation forests to agricultural lands with no riparian buffer. Dippers were captured by hand net at winter roosts from September to February, ringed, sexed, aged and measured. Dippers were sexed based on wing length (O'Halloran et al. 1992) and aged as juveniles (first winter, pre-breeding) or adults (second winter or older) following Svensson (1992). Body mass was measured with electronic scales to the nearest 0.1 g.

Juvenile and adult dippers undergo a complete body moult in July-August (Demongin 2016), so feather corticosterone sampled in the winter time reflected

processes occurring in the lead up to this moult period. Feathers were sampled from the rump of each bird, as this minimised discomfort to the birds (feathers from this area are easier to remove). Samples were obtained by pinching feathers between the thumb and index finger and pulling sharply, repeating the procedure two to three times and storing the sampled feathers from each bird in individual paper envelopes (see below for quantities). Feather samples were obtained from 63 juvenile and 115 adult birds.

All fieldwork was carried out under licence from the National Parks and Wildlife Service and the British Trust for Ornithology. Feather sampling was carried out under licence from the National Parks and Wildlife Service and the Health Products Regulatory Authority in accordance with EU legislation.

2.2 Feather corticosterone analysis

From each individual sample we took enough feathers to reach a minimum weight of 20 mg (approximately 15 feathers, average total length of 44.5 ± 3.1 cm). We used an optimized protocol for extracting corticosterone from feathers (Monclús et al., 2018). Feathers from each individual were minced with a ball-mill (Retsch, MM2 type, Germany) for 2 min at 25 Hz. Then, 1.5 mL of methanol was added and samples were placed in a vortex for 30 min at room temperature. Samples were incubated overnight at 32 ºC for steroid extraction (G24 Environmental Incubator Shaker; New Brunswick Scientific, Edison, NJ), after which samples were centrifuged (Hermle Z300K; Hermle Labortechnik, Wehingen, Germany) at 6000 rpm for 20 min at 23 ºC, and 1 mL of supernatant was transferred to a new aliquot and placed in an oven at 37 ºC until dry. Dried extracts were reconstituted with 0.25 mL of enzyme immunoassay (EIA) buffer provided by the EIA kit (Neogen Corporation, Ayr, UK), shaken for 1 min and immediately frozen at -20 ºC. Feather corticosterone concentrations were quantified using a competitive EIA kit (Neogen Corporation, Ayr, UK). Following Bortolotti et al. (2008), corticosterone values were expressed as a function of feather length (pg mm-1 feather).

Extracts from 30 random samples were used to biochemically validate the EIA (see Sheriff et al., 2011). The sensitivity of the assay was 0.11 pg corticosterone/ml for

feather extracts. Intra-assay and inter-assay coefficients of variation were 5.74% and 15.9%, respectively. In the dilution test, the efficiency of corticosterone extraction was 96.5 ± 14.94% (R2=99%) and the obtained and expected corticosterone concentrations were significantly correlated ($r=0.87$, $p<0.01$). The average recovery percentage from the spike-and-recovery test was 103.86 ± 28.23%. The cross-reactivity of the corticosterone antibody was as follows: 38% deoxycorticosterone; 19% 6-hydroxycorticosterone; 5.1% progesterone; 2.7% tetrahydrocorticosterone; 1.5% prednisolone; 1.1% cortisol. Steroids with cross-reactivity <0.9% are not presented.

2.3 Land use

All rivers were mapped using ArcMap 10.2 (ESRI, Redlands, California). Previous work in our study system showed that feather corticosterone of dipper nestlings was influenced by land use in the riparian corridor upstream from each nest (see Chapter 3). Unlike nestlings, however, juvenile and adult birds are not as spatially constrained and may use different sections of a river and thus be influenced by patterns occurring across the entire river length. We therefore calculated land use in the riparian corridor (hereafter 'riparian land use') for each river in the study area. This was calculated by creating a 125m buffer on each side of the river, following a corridor across the length of each river and through all tributaries. We used 2012 CORINE Landcover data obtained from the Environmental Protection Agency (EPA) geoportal (http://gis.epa.ie/) to characterise the percentage of farmland (pasture and all other agricultural uses) and forest (plantation and natural forestry) cover in the riparian buffer. Farmland and forest cover in the riparian buffers were strongly correlated ($r = -0.91$). As riparian forests are a strong predictor of dipper abundance (Buckton and Ormerod 1997) and play a key role in population dynamics of their macroinvertebrate prey (Broadmeadow and Nisbet 2004) we carried out analysis using only values of riparian forest cover.

2.4 Statistical analysis

We used generalised linear mixed models (GLMMs, Gaussian distribution, identity link) to test the effect of land use on dipper feather corticosterone concentrations. As

we expected explanatory variables to have different effects on each age class, we built separate models for juvenile and for adult birds. Response variables were thus juvenile and adult feather corticosterone (pg / mm) and fixed effects included sex, sampling year (as a factor: winter 2014/15 and winter 2015/16), body mass (g) and forest cover in the upstream riparian corridor (%). Both models included river as a random effect to account for other differences between rivers. In the case of adult birds, some individuals (n = 22) were sampled in both years. We therefore also included individual as a random effect in the model for adult dippers.

We built a similar model with feather corticosterone concentrations of all individuals to evaluate differences between age classes and sexes. Fixed effects included age class (juvenile / adult), sex (female / male), sampling year (as a factor) and body mass (g). River and individual were included as random effects.

Some individuals captured as juveniles or adults had been previously ringed as nestlings. We used data from these individuals to provide a tentative insight into effects of early life conditions on later life feather corticosterone concentrations., while acknowledging the limitations of a small sample size (n = 18). Previous work has shown that nestling feather corticosterone levels are influenced by brood size and riparian forest cover upstream from the nest (see Chapter 3 for details). We limited the complexity of the models by building a generalised linear model (GLM) to test the effects of brood size and riparian forest cover upstream from the nest on later life feather corticosterone concentrations. The only fixed effect relating to later life conditions was sampling year. It must be noted that the GLM approach for these models precluded the use of river as a random effect. However, differences between conditional and marginal R^2 values of the previous models indicated that the random term in those models (river) explained a low proportion of the variance (conditional R^2 – marginal $R^2 < 0.02$ in all GLMM models).

We calculated R^2 values for all models and tested all models for collinearity using variance inflation factor (all VIF < 2). Alternative models obtained by step-wise selection and retaining only significant variables produced similar results (same significant variables) to those presented here. All statistical analyses were performed

in R 3.4.3 (www.r-project.org). We used *lmer* package for generalised linear mixed models and *MuMIn* package to calculate R^2 values.

3 Results

Riparian forest cover had no significant effect on feather corticosterone levels in juvenile or adult dippers (Table 4.1). Sex, age class and body mass did not affect corticosterone values in any of our models, but year was significant in all models (Tables 4.1 and 4.2, Fig. 4.1). Birds sampled in the second winter of our study (2015/16) had significantly higher feather corticosterone values than those sampled the previous winter in both models. This difference was larger in the model for juvenile feather corticosterone (model estimate: 0.263 ± 0.076 pg / mm) than in the model for adult feather corticosterone (model estimate: 0.171 ± 0.04). The model for juvenile dipper feather corticosterone (R^2 = 0.19) also explained more variance than the model built for adult birds (R^2 = 0.15).

Table 4.1. Generalised linear mixed models describing feather corticosterone concentrations (pg / mm) in juvenile (n = 63) and adult (n = 115) dippers in relation to riparian land use. Random effects were 'river' (both models) and 'individual' (adult model). Marginal R^2 values were 0.19 and 0.15 for juvenile and adult models respectively. Significant factors are highlighted in bold.

	Juveniles			Adults		
	Est. ± SE	T-value	p	Est. ± SE	T-value	p
Intercept	0.751 ± 0.67	1.12	0.262	0.044 ± 0.326	0.13	0.894
Sex (male)	0.035 ± 0.142	0.25	0.805	0.009 ± 0.067	0.14	0.888
Body mass	1.030 ± 1.146	0.90	0.369	0.269 ± 0.616	0.44	0.662
Year (winter 15/16)	**0.263 ± 0.076**	**3.46**	**0.001**	**0.171 ± 0.04**	**4.24**	**0.000**
Riparian forest cover	-0.009 ± 0.011	-0.77	0.441	0.003 ± 0.005	0.60	0.550

Table 4.2. Generalised linear mixed model describing feather corticosterone concentrations (pg / mm) in dippers (n = 161) in relation to individual sex and age class. Random effects were 'river' and 'individual'. Marginal R^2 for the model was 0.15. Significant factors are highlighted in bold.

