

Specialist river birds as bioindicators of freshwater ecosystem health in the face of complex environmental change

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GENERAL ABSTRACT

Rivers are one of the most important and sensitive ecosystems globally, subject to environmental pressures integrated across local, landscape and catchment scales. There is a growing need to effectively assess their ecological health to inform management strategies for their restoration and conservation, yet detecting the impacts of multiple integrated stressors is also challenging. Bioindicators can reflect the state of an environment and offer a relatively cheap alternative or complementary approach to traditional direct measures. Predatory, obligate riverine birds are promising candidates for indicating riverine health, with White-throated Dipper at the forefront of research due to their sensitivity to a broad range of pressures. However, other riverine specialists such as Grey Wagtail and Common Sandpiper that have divergent life histories and ecologies may improve capture of the intersection of riverine, riparian, and nearby terrestrial ecosystems that ultimately affect riverine health.

This thesis examines the responses of these focal species to integrated stressors affecting riverine and riparian ecosystems in Britain, progressing our understanding of their potential role as broad indicators of ecological health. Chapter 2 explores the environmental drivers of spatial variation in occupancy and abundance of the three species. Findings demonstrate that occupancy, and to a lesser extent, abundance is controlled by underlying physiography and land cover at channel, local landscape, and catchment scales, upscaling existing knowledge to catchment-scale pressures. Chapter 3 examines responses to varying weather conditions. This analysis highlights the multiple direct and indirect pressures that temperature and rainfall impose, but the varying effects on these species likely reflects their contrasting breeding strategies. Chapter 4 investigates the association between Dipper breeding performance, breeding density and clutch initiation in a well-studied catchment. Findings suggest that clutch initiation date is a stronger driver of breeding performance than breeding density, but high variability within and among years may be obscured by overall trends.

DECLARATION OF AUTHORSHIP

I, Rachel S. Steenson, declare that I have composed this thesis and that it embodies the results of my own research. Where appropriate I have acknowledged the nature and extent of work carried out in collaboration with others. All research material has been duly acknowledged and cited.

Signed: 

Date: 28/03/2024

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TABLE OF CONTENTS

General abstract.....	3
Declaration of Authorship.....	4
Acknowledgements	5
List of Figures.....	10
List of Tables	12
List of Appendices	14
Chapter 1: General Introduction.....	17
1.1. Threats to riverine ecosystems.....	17
1.1.1. Acidification.....	19
1.1.2. Land use management.....	20
1.1.3. Climate change.....	27
1.1.4. Brownification	28
1.1.5. Invasive species.....	29
1.2. Status of riverine communities.....	31
1.2.1. Decline in riverine bird populations.....	31
1.3. Bioindicators for ecosystem health.....	34
1.3.1. What is a bioindicator?.....	34
1.3.2. Common riverine bioindicators	34
1.3.3. Evidence of birds as bioindicators	35
1.3.4. Dippers as bioindicators.....	35
1.3.5. Other options for avian bioindicators in riverine ecosystems	38
1.4. Research overview	43
Chapter 2: Environmental drivers of spatial variation in occupancy and abundance of three declining riverine birds	45
2.1. Abstract.....	45
2.2. Introduction.....	45
2.3. Methods	48
2.3.1. Bird survey data.....	48
2.3.2. Environmental data	49

2.3.3. Modelling approach.....	53
2.4. Results.....	56
2.4.1. Occupancy.....	56
2.4.2. Abundance.....	59
2.5. Discussion.....	62
2.5.1. Species responses to environmental variables.....	63
2.5.2. Managing rivers for the benefit of river birds.....	67
2.6. Appendix.....	68
Chapter 3: Is the abundance of riverine birds influenced by climate conditions?	79
3.1. Abstract.....	79
3.2. Introduction.....	79
3.3. Methods.....	81
3.3.1. Bird survey data.....	81
3.3.2. Climate data.....	83
3.3.3. Modelling approach.....	85
3.4. Results.....	87
3.4.1. Abundance trends for focal species.....	87
3.4.2. Comparative species' sensitivity to climate indices.....	87
3.4.3. Full species-level responses to climate conditions.....	89
3.5. Discussion.....	92
3.5.1. Species' responses towards climate conditions.....	93
3.5.2. Management strategies.....	96
3.6. Appendix.....	97
Chapter 4: Long term breeding performance of White-throated Dipper (<i>Cinclus cinclus</i>) in a Scottish catchment.....	114
4.1. Abstract.....	114
4.2. Introduction.....	114
4.3. Methods.....	117
4.3.1. Study area and survey history.....	117
4.3.2. Data.....	120