	Est. ± SE	T-value	p
Intercept	0.301 ± 0.291	1.03	0.302
Sex (male)	0.009 ± 0.062	0.15	0.882
Age (adult)	-0.025 ± 0.037	-0.67	0.500
Body mass	0.000 ± 0.005	-0.03	0.973
Year (winter 15/16)	**0.205 ± 0.036**	**5.71**	**0.000**

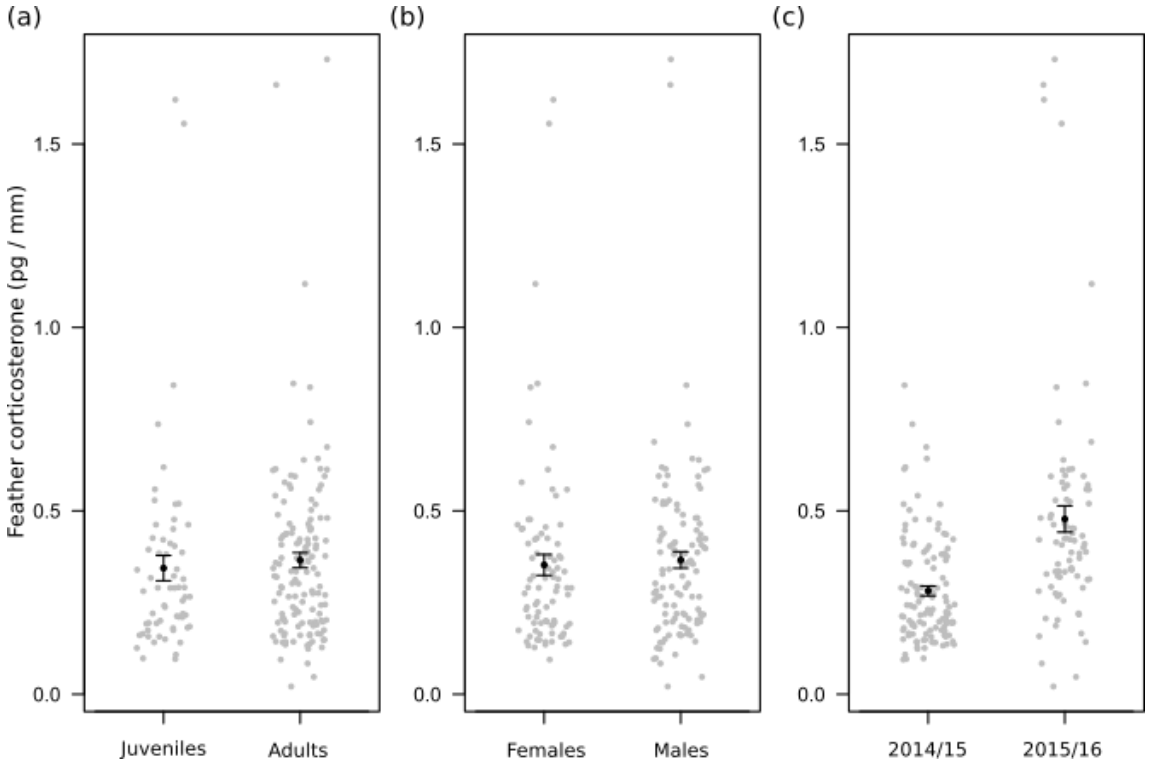


Figure 4.1. Dipper feather corticosterone concentrations by age class, sex and sampling year (n = 161).

The model assessing the influence of early life conditions indicate that brood size but not land use had a significant effect on feather corticosterone in later life (Table 4.3, Fig. 4.2). Juvenile and adult dippers that fledged from nests with larger broods had lower feather corticosterone values than those from nests with smaller broods.

Table 4.3. Generalised linear model describing feather corticosterone concentrations (pg / mm) in dippers in relation to early life conditions (brood size in the nest and riparian forest cover upstream from the nest) for a small subset of birds ringed as nestlings (n = 18). Marginal R^2 value was 0.44, significant factors are highlighted in bold.

	Est. ± SE	T-value	P
Intercept	0.571 ± 0.109	5.23	0.000
Year (winter 15/16)	**0.126 ± 0.049**	**2.77**	**0.011**
Brood size	**-0.087 ± 0.028**	**-3.16**	**0.002**
Nest riparian forest cover	0.007 ± 0.262	-0.03	0.978

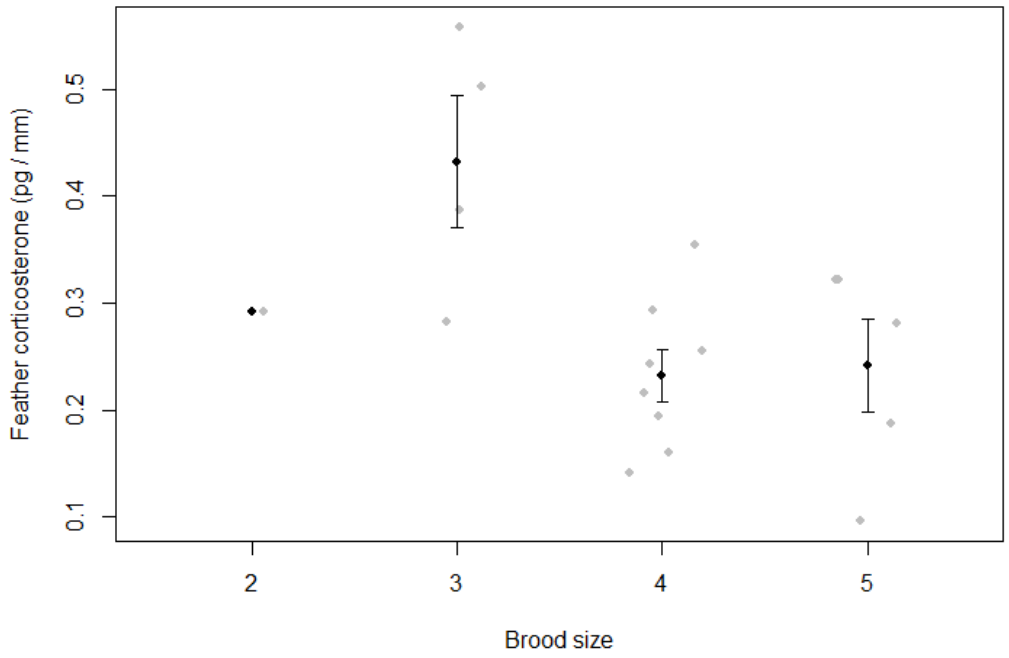


Figure 4.2. Feather corticosterone concentrations in juvenile and adult dippers in relation to early life conditions (brood size) for a small subset of birds ringed as nestlings (n = 18).

4 Discussion

4.1 Environmental effects on feather corticosterone

Juvenile and adult dipper feather corticosterone levels showed no relationship with riparian land use but varied strongly across years. As our study spanned a large geographical area, weather patterns are the most plausible factor to explain consistent yearly variations across all rivers over such a large scale. The two years of the study were characterised by contrasting weather patterns. Compared to long-term averages (LTA) from 1981-2010, the first study year (2014/15) was relatively warm (0.5 to 1.0 ° C warmer than LTA) and one of the wettest on record (150-250% more winter rainfall than LTA) (Met Éireann 2015). In contrast, the following year was relatively cold (0.5 to 1.0 ° C colder than LTA) and was characterised by a drier winter closer to the average (25-100% of LTA rainfall) (Met Éireann 2016). Apart from direct effects on dipper metabolic rates and energy expenditure, such weather patterns have important consequences for river ecosystems, influencing flow rates and water temperatures. River flow rates and water temperatures are crucial in determining

population dynamics (abundance and phenology) and accessibility of freshwater macroinvertebrates that dippers depend on (Taylor and O'Halloran 2001). These dynamics are particularly relevant during spring and summer, in the lead up to the moult period and deposition of corticosterone during growth of the feathers sampled. The weather conditions recorded during the first study year (warm and wet) are linked to increased macroinvertebrate population growth, while conditions during the second year may have been a limiting factor for macroinvertebrates (Vannote and Sweeney 1980, Durance and Ormerod 2007). Such fluctuations in prey abundance mediated by weather patterns could explain the higher values of feather corticosterone in the drier and colder year (2015/16). Regardless of the underlying mechanism, our findings indicate that feather corticosterone levels in juvenile and adult dippers are more sensitive to annual variations in conditions than to land use. This contrasts with effects found for nestlings in the same study system, whose feather corticosterone was negatively related to riparian forest cover upstream from the nest (see Table 3.1 in Chapter 3).

Land use type, habitat quality and fragmentation has been related to different measures of glucocorticoids in fish, amphibians, birds and mammals (Janin et al. 2011, Creel et al. 2013, Blevins et al. 2014, Jankowski et al. 2014). However, other studies on amphibians, reptiles and birds have found no such relationships (Chávez-Zichinelli et al. 2010, Hopkins and DuRant 2011, Halliday et al. 2015). Weather effects on glucocorticoids are similarly disparate across bird and mammal species (Creel et al. 2002, Wingfield and Ramenofsky 2011, Bechshøft et al. 2013). Effects of extreme weather events have been reported in faecal and blood glucocorticoid concentrations in songbirds (Liu et al. 2018, Krause et al. 2018) while large scale weather and climatic patterns have been linked to glucocorticoid concentrations in birds and mammals (Bechshøft et al. 2013, Treen et al. 2015). Variations in physiological sensitivity and responses to land use and weather thus appear to be species specific. Indeed, work on multiple fish species occupying the same habitats indicated different effects of catchment land use on corticosterone concentrations (King et al. 2016). Our findings would appear to suggest that sensitivity and responses to land use and weather may also be dependent on life stage. Specifically, during early development, land use influenced feather corticosterone levels in nestling dippers (Chapter 3), but once birds had fledged this land use signal was no

longer apparent. Instead, for fledged birds (juveniles and adults), weather patterns became the prime mediator of changes in feather corticosterone. Previous work has found variation in corticosterone response to environmental factors in relation to age in reptiles and birds (Josserand et al. 2017, Cīrule et al. 2017). In our study, it is likely that changes in exposure to environmental factors across different life stages influenced the patterns observed. Nestlings are restricted to the nest, and are thus exposed to fewer external stressors than free-roaming juveniles or adults. Furthermore, as juvenile and adult birds are highly mobile within (and even between) catchments, they are less likely to be influenced by riparian land use in any specific area. Instead, exposure to other factors (such as weather) is likely to have a stronger effect on corticosterone patterns. A better understanding of climate effects on feather corticosterone was limited by the temporal scale of our study. Work on nestlings covered a single year (Chapter 3) and data on adult corticosterone covered two years. While this provides insight into the feather corticosterone patterns discussed above, it limits our ability to determine the effects of weather on nestlings or to determine what specific meteorological variables and time periods influenced juvenile and adult dippers.

We found no differences between juveniles and adults or females and males, either in their response to environmental factors (Table 4.1) or in overall feather corticosterone concentrations (Table 4.2). This is surprising, as we expected that reproductive efforts would affect adult and male and female corticosterone levels differently. Reproduction is energetically costly (Wiersma et al. 2004, Welcker et al. 2015), and has been linked to corticosterone concentrations in birds (Bókony et al. 2009, Hau et al. 2010, Krause et al. 2016). Furthermore, male and female roles are differentiated during breeding with males nest-guarding while females incubate and brood (Ormerod and Tyler 2005). The lack of differences between juveniles and adult birds and between females and males could be explained by homogenous corticosterone production independent of sex and age class in this species, or it could reflect a temporal lag between any breeding season effects on corticosterone production and feather growth. It is possible that at the time of moult, any physiological effects of breeding have subsided and are no longer apparent in circulating corticosterone concentrations during the feather growth period.

4.2 Early life conditions and corticosterone

Although limited by small sample sizes, our findings on early life conditions provide insight into the effects of early development on later life corticosterone levels. Our results suggest that brood size but not land use upstream from the nest may be related to feather corticosterone in juveniles and adults. Although during early development nestlings from larger broods had higher levels of feather corticosterone (Chapter 3), in later life juvenile and adult dippers originating from larger broods had lower levels of feather corticosterone. Adverse conditions in early development can have positive effects in later life. In mammals, increased variability in ecological conditions during development has been linked to increased fitness and longevity (Marshall et al. 2017). In passerines, increased sibling competition in the nest was linked to increased foraging efficiency and body condition in later life (Andrews et al. 2015). In other passerines, individual patterns of glucocorticoid secretion appear to be fixed in early development (see Rensel and Schoech 2011 and references therein). If this is the case in dippers, it is possible that sibling-competition-induced stress may influence later life patterns in corticosterone.

4.3 Conclusions

Changes in life-stage-specific physiological sensitivity and responses to environmental factors in dippers appear to occur when birds achieve independence, with no noticeable variations at later stages (i.e. between juveniles and adults). The effects of climate and land use depended on life stage. A land use signal was apparent in nestlings but not in later life when yearly variations in conditions were more relevant. This finding highlights the importance of considering the effect of global change drivers across different life stages. Future work should study the variation in physiological sensitivity and responses to environmental change across different life stages, with a particular focus on longitudinal studies monitoring individual physiology throughout their life.

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Chapter 5

Temporal trends in female and male morphological traits in a dimorphic river songbird



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Abstract

Changes in morphology have been suggested as the third main response of species to global change, after shifts in distribution and phenology. Allometric trends resulting from these changes in morphology can provide insight into underlying mechanisms. Using a 27-year dataset of 1738 measures from 868 individuals we assessed variation in body mass, tarsus length and wing length in a dimorphic songbird adapted to aquatic life and underwater foraging. We detected different changes in female and male morphology over time which resulted in similar patterns for both sexes: female body mass and tarsus length increased, while male wing length decreased during the study, resulting in a relative shortening of wing length with respect to body size in both sexes. Increased rainfall, river flow and frequency of floods during the study period may have resulted in the observed shortening of wings relative to body size, which are advantageous for underwater foraging in deeper and faster flowing water. These trends may provide evidence of climate-change induced phenotypic change mediated by direct changes to the physical environment of the species. However, information on underlying genetic mechanisms will be necessary to determine whether these changes are indicative of natural selection or of phenotypic plasticity.

Keywords: Allometry, *Cinclus cinclus*, climate change, morphology, phenotypic change, white-throated dipper.

1 Introduction

Body size, morphology and allometry are defining traits of animal species, influencing all aspects of their physiology and ecology (Schmidt-Nielsen 1984, West et al. 1997). These traits often show geographical or temporal variation within species, which are generally assumed to reflect population adaptations to local environmental and biological conditions and interactions (Yom-Tov and Geffen 2011). Variation in morphological traits can have a direct influence on individual life-histories, reproductive success and survival, population dynamics and population responses to changing environments (Peters and Peters 1986, Nee et al. 1991). Contemporary changes in phenotypic traits of vertebrates have been widely attributed to environmental change resulting from climate warming (Chamaillé-Jammes et al. 2006, Meiri et al. 2009, Buskirk et al. 2010, Caruso et al. 2014). For instance, reports of shrinking body size across different taxa has led to the suggestion that this pattern may reflect a universal response to climate change (Gardner et al. 2011, Sheridan and Bickford 2011).

Skeletal size and body mass are regularly used measures in studies of morphological variation. In most endotherms, variation in these two traits arises from different processes. Skeletal size is largely determined during growth and development in early life stages and is independent of fluctuating energetic reserves (Lindström 1999). Body mass is a composite of skeletal mass and storage mass, and is often used as an indicator of energy reserves and body condition (Labocha and Hayes 2012). Body mass can vary during an individual's lifetime in relation to different life stages, such as migration or breeding (Maggini and Bairlein 2010, Sibly et al. 2012), but also in response to environmental change (Ozgul et al. 2010). Because different factors influence skeletal size and body mass, changes in these traits can reflect responses to different processes. Despite this, many studies analysing patterns in species' body size have used skeletal size and body mass interchangeably (see Canale et al. 2016).

In many species sexual dimorphism is an additional contributor to intraspecific variation in skeletal size and body mass. Morphological dimorphism can be explained by sexual selection, inter-sex food competition and reproductive role division (Hedrick and Temeles 1989, Fairbairn 1997). Changes in morphology of dimorphic

species are particularly interesting, as they can follow different patterns: variation can occur for one or for both sexes, and when it occurs for both sexes it can follow the same or different patterns for each sex (e.g. increase in value of a trait for females and decrease in value of the same trait for males). In some dimorphic species, rates of latitudinal or geographical change in morphology have been found to differ between males and females (Schäuble 2004, Blanckenhorn et al. 2006). In species with marked seasonal investment in reproduction (Rughetti and Festa-Bianchet 2011) such as deer, differences between male and female morphology vary throughout the year. However, long-term studies on morphological variation in dimorphic species are lacking.

Here we focus on a dimorphic songbird closely linked to river systems for all aspects of its life cycle, the white-throated dipper *Cinclus cinclus*. Dippers forage in fast flowing waters, swimming and diving in search of macroinvertebrate prey (Ormerod and Tyler 2005). Underwater foraging imposes unique biomechanical challenges and constraints which shape the body size and allometric relationships of diving birds (Lovvorn and Jones 1994, Thaxter et al. 2010) and, in the case of dippers, this results in relatively short wings and long tarsus compared to other terrestrial birds of similar size (Cramp and Brooks 1988, Tyler and Ormerod 1994, Robinson 2018). Dippers, with their unique biology, can help us understand how river species are responding to contemporary environmental change. River flow rates influence dipper population densities (Royan et al. 2015) and energy budgets (O'Halloran et al. 1990, D'Amico and Hémery 2007), but little work is available on how river flow relates to morphological adaptations to river life. Here we use 27 years of data to test for variation in dipper body mass, tarsus and wing length measurements in relation to flow rates. River flow rates are linked to physical river characteristics (i.e. river gradient) and to weather patterns (i.e. rainfall and runoff into rivers). By using data from 13 rivers with different gradients, and thus different flow rates, during a period of increased variation in precipitation and frequency of flood events (Kiely et al. 2013), we aim to evaluate whether and to what extent dipper morphology changed over time. We expect wing and tarsus length to be related to river gradient (shorter wings and longer tarsus for birds in rivers with steeper gradients) and to change over time (shortening of wings and lengthening of tarsus concurrent to increasing

variation in precipitation and river flow). If any changes in morphology do occur, we expect these to be similar for both female and male dippers.

2 Methods

2.1 Dipper monitoring

Adult dipper biometric data were collected as part of long-term monitoring of populations on rivers in south-west Ireland. Monitored rivers are second or third order streams characterised by fast flowing, shallow waters. Dippers were captured by hand net at winter roosts (September to February) during 27 years from 1989-2016 (no data for 2010), ringed, sexed, aged and measured. Dippers were sexed based on wing length (O'Halloran et al. 1992) and aged as juveniles (first winter) or adults (second winter or older) following Svensson (1992). Birds were weighed using spring pesolas until 2002 (± 0.2 g) and electronic scales thereafter (± 0.1 g). Tarsus length was measured using callipers (± 0.1 mm) and wing length using a ruler (± 1 mm). Dippers recaptured on subsequent years were processed and measured in the same way as new birds. See O'Halloran et al. (1992) for further details on fieldwork. All roosts were mapped using ArcMap 10.2 (ESRI, Redlands, California) to characterise river stretch gradient as this influences water velocity and flow (Flint 1974). River gradient data (river bed slope in m/km) were obtained from the Environmental Protection Agency (EPA) geoportal (http://gis.epa.ie/).