4.3.3. Modelling approach.....	123
4.4. Results.....	124
4.4.1. Noteworthy nests.....	124
4.4.2. Breeding performance	130
4.5. Discussion.....	140
4.5.1. Variation in breeding density and clutch initiation within the South Esk catchment 140	
4.5.2. Association between year, breeding density, clutch initiation, and breeding performance.....	141
4.5.3. Comparison with national metrics and trends.....	143
4.5.4. Conclusions.....	144
4.6. Appendix.....	145
Chapter 5: General Discussion.....	156
5.1. Summary of research.....	156
5.2. Implications for conservation and biodiversity of riverine ecosystems	160
5.2.1. Birds as bioindicators.....	160
5.2.2. Lessons for managing rivers for riverine biodiversity	161
5.2.3. Reflection on changes in river and catchment management	162
5.3. Research complications from Covid-19.....	163
5.4. Future research	165
5.4.1. Development of analyses in this thesis	166
5.4.2. The next steps	169
5.5. Conclusion	171
References	173

LIST OF FIGURES

Figure	Title	Page
CHAPTER 1		
1.1	Flowchart summarising the direct and indirect pressures within freshwater ecosystems.	18
1.2	Example of poor practice in conifer plantation.	21
1.3	Example of mine drainage evidence in rivers.	23
1.4	Example of varying flow regimes from a hydroelectric dam with stepped spillway.	26
1.5	Example water colour variability due to differences in the concentration of DOM and iron.	29
1.6	Smoothed population trends for five bird species commonly associated with the riverine environment between 1974 and 2021.	33
1.7	Global distribution of Cinclidae species.	37
1.8	Dipper breeding (orange) and winter (blue) distributions in Great Britain.	38
1.9	Distribution maps for Grey Wagtail.	40
1.10	Distribution maps for Common Sandpiper.	42
CHAPTER 2		
2.1	Site locations included in each species' dataset.	49
2.2	Forest plot of GLMM output for Dipper, Common Sandpiper and Grey Wagtail occupancy.	57
2.3	Marginal effect plots of species occupancy and histograms of the individual site ranges for significant/marginal explanatory variables	58
2.4	Forest plot of GLMM output for Dipper, Common Sandpiper and Grey Wagtail abundance.	60
2.5	Marginal effect plots of species abundance (birds/km) and histograms of the individual site ranges for significant/marginal explanatory variables.	61
CHAPTER 3		
3.1	Maps showing the site locations that are included in each species' dataset.	83
3.2	Trends for species abundance (birds/km) from 1998 to 2019.	87
3.3	Diagram summarising species sensitivity to length of Winter (A) and Breeding (B) climate indices.	88
3.4	Partial effect plots of species abundance for species-specific responses to climate indices.	90
CHAPTER 4		
4.1	Metrics for Dipper breeding performance, estimated from data collected throughout the UK.	116
4.2	Study area location	119
4.3	Two Dipper nests positioned in trees.	126
4.4	Dipper nest positioned in a crack within an old railway bridge support, Gorewater.	127