We excluded rivers with data on fewer than 10 individuals from our analysis (n = 99 measurements from 77 individuals), resulting in a final dataset of 769 measurements from 409 females and 969 measurements from 459 males captured on 13 rivers during the study. All fieldwork was carried out under licence from the National Parks and Wildlife Service and the British Trust for Ornithology.

2.2 Statistical analysis

We built generalised linear mixed models (GLMM's) with a gaussian family and identity link to assess variation of different male and female dipper morphologic traits over time and with respect to bird age class and river gradient. To this end we

built models for body mass (g), tarsus length (mm) and wing length (mm). As dippers are dimorphic and traits may be responding to different pressures in each sex, we built separate models for females and males for each morphological trait. All models had the same structure: year (as continuous), dipper age class (juvenile or adult) and river gradient (m/km) were fixed effects in all models. Year was also included as a random effect to account for annual variation. To account for seasonal biometric variations, we included month of capture (September = 1, October = 2, etc.) as a random effect. Juvenile and adult dippers undergo a full moult in July-August (Demongin 2016), and thereafter wing length measurements can vary due to feather wear depending on time of capture (own obs.). In other populations weight has also been found to vary during winter (Ormerod et al. 1986), though this appears not to be the case in Ireland (O'Halloran et al. 1992). Finally, we included ringer as a random effect to control for observer bias. Alternative models obtained by step-wise selection and retaining only significant variables produced similar results (same significant variables) to those presented here. All statistical analyses were performed in R 3.4.3 (www.r-project.org). We used *lmer* package for generalised linear mixed models.

3 Results

Table 5.1 presents summary values of the different dipper morphological traits measured during the study. We found significant variation in several morphological traits over time in both females and males (Table 5.2, Fig. 5.1). Female body mass and tarsus length increased over the course of the study, and shortening of wing length approached significance ($p = 0.063$). Male wing length decreased significantly, but tarsus length and body mass were stable over time. Body mass and wing length were significantly affected by age class, with values for both traits increasing in older birds. Data for a subset of birds for which it was possible to accurately determine calendar age suggests that body mass and wing length may peak at different ages for females and males (see Appendix S5.1). Tarsus length on the other hand, showed no change with age class. Finally, river gradient was not significant in any of the models tested, but was marginally non-significant ($p = 0.053$) in the model for male tarsus.

Table 5.1. Mean ± SD of morphological traits (mass, tarsus length and wing length) measured on dippers from 1987 to 2016.

	Juvenile females (n = 257)	Adult females (n = 228)	Juvenile males (n = 285)	Adult males (n = 284)
Mass (g)	61.5 ± 3.3	59.5 ± 3.1	70.6 ± 3.2	72.2 ± 3.6
Tarsus length (mm)	32.7 ± 0.9	32.6 ± 0.8	34.7 ± 0.9	34.8 ± 0.8
Wing length (mm)	89.7 ± 1.6	88.9 ± 1.8	96.8 ± 1.7	98.1 ± 1.9

To determine whether temporal trends in morphological traits were significantly different between female and male dippers we performed post-hoc GLMM analysis using all data (female and male combined). GLMM's had the same structure as those in Table 5.2, but included the fixed effect sex in interaction with year. Temporal trends were significantly different between female and male dippers for mass ($p = 0.021$) and tarsus length ($p = 0.016$), but not for wing length ($p = 0.021$). Full details of these models are available in Appendix S5.2.

Table 5.2. Results of GLMM analysis of female and male dipper body mass, tarsus length and wing length from 1987 to 2016. All models included year, month, individual and ringer as random effects. Age class category 'adult' is compared to 'juvenile' which was the reference category in the model. Significant effects are highlighted in bold.

Response	Factor	Females			Males		
		Est. ± SE	T-value	p	Est. ± SE	T-value	p
Mass (g)	Intercept	-36.46 ± 46.50	-0.78	0.433	33.24 ± 41.51	0.80	0.423
	Year	**0.05 ± 0.02**	**2.05**	**0.040**	0.02 ± 0.02	0.89	0.376
	Age (adults)	**1.78 ± 0.21**	**8.66**	**0.000**	**1.41 ± 0.17**	**8.24**	**0.000**
	Gradient	0.02 ± 0.02	0.89	0.371	-0.03 ± 0.03	-1.16	0.248
Tarsus length (mm)	Intercept	5.20 ± 11.06	0.47	0.638	35.30 ± 10.79	3.28	0.001
	Year	**0.01 ± 0.00**	**2.49**	**0.013**	0.00 ± 0.01	-0.03	0.974
	Age (adults)	0.06 ± 0.05	1.16	0.244	0.06 ± 0.05	1.25	0.212
	Gradient	0.00 ± 0.01	-0.19	0.846	-0.01 ± 0.01	-1.93	0.053
Wing length (mm)	Intercept	130.65 ± 22.49	5.81	0.000	153.41 ± 23.13	6.63	0.000
	Year	-0.02 ± 0.01	-1.86	0.063	**-0.03 ± 0.01**	**-2.45**	**0.014**
	Age (adults)	**0.70 ± 0.10**	**7.11**	**0.000**	**1.29 ± 0.09**	**14.35**	**0.000**
	Gradient	0.00 ± 0.01	0.07	0.943	0.00 ± 0.01	0.05	0.957

4 Discussion

4.1 Temporal variation in morphology

Results indicate that dipper morphology changed during the study, but did so differentially for females and males (Fig. 5.1, Appendix S5.2). Female body mass and tarsus length increased during the study period. Tarsus length is indicative of skeletal size and as such is determined in early development (O'Halloran et al. 1992), whereas body mass can fluctuate depending on environmental conditions but also depends on skeletal size (Canale et al. 2016). An increase in tarsus length coupled with increasing

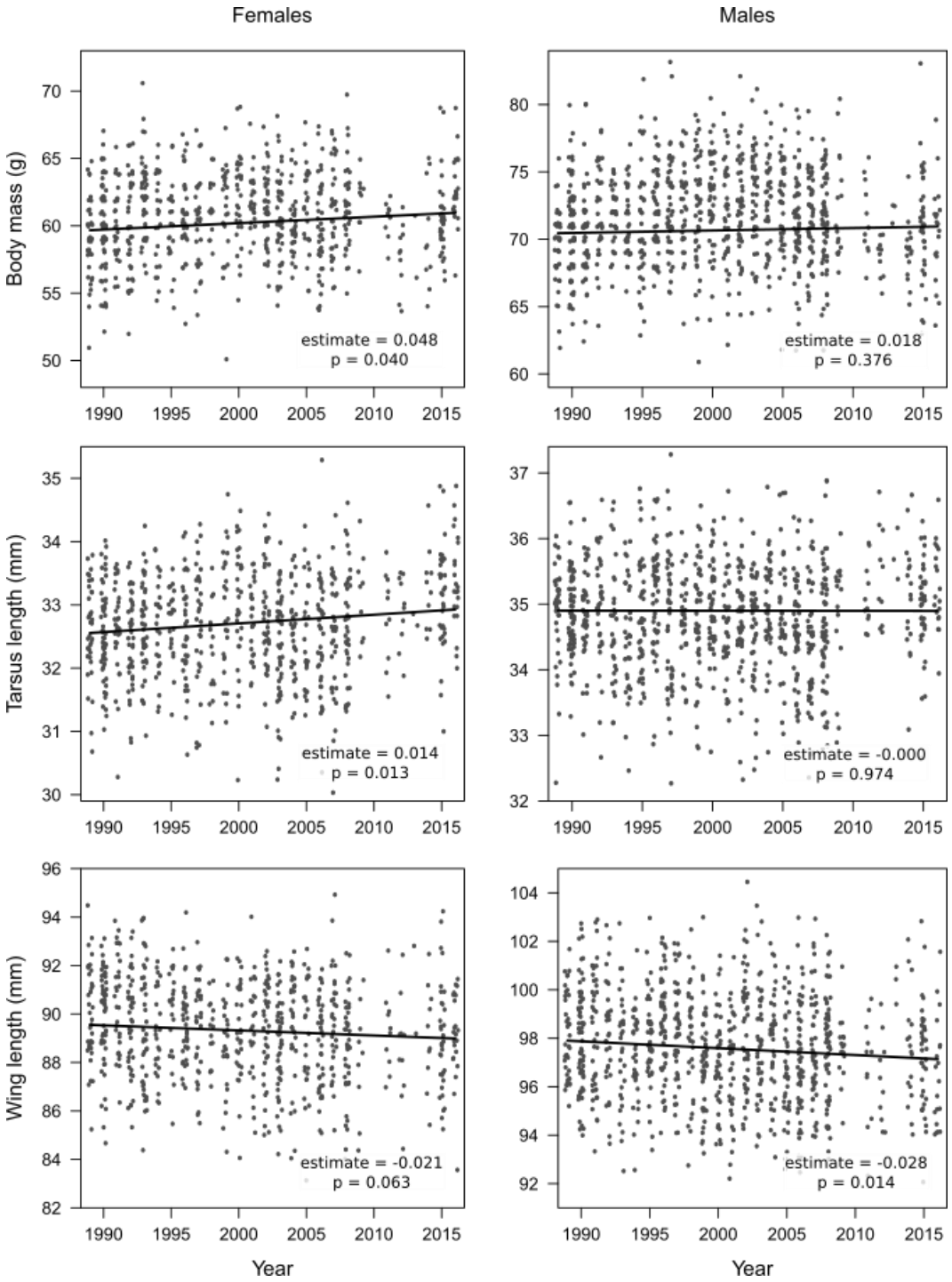


Figure 5.1. Modelled effect of year for female (n = 769 measurements; 409 individuals) and male (n = 969 measurements; 459 individuals) dipper body mass (g), tarsus length (mm) and wing length (mm) for the period 1989-2016. Estimate and p-values for year effects from the corresponding model are indicated for each trait.

body mass suggests an overall increase in body size. Despite this increase in size, female dipper wing length appeared to remain stable (or even shorten, see Table 5.2 and Fig. 5.1) during the study, indicating an overall relative shortening of the wing in relation to body size. On the other hand, male dipper wing length decreased while body mass and tarsus length remained constant. Therefore, similar to the pattern

observed in females, male dippers experienced a shortening of the wing in relation to body size.

Body size trends in relation to climate change have been mostly explained by temperature effects on metabolism and heat maintenance or through indirect effects on food availability mediated by changes to primary productivity (Yom-Tov and Geffen 2011, Gardner et al. 2011, Dubos et al. 2018). In some cases, however, climate change can have a more direct effect on foraging ecology when the constraints imposed by physical habitat characteristics affect foraging success. For example, snow and ice cover have been shown to influence prey availability and hunting success, with corresponding changes in morphology, for Eurasian lynx *Lynx lynx* (Yom-Tov et al. 2011), Eurasian otter *Lutra lutra* (Yom-Tov et al. 2010) and polar bears *Ursus maritimus* (Rode et al. 2010). Dipper foraging ecology is similarly affected by physical characteristics of river systems which can fluctuate considerably. Despite their ability to dive in search of prey, their foraging behaviour is optimised for intermediate values of river flow (O'Halloran et al. 1990). In fact, dippers show flood avoidance behaviour, relocating to smaller tributaries where food abundance may be compromised (Hong et al. 2018) and incorporating prey of terrestrial origin to their diet during periods of extreme flow (Taylor and O'Halloran 2001). In Ireland, precipitation and stream flow have increased over the second half of the twentieth century (Kiely 1999) with projections for increasing winter discharge and decreasing summer discharge in the coming decades (Steele-Dunne et al. 2008, Bastola et al. 2011). These changes in precipitation and flow are parallel to increasing frequency of extreme events. For example, 2006-2015 was the wettest decade in Ireland in 300 years (Murphy et al. 2018), and was characterised by an increased frequency of flood events (Nolan 2015, Nolan et al. 2017).

Dipper allometric scaling (i.e. relatively long tarsus and short wings) is an adaptation to foraging in fast-flowing rivers (Tyler and Ormerod 1994). The decrease in wing to body size ratio of both females and males during the study period may thus be a consequence of recent increases in river flow in our study area. A study of a small number of birds (17 females and 15 males) in south-eastern Spain revealed that both female and male dippers underwent an increase in wing-tarsus ratio over a 20-year period (see Fig. 5.2) during which body mass remained constant (Moreno-Rueda and

Rivas 2007). Although sample size was limited, the authors linked this to a concurrent decline in water flow in the area, which they proposed would lead to a dietary shift towards terrestrial and aerial prey. This would result in selective pressure for an increase in relative wing length, more similar to that of similar-sized terrestrial species (Moreno-Rueda and Rivas 2007). Climate and river flow trends in our study are the opposite of those described by Moreno-Rueda and Rivas (2007), as are the trends we observed (see Fig. 5.2). The need to forage in conditions of increased river flow could thus be expected to favour a body plan with shorter wings better suited for aquatic life.

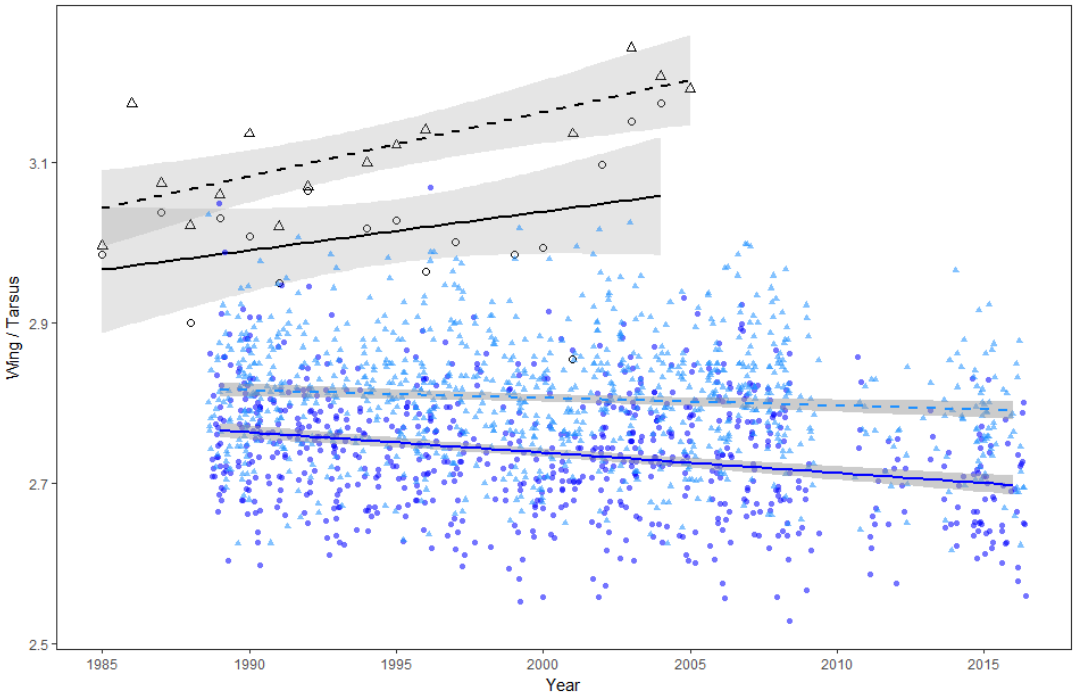


Figure 5.2. Changes in wing and tarsus length ratios in dippers in southern Ireland 1989-2016 (current study, blue) and south-eastern Spain 1985-2005 (Moreno-Rueda and Rivas 2007, black). Circles and continuous lines represent females, triangles and dashed lines represent males, shaded areas represent 95% confidence intervals. Sample sizes: Ireland females (n = 769 measurements; 409 individuals), males (n = 969 measurements; 459 individuals); Spain females (n = 17), males (n = 15). South-eastern Spain data extracted from Figure 1 in Moreno-Rueda and Rivas (2007).

The main challenge of studies of morphological change lies in distinguishing effects of natural selection from phenotypic plasticity (Yom-Tov and Geffen 2011). Indeed, the main criticism of many studies reporting evidence of selective processes is that such inferences may, in some cases, be inconclusive (Merilä and Hendry 2014). Winter survival of different dipper species is affected by river flow conditions (Chiu et al. 2013, Sánchez et al. 2017) and survival of females and males has been found to

differ in response to weather (Marzolin 2002). This suggests that river flow may indeed be a source of selective pressure on dipper populations. The changing weather and river flow patterns in the last decades would also appear to support the possible adaptive nature of the patterns we observed, but it is not possible to make a definitive distinction between natural selection and phenotypic plasticity in our study.

4.2 Dipper age class and river gradient

In addition to the temporal patterns observed for some morphological traits, we also found changes linked to individual age class. Body mass and wing length increased from juveniles to adults, but tarsus length remained constant. This supports previous work which indicated that maximum tarsus length is achieved in early development (O'Halloran et al. 1992), which is typical of the pattern of skeletal growth in vertebrates (Canale et al. 2016). When analysed by calendar age (Appendix S5.1), these traits appeared to reach their maximum value at different ages in each sex. These differences may be linked to sexual dimorphism and differential development and growth curves for each sex. Although we suggest that temporal variation in morphology may be linked to flow rates, and rivers in our study vary in gradient (range 0.001-0.280 m/km) and thus flow rates, our analysis revealed no links between morphological traits and river gradient. A possible explanation for the lack of river gradient effect on morphology is that our study area covers a single dipper population, with most rivers within dispersal distance of each other (O'Halloran et al. 2000). This may preclude the possibility of geographical phenotypic variation between birds occupying different rivers.

4.3 Conclusions

Our results indicate differential changes in morphological traits in female and male dippers over a short time period (less than three decades). We observed parallel trends resulting from changes in different morphological traits in each sex. While it is not possible to discern whether these changes are the result of phenotypic plasticity or natural selection, we propose that they may be a response to changes in river flow dynamics as a consequence of climate change. These findings highlight the importance of the physical environment in determining morphometric changes in

species adapted to river life. However, it is unclear whether such changes may have other beneficial or detrimental consequences for individual life-histories (e.g. reproduction, metabolism, flight and dispersal). Further work will be required to fully understand the underlying mechanisms behind these changes, but we suggest that studies encompassing multiple morphological traits in dimorphic species can be particularly useful in helping us understand species' phenotypic responses to global change.

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Supporting information

Patterns in female and male dipper body mass, tarsus length and wing length by calendar age (Appendix S5.1) and models testing for significance of differences between temporal trends in females and males (Appendix S5.2) are available at the end of this chapter.