4.5	Dipper nest positioned under an overhanging bank and constructed primarily of grass, Gorewater.	128
4.6	Example of three old Dipper nests at a single site that were not re-used.	129
4.7	Culvert nest, which was active in all three study periods.	129
4.8	Breeding density (pairs/km) in the study area.	130
4.9	Marginal effects of (A) year, (B) elevation and (C) breeding density on Clutch initiation date for first breeding attempts.	132
4.10	Histograms (A, E) and marginal effects of year (B, F), breeding density (C, G), and clutch initiation date (D, H) on clutch size and brood size respectively.	133
4.11	Nestling biometrics.	135
4.12	Probability of survival (P_{survival}) for year (A), breeding density (B), and clutch initiation date (C).	137
4.13	Probability of second breeding attempts following a successful first (P_{second}) for individual years (A), year trend (B), breeding density (C), and clutch initiation date (D).	139
CHAPTER 5		
5.1	Dipper nestlings waiting at the nest entrance for food.	160
5.2	The iconic viaduct over the Big Water of Fleet, above Gatehouse of Fleet in Galloway.	164
5.3	Example paper nest records from Mike Nicholl.	165
5.4	Colour-ringed Dipper fledgling in the River South Esk study system.	168
5.5	Details of long-term nest record data collected in Perthshire and Angus, Scotland.	169

LIST OF TABLES

Table	Title	Page
CHAPTER 1		
1.1	Population estimates, conservation status and trends for five bird species commonly associated with riverine habitats in Britain.	32
CHAPTER 2		
2.1	Detail on datasets used to extract variables for analysis.	50
2.2	Inclusion of bird survey data in occupancy and abundance models.	55
CHAPTER 3		
3.1	Climate variables considered for analysis	84
3.2	Multivariate Generalised additive mixed model (GAMM) output by species	91
CHAPTER 4		
4.1	Data collected during nest monitoring, with availability depending on study period.	121
4.2	Time periods used for estimation of key dates associated with breeding Dippers.	121
4.3	Output from type-II analysis of deviance, evaluating the effects of year and site on breeding density.	131
4.4	Output from Generalized Linear model (GLM) evaluating the effects of year (factor) and site on breeding density.	131
4.5	Output from Linear model (LM) evaluating the effects of year, elevation, and breeding density on clutch initiation date for first breeding attempts.	132
4.6	Output from type-II analysis of variance, evaluating the effects of year, elevation, and breeding density on clutch initiation date for first breeding attempts.	132
4.7	Output from Linear model (LM) evaluating the effects of year, clutch initiation date and breeding density on clutch size.	133
4.8	Output from type-II analysis of variance, evaluating the effects of year, clutch initiation date and breeding density on clutch size.	133
4.9	Output from Linear model (LM) evaluating the effects of year, clutch initiation date and breeding density on brood size.	134
4.10	Output from type-II analysis of variance, evaluating the effects of year, clutch initiation date and breeding density on brood size.	134
4.11	Output from Linear Mixed-effect Model (LMM) evaluating the effects of age on nestling weight and tarsus length.	136
4.12	Output from Linear Mixed-effect Model (LMM) evaluating the effects of tarsus length and study period (i.e. 1990/91 vs. 2021/22) on nestling weight, including an interaction term.	136
4.13	Output from Linear mixed-effect model (LMM) evaluating the effects of year, clutch initiation date, brood size and breeding density on residuals of nestling weight.	137
4.14	Output from Generalised linear model (GLM) evaluating the effects of year (factor) on the probability of survival.	138

4.15	Generalised linear model (GLM) evaluating the effects of clutch initiation date and breeding density on the probability of survival.	138
4.16	Output from Generalised linear model (GLM) evaluating the effects of year (factor) on the probability of a second breeding attempt.	139
4.17	Generalised linear model (GLM) evaluating the effects of clutch initiation date and breeding density on the probability of a second breeding attempt.	140

CHAPTER 5

5.1	Summary of results from chapters 2 and 3	159
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LIST OF APPENDICES

Appendix	Title	Page
CHAPTER 2		
A2.1	BTO WBBS data	68
	<i>Figure A2.1-1: Histograms of the relative number of each species included in data</i>	68
A2.2	Description and use of spatial scale for each environmental variable	69
	<i>Figure A2.2-1: Description of data extraction areas for each WBBS survey site.</i>	69
	<i>Table A2.2-1: Summary of spatial scales for environmental variables used in analysis.</i>	69
A2.3	Value range of environmental variables by species	70
	<i>Figure A2.3-1: Histograms of explanatory variable values for Dipper.</i>	70
	<i>Figure A2.3-2: Histograms of explanatory variable values for Grey Wagtail.</i>	71
	<i>Figure A2.3-3: Histograms of explanatory variable values for Common Sandpiper.</i>	72
A2.4	Effect of survey effort on occupancy and abundance	73
	<i>Figure A2.4-1: Linear association between survey effort and (A) occupancy and (B) abundance</i>	73
	<i>Table A2.4-1: LM output for occupancy and survey effort of the three species.</i>	73
	<i>Table A2.4-2: LM output for abundance and survey effort of the three species.</i>	73
A2.5	Buffer sizes for land cover variables by species	74
	<i>Table A2.5-1: Details of reach level land cover buffer sizes for each species.</i>	74
A2.6	Correlation test results	75
	<i>Figure A2.6-1: Correlation plot of explanatory variables at sites in the bird survey data.</i>	75
A2.7	Model structures	76
	<i>Table A2.7-1: Final multivariate occupancy model structures.</i>	76
	<i>Table A2.7-2: Final multivariate abundance model structures.</i>	76
A2.8	Model outputs	77
	<i>Table A2.8-1: GLMM output for occupancy by species.</i>	77
	<i>Table A2.8-2: GLMM output for abundance by species.</i>	78
CHAPTER 3		
A3.1	Example of HAD-UK climate data	97
	<i>Figure A3.1-1: Example raw climate data.</i>	97
A3.2	Model selection for species abundance trends	98
	<i>Figure A3.2-1: GAMs of species abundance trends.</i>	98
	<i>Table A3.2-1: Comparison of GAIC values of the three smoothing methods</i>	99
	<i>Table A3.2-2: Generalized Akaike information criterion (GAIC) for species abundance trend model comparison.</i>	99
A3.3	Effect of survey effort on occupancy and abundance	100

	<i>Figure A3.3-1: Linear association between survey effort and abundance, including zero counts.</i>	100
	<i>Table A3.3-1: LM output for occupancy and survey effort of the three species.</i>	100
A3.4	Annual variation in climate indices	101
	<i>Figure A3.4-1: Annual variation in climate variables.</i>	101
	<i>Figure A3.4-2: Scaled and centred annual variation in climate variables.</i>	102
A3.5	Detrending species abundance and climate data	103
	<i>Figure A3.5-1: Raw and detrended pooled bird count (abundance) data by species.</i>	103
	<i>Figure A3.5-2: Comparison of trends present in the climate variables.</i>	104
A3.6	Univariate GAM results	105
	<i>Table A3.6-1: Results of univariate GAMMs between bird abundance and all climatic variables.</i>	105
	<i>Figure A3.6-1: Partial effect plots for univariate GAMMs between Dipper abundance and each climate variable.</i>	106
	<i>Figure A3.6-2: Partial effect plots for univariate GAMMs between Grey Wagtail abundance and each climate variable.</i>	107
	<i>Figure A3.6-3: Partial effect plots for univariate GAMMs between Common Sandpiper abundance and each climate variable.</i>	108
A3.7	Correlation test results	109
	<i>Figure A3.7-1: Correlation test results.</i>	109
A3.8	Multivariate model selection	110
	<i>Table A3.8-1: Multivariate GAMM structure for Dipper.</i>	110
	<i>Table A3.8-2: Multivariate GAMM structure for Grey Wagtail.</i>	110
	<i>Table A3.8-3: Multivariate GAMM structure for Common Sandpiper.</i>	111
A3.9	Multivariate model outputs	112
	<i>Table A3.9-1: Output from Generalised additive mixed model (GAMM) evaluating the effects of climate indices on Dipper breeding abundance.</i>	112
	<i>Table A3.9-2: Output from Generalised additive mixed model (GAMM) evaluating the effects of climate indices on Grey Wagtail breeding abundance.</i>	112
	<i>Table A3.9-3: Output from Generalised additive mixed model (GAMM) evaluating the effects of climate indices on Common Sandpiper breeding abundance.</i>	112
A3.10	Concurvity test results	113
	<i>Figure A3.10-1: Concurvity test results for the (A) Dipper, (B) Grey Wagtail and (C) Common Sandpiper multivariate GAMMs.</i>	113