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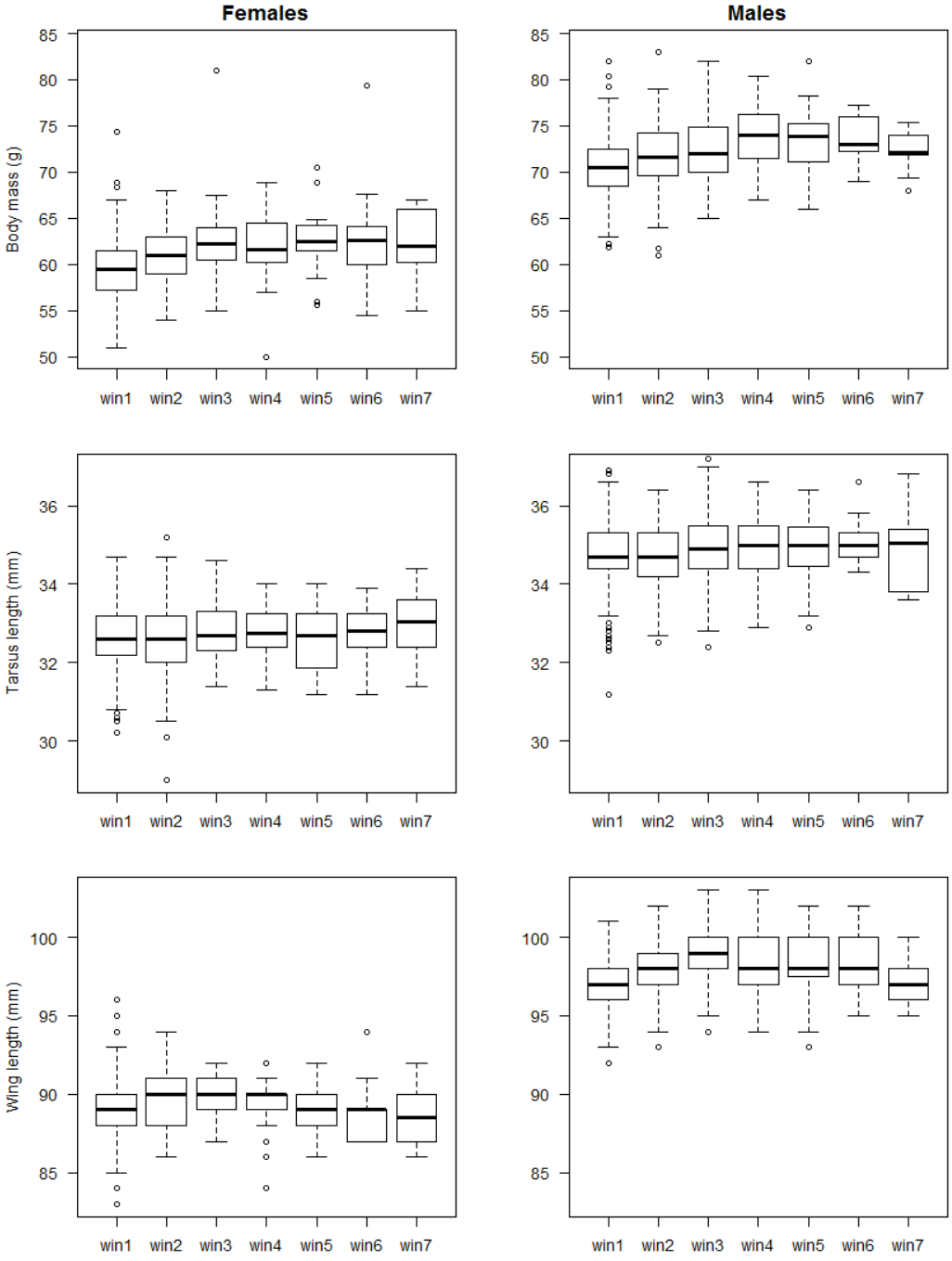
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Supporting information

Appendix S5.1. Female and male dipper body mass, tarsus length and wing length by calendar age. In the field, it is only possible to distinguish dipper juveniles (first winter) from adults (second winter or older). However, by subsetting data to measurements of birds captured as juveniles and their measurements on subsequent recaptures it is possible to represent morphological measurements of birds at increasing ages. Sample sizes are: females (n = 554 measurements, 291 individuals), males (n = 707 measurements, 320 individuals). Note that male birds older than 7th winter are not represented here due to small sample sizes (winter 8, n = 3; winter 9, n = 1).



Appendix S5.1. Results of post-hoc GLMM analysis to test significance of differences in temporal trends of morphological traits (mass, tarsus length and wing length) in female and male dippers. All models included year, month, individual and ringer as random effects. Age class category 'adult' is compared to 'juvenile' which was fixed in the model. Significant effects are highlighted in bold.

Response	Factor	Est. ± SE	T-value	p
Mass (g)	Intercept	-62.46 ± 45.3	-1.38	0.168
	Age (adults)	**0.06 ± 0.02**	**2.72**	**0.007**
	Gradient	**122.69 ± 48.45**	**2.53**	**0.011**
	Year	**-1.56 ± 0.13**	**-11.80**	**0.000**
	Sex (male)	0.00 ± 0.02	0.06	0.951
	Year*Sex	**-0.06 ± 0.02**	**-2.31**	**0.021**
Tarsus length (mm)	Intercept	4.9 ± 10.84	0.45	0.652
	Age (adults)	**0.01 ± 0.01**	**2.58**	**0.010**
	Gradient	**32.15 ± 12.5**	**2.57**	**0.010**
	Year	-0.06 ± 0.03	-1.82	0.069
	Sex (male)	-0.01 ± 0.00	-1.46	0.143
	Year*Sex	**-0.02 ± 0.01**	**-2.40**	**0.016**
Wing length (mm)	Intercept	136.15 ± 23.82	5.72	0.000
	Age (adults)	-0.02 ± 0.01	-1.95	0.051
	Gradient	-3.41 ± 26.36	-0.13	0.897
	Year	**-1.04 ± 0.07**	**-15.60**	**0.000**
	Sex (male)	0.00 ± 0.01	0.05	0.962
	Year*Sex	0.01 ± 0.01	0.44	0.663

Chapter 6

Discussion



1 Responses of dippers to global change

How species respond to environmental and global change varies considerably: some species are thriving in the current human-altered ecological context while others face extinction. However, responses to global change are not universal across or within species, but rather arise as the result of complex processes. The response of an individual species to global change has multiple components. Various life stages and ecological traits can have variable responses to the different drivers of global change. It is the combination of all these interactions that determines if and how a species adapts to human-induced environmental change. While attempting to identify and understand every individual factor involved in a species' response may be unrealistic (and perhaps negligent in the case of those facing extinction), overly simplistic approaches risk drawing erroneous conclusions and confounding our understanding of these processes. This thesis aimed at navigating a 'middle ground', investigating how different ecological traits of a species closely linked to rivers, the white-throated dipper *Cinclus cinclus*, were affected by the drivers of global change which are most relevant in these systems. The main findings of this work were: (i) breeding phenology was influenced by climate and land use at multiple scales, but the effect of their interaction was only significant at local scales; (ii) land use influenced stress hormone concentrations but not morphology in nestlings; (iii) at later life stages, stress hormones were not related to land use but appeared to reflect weather patterns; and (iv) changes in female and male dipper phenotype over time occurred parallel to changes in climate. The broader implications of these results are discussed below.

River systems are highly sensitive to climate change (Nijssen et al. 2001, Hirabayashi et al. 2013). As a species closely connected to rivers throughout its life cycle, dippers are vulnerable to climate-change-induced effects on these systems. Climate has been linked to changes in dipper foraging behaviour (Da Prato 1981, Taylor and O'Halloran 2001), breeding phenology (Chapter 2), physiology (Chapter 4), morphology (Moreno-Rueda and Rivas 2007, Chapter 5), individual survival (Chiu et al. 2013, Sánchez et al. 2017) and population dynamics (Sæther et al. 2000, Nilsson et al. 2011). Indeed, climate appeared to be the dominating driver for the species in this

study, overriding land use when effects of the two drivers were compared (Chapters 2 and 4). Increased rainfall and warming temperatures in early spring were associated with advanced lay dates (Chapter 2) and reduced stress hormone levels (Chapter 4), indicating how dippers are in this study system are responding to current climate trends. Changes in stress hormones and in allometric relationships indicate that the species may have the ability to adjust its physiology and morphology to environmental changes, though whether this is the result of selection processes or phenotypic plasticity remains unclear (Chapters 3, 4 and 5). Although dippers may be able to respond to, and even track progressive changes in climate, this interpretation fails to consider the increased stochasticity associated with climate change. This is exemplified by the findings presented in Chapter 4. Despite general trends for increasing temperature and rainfall, weather patterns varied considerably over the two seasons covered in that chapter: an above average warm, wet year (in line with future climate projections) followed by a colder and drier year (similar to past long term averages). Juvenile and adult stress hormone levels were lower during the first year, but higher during the second. Although this suggests that dipper physiology may be able to cope with future climate projections, it presents a different scenario to that of a response tracking a progressive environmental change. Increased yearly variation in weather patterns would suggest that fluctuations in production of stress hormones may also increase, but it is unclear what effect strong yearly fluctuations in stress hormone production would have on individuals over their lifetime. Therefore, although this thesis provides information on immediate responses to climate, further work will be necessary to fully understand how climate change is affecting individuals throughout their life and what effects this may have at a population level.