CHAPTER 4

A4.1	Dipper nests construction and positioning	145
	<i>A4.1-1: Dipper nest construction</i>	145
	<i>Figure A4.1-2: Example Dipper nest positioning.</i>	146
A4.2	Use of endoscope for nest monitoring	147
	<i>Figure A4.2-1: Endoscope used to view inside of otherwise inaccessible nests.</i>	147

	<i>Figure A4.2-2: Example views using an endoscope to monitor Dipper nests.</i>	147
A4.3	Examples of Dipper nestling development at 6 to 12 days old	148
	<i>Figure A4.3-1: Images demonstrating development of Dipper nestlings at (A) six, (B) seven, (C) eight, (D) nine, (E) ten, (F) eleven and (G) twelve days old (day zero = day of hatching).</i>	148
A4.4	Data collection techniques used during nestling ringing.	149
	<i>Figure A4.4-1: Images showing data collection methods during nestling ringing.</i>	149
A4.5	Comparison of tarsi measurement methods.	150
	<i>Figure A4.5-1: Methods for measuring (a) minimum and (b) maximum tarsi on birds.</i>	150
	<i>Figure A4.5-2: Comparison of tarsus length (mm) methods against weight (g).</i>	150
	<i>Table A4.5-1: Summary statistics for minimum tarsus measurements.</i>	151
A4.6	Nest and territory position maps.	152
	<i>Figure A4.6-1: Location of active nests surveyed on the River South Esk in 1979, 1980 and 1981.</i>	152
	<i>Figure A4.6-2: Location of active nests surveyed on the River South Esk in 1982, 1983 and 1984.</i>	153
	<i>Figure A4.6-3: Location of active nests surveyed on the River South Esk in 1985, 1986 and 1990.</i>	154
	<i>Figure A4.6-4: Location of active nests surveyed on the River South Esk in 1991, 2021 and 2022.</i>	155

CHAPTER 1: GENERAL INTRODUCTION

Running waters are one of the most important, and at-risk ecosystems in the world. They are a major processing and transport system for energy, organisms and solutes from both terrestrial and autochthonous sources, can integrate environmental pressures across habitats within their watershed through vast drainage networks and act as an indicator of ecological degradation both locally and elsewhere within the catchment (Vannote et al., 1980; Durance & Ormerod, 2009; Allen et al., 2024). Freshwaters host a disproportionately high species richness compared with other habitats, supporting 6% of described species despite only comprising 0.8% of Earth's surface (Dudgeon et al., 2006; Miranda, Hermoso & Hassall, 2019; Reid et al., 2019), but also provide food and drinking water, offer an environment for tourism and recreation, and support industry, agriculture, navigation, waste disposal and electricity generation (Critchlow-Watton et al., 2014; WWF, 2022). Paradoxically, many of these services also impose chemical, biological or physical pressures on watercourses that can negatively affect ecological health, thereby impacting the quality and delivery of these services (Miranda, Hermoso & Hassall, 2019). Effective monitoring to understand how freshwater ecosystem health responds to, and recovers from, multiple stressors on a spectrum of spatial scales is challenging, but crucial to ensure that watercourses are improved, restored, and protected as resources for nature and humans alike. This introductory chapter firstly examines threats to riverine ecosystems and the consequent impacts on communities, before discussing how specialist riverine birds may be utilised as indicators for ecosystem health and quality.

1.1. Threats to riverine ecosystems

Globally, there are a range of threats to riverine ecosystems, which can be broadly grouped into five integrated categories: (1) water pollution; (2) habitat degradation; (3) flow modification; (4) species invasions; and (5) over-exploitation (Dudgeon et al., 2006; Haase et al., 2023). With the exception of over-exploitation, which primarily affects vertebrate taxa, these groups impose stresses on all taxa within lotic ecosystems; all five are potentially further exacerbated by climate change and riparian/catchment-scale land management. The following sections will discuss the threats to riverine ecosystems posed by water pollution, habitat degradation and flow modification in terms of the processes and land uses that impose such pressures (Figure 1.1) within a European context. The potential impacts of species invasions on rivers will be discussed briefly, but assessing the impacts of over-exploitation is beyond the scope of this thesis and will not be discussed here.

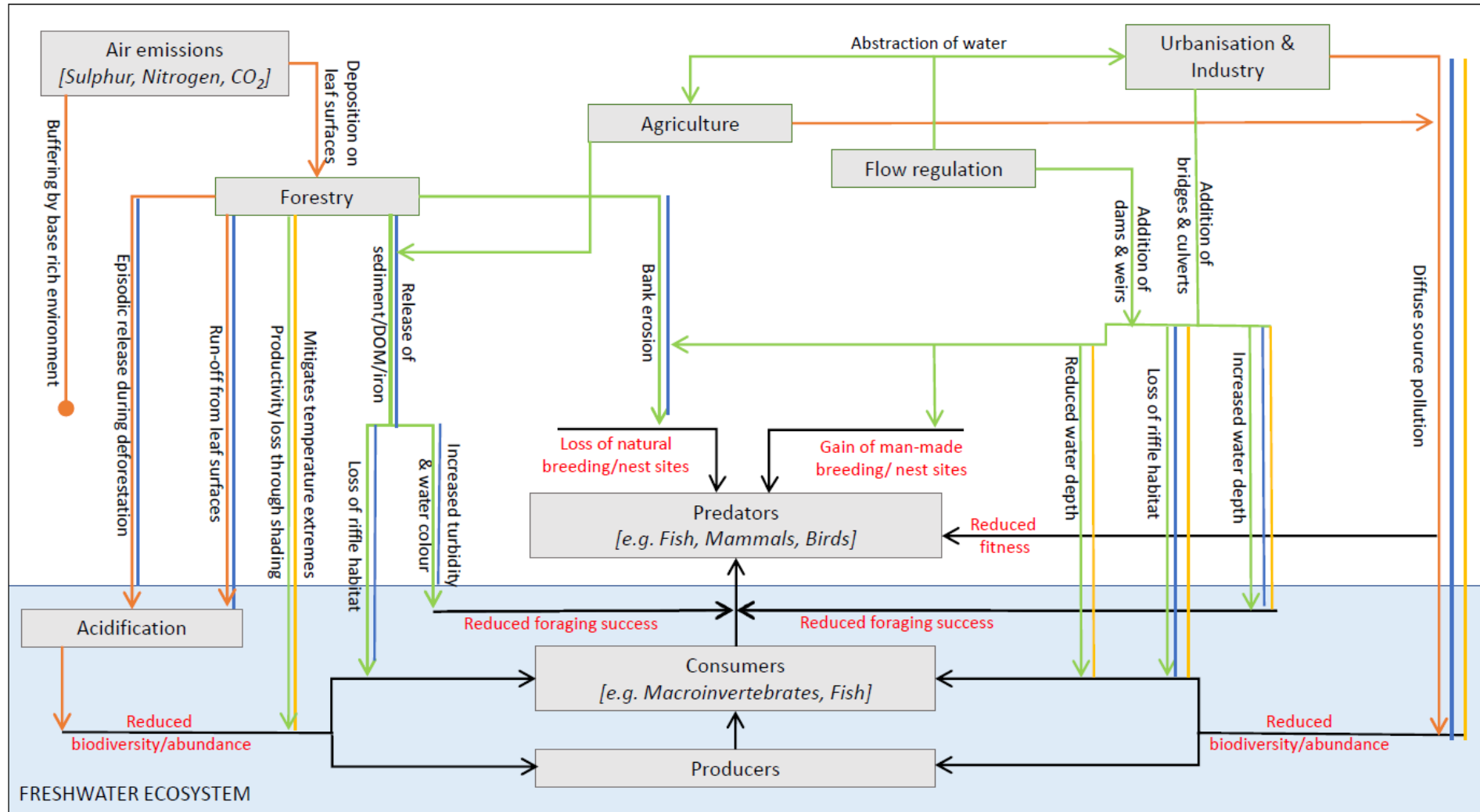


Figure 1.1: Flowchart summarising the direct and indirect pressures within freshwater ecosystems. Examples of effects on producers, consumers and predators are highlighted in red text; green and orange arrows represent habitat modification and pollution respectively; blue lines indicate processes that are exacerbated by precipitation; yellow lines indicate processes that affect local temperature regimes.

1.1.1. Acidification

Watercourses may exhibit a broad range in pH naturally (< 4 - 12), particularly in areas rich in dissolved organic matter (e.g. bogs) or endorheic basins. Acidification occurs where the natural pH is lowered through anthropogenic activity, and has largely been attributed to ‘strong’ acid deposition from sulphur and nitrogen emissions from coal-fired power stations and vehicle exhausts (Hildrew & Ormerod, 1995; Hasler et al., 2018), and more recently ‘weak’ acid deposition from carbon dioxide (Hasler et al., 2018), both of which are subsequently introduced to the catchment through acid rain and runoff. The degree of acidification can be exacerbated by poor management of afforestation (see section 1.1.2; Gee and Stoner, 1989; Ormerod *et al.