Alongside climate, catchment land use is one of the main drivers of change to river systems (Reynard et al. 2001, Coulthard and Macklin 2001). Riparian forest cover has been found to influence dipper population density (Logie et al. 1996), while urban cover has been linked to concentrations of contaminants in eggs (Morrissey et al. 2013). Perhaps the best-studied effect of land use on dippers is in relation to catchments dominated by commercial coniferous forestry linked to river acidification. Dipper energetic expenditure (O'Halloran et al. 1990), foraging, physiology (Tyler and Ormerod 1992), breeding phenology and success (Ormerod et

al. 1991), and population density (Logie et al. 1996) have been shown to vary in relation to forestry-mediated acidification. The catchments studied in this thesis, however, were largely dominated by farmland, and where forest occurred, its cover was below thresholds that result in river acidification. Despite this, land use mediated effects still had an effect on dipper breeding phenology (Chapter 2) and stress hormone levels in nestlings (Chapter 3), but not in juvenile or adult birds (Chapter 4). Catchments with high farmland cover were linked to earlier lay dates but produced nestlings with higher stress hormone concentrations. Relationships with forest cover were the opposite, partly due to the negative correlation between these two land covers in the study system, but also to the different effects of each land use on rivers. In areas dominated by farmland, rivers are more exposed to external factors and disturbance, resulting in higher fluctuations in temperature, river flow and nutrient loads from run-off. Seasonal effects (e.g. increasing temperatures in spring) would be more patent in these conditions, which would explain the earlier lay dates described in Chapter 2, as phenological cues for breeding would occur earlier. Conversely, rivers in areas dominated by forest are less prone to fluctuations as tree cover buffers changes in water temperature and root systems reduce run-off, resulting in more stable systems. These patterns explain the differences in lay dates between farmland and forest areas, but also give insights into the apparent effects of land use on nestling stress hormone concentrations described in Chapter 3. The stability of forest systems also makes them more predictable, reducing fluctuations in food availability during nestling development. These findings suggest that anthropogenic land uses may be acting as an ecological trap for dippers: farmland cover triggers earlier breeding but increased nestling stress hormone production. The possible effects at a population scale, however, remain unexplored. For example, evaluating whether earlier breeding in farmland areas is associated with higher breeding densities would add evidence to the ecological trap scenario and shed light on population effects.

Effects of global change drivers varied across the different dipper life stages assessed. For instance, land use effects on stress hormones varied with age (Chapters 3 and 4). In early life, farmland cover was linked to higher concentrations of corticosterone, but this relationship was not maintained in juvenile or adult birds for which yearly variation in climate appeared to bear a stronger influence on hormone levels. The

loss of a land use signal in free-roaming juvenile and adult dippers shows that at these stages other factors may play a more important role in influencing stress hormones. Although climate patterns were concurrent to changes in stress hormone levels (Chapter 4) and morphology (Chapter 5) in juvenile and adult birds, comparison of climate effects with earlier life stages was not possible. First, assessment of climate effects on nestling stress hormone levels was not possible as data was collected in a single year. Second, morphological changes described in juvenile and adult birds were sex-specific, but sex-determination of nestlings was not carried out as it would have required genetic testing. Despite these limitations, the work presented here suggests that a possible ontogenetic pattern that requires attention is whether the influence of land use may be stronger during early development while climate bears a stronger effect in later life.

2 Conclusions and future directions

This thesis highlights how global change effects on dippers vary depending on the drivers, scales, ecological traits, and life stages considered. Although the Irish context provides a relatively homogeneous study system (i.e. temperate climate, low rate of geographical or temporal change in land use, narrow range of water chemistry variation compared to other studies), three aspects of the study made it possible to detect effects of global change on dippers: (i) the multi-scale approach used in Chapter 2 (and in preliminary analyses of Chapters 3 and 4 to select land use scales); (ii) the use of long-term data (Chapters 2, 3 and 5); and (iii) the use of multiple response variables (Chapters 3 and 5) and, in particular, of physiological parameters which are more direct measures and show higher sensitivity to environmental change than traditional measures (Chapters 3 and 4). This showcases the value of incorporating multiple approaches to achieve a comprehensive understanding of the processes involved in species' responses to global change. Identifying factors that influence key aspects of a species' ecology and understanding the nature of these effects is pivotal to be able to minimise the impacts of global change. Although this work improves current understanding of how dippers in particular, and river species in general are affected by global change, it also raises further questions.

Chapter 2 describes the combined effects of climate and land use on breeding phenology. In this context, it would be interesting to study whether and how the effects of climate and land use vary across other phases of the breeding cycle. Although Chapter 3 tackles one aspect (effects of land use on nestling morphology and physiology), it does not explore the effects of climate on nestling condition. Furthermore, the effects of global change on territory occupancy, breeding density, timing of nest failure or breeding success rate remain unexplored. While the first two (occupancy and breeding density) would require further data collection, the existing data could be used to investigate changes in timing of nest failure and in breeding success. These could be studied with a similar approach to that used in Chapter 2 (multi-scale analysis of effects of climate, land use and their interactions), while sliding window analysis could be used to explore the influence of climate on long-term nestling biometric data used in Chapter 3.

The role of climate in physiology, and its effects on stress hormones emerges as a topic in Chapter 4. In the work presented here, it was not possible to assess the direct effects of climate on stress hormones. In Chapter 3, feather sampling was carried out in a single year and sample size was insufficient to assess within-year variation in relation to weather. In Chapter 4, weather patterns were so different in the two sampling years that preliminary analysis indicated highly significant effects of all weather variables assessed (i.e. rain, temperature, NAO) during all time periods prior to feather growth. These limitations could be overcome with larger samples covering more years. Feather samples were collected in additional years but not analysed for corticosterone due to limited resources. These samples could be used to improve sample sizes and temporal coverage to enable analysis of the effects of climate on stress hormone levels of nestlings, juveniles and adults.

Another topic emerging from this thesis is the precise role of factors intrinsic (e.g. nest structure, brood size) and extrinsic (e.g. land use, climate) to the nest in determining nestling morphology and physiology (Chapter 3). One possible avenue for future work could focus on the nest microclimate. Dipper nests are enclosed, and thus provide more protection from environmental factors than those of other bird species that build open nests. By using temperature and humidity loggers, it would be

possible to investigate how dipper nest microclimate varies in relation to external climate, nest structure (i.e. full domes, domes encased in man-made structures, nest boxes), or to brood size (e.g. temperature is likely to be different in nests with 2 or 5 nestlings). Brood manipulation or cross-fostering experiments would further aid these investigations and also give insight into the precise role of sibling competition in determining nestling condition. Understanding how intrinsic factors such as nest microclimate or sibling competition influence nestling condition would help us understand the relative importance of extrinsic factors such as climate (discussed above) or land use (Chapter 3).

Although dippers are responding to global change, the evolutionary potential of the species remains unexplored. The heritability of the traits studied here (phenological, physiological and morphological) will influence whether dippers can successfully adapt to changes in their environment (Visser 2008). Survival rates and fitness of the phenotypes associated with these traits will influence whether the responses described here are sufficient to cope with current and future trends of environmental change. For example, Chapter 5 describes changes in morphological traits (tarsus length, wing length and body mass) in female and male dippers, possibly linked to changes in river flow rates. These traits are likely to have a significant heritable component (Jensen et al. 2003), but investigating whether they are linked to differential survival and fitness is key to understanding whether dippers are likely to adapt to increasing rates of environmental change. The existing data could be used to perform mark-recapture survival analysis of individuals with known phenotypes (see Appendix S5.2). Furthermore, simple lab or field experiments with dippers in captivity (see for example Jenkins and Ormerod 1996) could investigate foraging efficiency and limitations of different phenotypes under varying flow conditions. These studies would inform on the adaptive nature of variation in morphological traits and whether natural selection plays a role in the observed changes.

At a broader scale, it is necessary to understand the variation of these responses across the species' range. Chapters 2 and 5 give insight into the potential importance of comparing responses between populations (Fig. 2.5 and 5.2). For instance, Fig. 2.5 showcases variations in lay date between this study (lay dates constant over time) and

British and French populations (significant advance in lay dates, Marzolin and D'Amico 2017, Massimino et al. 2017). Information on land use for these other populations would shed light on these patterns and the reasons for this variation in phenology. Similarly, it would be interesting to compare the allometric trends described in Chapter 5 (reduction in wing length relative to body size) with other populations exposed to different climatic patterns. Although based on a limited sample size, the opposite trends from another population under different climatic patterns shown in Figure 5.2 give an idea of the potential of this approach. Integration of data on phenological or morphological change from multiple populations would give insight into the spatial patterns and rates of phenotypic responses to climate change. Such integrative approaches are necessary if we are to understand and minimise the impacts of global change.

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Chapter 7

Appendix: additional research



In addition to the work presented in this thesis, I was also involved in the following research during my PhD.

1 Effects of wind energy development and associated changes in land use on bird densities in upland areas

Darío Fernández Bellon, Mark W. Wilson, Sandra Irwin & John O'Halloran

Conservation Biology (*in press*)

Wind energy development is the most recent of many pressures on upland bird communities and their habitats. Studies of birds in relation to wind energy development have focused on effects of direct mortality, but the importance of indirect effects (e.g., displacement, habitat loss) on avian community diversity and stability is increasingly being recognized. We used a control-impact study in combination with a gradient design to assess the effects of wind farms on upland bird densities and on bird species grouped by habitat association (forest and open-habitat species). We conducted 506 point count surveys at 12 wind farm and 12 control sites in Ireland during two breeding seasons (2012 and 2013). Total bird densities were lower at wind farms than at control sites, and the greatest differences occurred close to turbines. Densities of forest species were significantly lower within 100 m of turbines than at greater distances, and this difference was mediated by habitat modifications associated with wind farm development. In particular, reductions in forest cover adjacent to turbines was linked to the observed decrease in densities of forest species. Open-habitat species' densities were lower at wind farms but were not related to distance from turbines and were negatively related to size of the wind farm. This suggests that, for these species, wind farm effects may occur at a landscape scale. Our findings indicate that the scale and intensity of the displacement effects of wind farms on upland birds depends on bird species' habitat associations and that the observed effects are mediated by changes in land use associated with wind farm construction. This highlights the importance of construction effects and siting of turbines, tracks, and other infrastructure in understanding the impacts of wind farms on biodiversity.

2 Video evidence of siblicide and cannibalism, movement of nestlings by adults, and interactions with predators in nesting Hen Harriers.

Darío Fernández Bellon, Mark W. Wilson, Sandra Irwin, Thomas C. Kelly, Barry O'Mahony & John O'Halloran

Journal of Raptor Research (2018): 52, 393-399 doi.org/10.3356/JRR-17-58.1

During a nest-camera study of hen harriers (*Circus cyaneus*), we recorded siblicide, cannibalism, movement of nestlings by adult birds, and interactions with predators. We deployed cameras at 13 nests across three study areas in Ireland between 2008 and 2010. At a nest with two well-developed nestlings (approximately 25–30 d old), the older nestling killed its sibling and fed on it. This was the first documented case

of siblicide in this species, to our knowledge. Recordings also revealed three other events of cannibalism in which one of the nestlings in a brood died from unknown causes and was then eaten by its siblings (n = 1), by the adult male (n = 1), or was used by the adult female to feed the remaining nestlings (n = 1). At two nests, recordings showed the adult female picking up and moving nestlings that were outside the nest cup. In addition, cameras recorded two instances of full brood predation by red fox (*Vulpes vulpes*) and an attack on a nest by a female Eurasian kestrel (*Falco tinnunculus*) that had no apparent consequences for the nestlings or the female hen harrier. The behaviors reported here, which are difficult to observe directly, may have important consequences for our understanding of productivity and population dynamics of hen harriers.

3 Activity patterns of breeding hen harriers *Circus cyaneus* assessed using nest cameras

Darío Fernández-Bellon, Mark W. Wilson, Sandra Irwin, Thomas C. Kelly, Barry O'Mahony & John O'Halloran

Bird Study (2017): 64, 557-561 https://doi.org/10.1080/00063657.2017.1383969

Nest camera footage from 13 hen harrier *Circus cyaneus* nests was analysed to document patterns of adult attendance, incubation, brooding and prey delivery rates. Nest attendance was high throughout the incubation stage and began to decrease when chicks were five days old. Chick provisioning increased gradually after hatching and peaked when the chicks were five days old. Daily activity rates were highest during the middle of the day, from 08:00 to 19:00 hours.

4 Breeding ecology and habitat selection of merlin *Falco columbarius* in forested landscapes

John Lusby, Ilse Corkery, Shane McGuiness, Darío Fernández-Bellon, Larry Toal, David Norriss, Dermot Breen, Aonghus O'Donaill, Damian Clarke, Sandra Irwin, John L. Quinn & John O'Halloran

Bird Study (2017): 64, 445-454 https://doi.org/10.1080/00063657.2017.1408565

Capsule: Long-term trends in merlin *Falco columbarius* breeding performance remained stable during a period of extensive afforestation in Ireland, where merlin predominantly select conifer plantations for nesting.
Aims: To determine breeding performance and habitat selection of merlin in a landscape significantly altered by afforestation.
Methods: We compiled data on merlin to determine long-term trends in breeding performance and to examine habitat selection in a country with one of the fastest rates of afforestation in Europe.
Results: Merlin predominantly nested in trees (99.5%; n = 183 pairs), with a strong preference for conifer plantations, which accounted for over 12 times more nests

than expected by random selection. Moors and heathland were strongly selected as land-uses adjacent to nest sites. Most nests were located within 10 m of the forest edge, and in forests aged between 31 and 40 years. Merlin showed positive selection for moors and heathland, peat bogs and natural grasslands within breeding territories, and breeding success was positively related to the proportion of these land-uses surrounding nests. Breeding was successful for 74% of nests (n = 300), and mean productivity was 2.1 young per breeding attempt (n = 265) between 1982 and 2014. Breeding parameters remained constant over the 33-year study period, despite an increase of more than 75% in forest cover during this time.
Conclusion: Merlin breeding performance showed no long-term effects of increased afforestation. Although merlin predominantly nested in conifer plantations, the presence of nearby open suitable foraging habitats influenced nest site selection and breeding success. The nesting preference of merlin makes them vulnerable to disturbance from forest operations, which requires mitigation.

5 Hen harrier *Circus cyaneus* population trends in relation to wind farms

Mark W. Wilson, Darío Fernández-Bellon, Sandra Irwin & John O'Halloran

Bird Study (2017): 64, 20-29 https://doi.org/10.1080/00063657.2016.1262815

Capsule: The data presented here demonstrate a considerable spatial overlap between wind farms and the breeding distribution of hen harriers in Ireland, but evidence for a negative impact of wind farms on their population is weak.
Aims: To assess the extent of the overlap between wind farms and breeding hen harriers and to investigate their potential impact on hen harrier population trends.
Methods: Data on hen harrier breeding distribution in 10 km × 10 km survey squares from national surveys were used in conjunction with information on the location of wind farms to examine whether, and to what extent, changes in hen harrier distribution and abundance between 2000 and 2010 were related to wind energy development.
Results: Of the 69 survey squares holding hen harriers during the 2010 breeding season, 28% also overlapped with one or more wind farms. Data from 36 of the squares with breeding hen harriers during the 2000 survey revealed a marginally non-significant negative relationship between wind farm presence and change in the number of breeding pairs between 2000 and 2010.
Conclusions: A considerable overlap exists between hen harrier breeding distribution and the location of wind farms in Ireland, particularly in areas between 200 and 400 m above sea level. The presence of wind farms is negatively related to hen harrier population trends in squares surveyed in 2000 and 2010, but this relationship is not statistically significant, and may not be causal. This is the first study to assess the influence of wind energy development on hen harriers at such a large geographic and population scale.

6 Density-dependent productivity in a colonial vulture at two spatial scales

Darío Fernández-Bellon, Ainara Cortés-Avizanda, Rafael Arenas & José Antonio Donázar

Ecology (2016): 97, 404-416 https://doi.org/10.1890/15-0357.1

Understanding how density dependence modifies demographic parameters in long-lived vertebrates is a challenge for ecologists. Two alternative hypotheses have been used to explain the mechanisms behind density-dependent effects on breeding output: habitat heterogeneity and individual adjustment (also known as interference competition). A number of studies have highlighted the importance of habitat heterogeneity in density dependence in territorial species, but less information exists on demographic processes in colonial species. For these, we expect density-dependent mechanisms to operate at two spatial scales: colony and breeding unit. In this study, we used long-term data from a recovering population of cinereous vultures (*Aegypius monachus*) in southern Spain. We analyzed a long-term data set with information on 2162 breeding attempts at four colonies over a nine-year period (2002–2010) to evaluate environmental and population parameters influencing breeding output. Our results suggest that breeding productivity is subject to density-dependent processes at the colony and the nest site scale and is best explained by interference competition. Factors intrinsic to each colony, as well as environmental constraints linked to physiography and human presence, also play a role in regulatory processes. We detected the existence of a trade-off between the disadvantages of nesting too close to conspecifics and the benefits of coloniality. These could be mediated by the agonistic interactions between breeding pairs and the benefits derived from social sharing of information by breeding individuals. We propose that this trade-off may play a role in defining colony structure and may hold true for other colonial breeding bird species. Our findings also have important management implications for the conservation of this threatened species.

7 Reproductive output of hen harriers *Circus cyaneus* in relation to wind turbine proximity

Darío Fernández-Bellon, Mark W. Wilson, Sandra Irwin & John O'Halloran

Irish Birds (2015): 10, 143-150 https://goo.gl/VqDLkz

Despite the growing importance of wind energy development in Ireland, and concerns about its potential ecological impact on birds, there is a notable lack of published scientific information in this area. As a bird of conservation concern, the hen harrier *Circus cyaneus* inhabits upland areas with potential for wind energy resources. This study assessed the breeding performance of hen harriers across Ireland in relation to wind farm development by analysing the breeding output from 84 nests located at varying distances from wind turbines. Three measures of breeding performance were investigated: (a) nest success (the proportion of nests that fledged one or more young), (b) fledged brood size (the average number of fledged chicks per successful nest), and (c) overall productivity of breeding pairs (the average number of fledged chicks across all nesting attempts). No statistically significant relationships were found between these breeding parameters and distance of the nest from the nearest wind turbine. However, lower nest success within 1 km of wind turbines than at greater distances was sufficiently close to statistical significance, and with a sufficiently small sample size, that this difference may be of biological relevance. Nests within 1 km of wind turbines which were successful had similar fledged brood sizes to those of nests at greater distances from turbines. These

findings support previous research which highlighted the importance of areas within a 1 km radius of raptor nests. Our results provide the first insight into the potential effects of wind turbines for breeding success of hen harriers, which should be taken into consideration in assessments of wind farm impacts on this vulnerable species. Further work is required to quantify (a) direct hen harrier mortality through collisions, (b) habitat loss and displacement caused by wind turbines and (c) to continue ongoing monitoring of breeding success in order to confirm whether the effect of wind farm proximity suggested here is consistent. This work will support the development of an integrated management strategy for hen harriers in Ireland.