*, 1989; Nisbet, 2001; Evans *et al.*, 2014; Broadmeadow *et al.*, 2019), the addition of fertilizers or reduction of lime application to agricultural land (Gee & Stoner, 1989; Goulding, 2016), disruption of peatland (Allan & Castillo, 2007; Monteith et al., 2014), and increases in precipitation (RoTAP, 2012). Conversely, the presence of base-rich soils, geology, dissolved organic carbon or vegetation in the catchment can act as a buffer and raise or stabilise the pH (Gee & Stoner, 1989; Allan & Castillo, 2007; Winterdahl, Bishop & Erlandsson, 2014). Consequently, a freshwater environment is prone to acidification under heavy acid deposition where the natural buffering capacity is also reduced or absent.

Recognition of acidification as a widespread environmental threat in the 1970s led to regulations on industrial emissions at both national and international scales (Malmqvist & Rundle, 2002), which alongside reductions in heavy industry and switching from coal to cleaner fuel sources, has resulted in significant reductions in sulphur emissions and deposition across Europe and North America. However, reductions in nitrogen emissions and deposition have been lower overall, and geographically highly variable. For example, the UK observed declines in sulphur and nitrogen emissions by 94% and 58% respectively, with subsequent reductions in acid deposition from sulphur dioxide and nitrogen oxides by 80% and 22% respectively (RoTAP, 2012). Despite these reductions, a “pollution legacy” exists where acidic compounds are retained in soil and vegetation, which has the potential to cause freshwater acidification if released in large volume through increased soil erosion and leaching, for example during deforestation or land drainage (Alewell et al., 2000; Evans et al., 2014).

Acidified streams and rivers have significantly reduced plant, invertebrate and vertebrate biodiversity when compared with neutral waterways of a similar physiography (Townsend, Hildrew & Francis, 1983; Ormerod, Tyler & Lewis, 1985; Ormerod et al., 1986, 1987; Ormerod & Tyler, 1987b; Vickery, 1991, 1992; Hildrew & Ormerod, 1995; Durance & Ormerod, 2007). While there is evidence of chemical recovery in multiple formerly acidified freshwater ecosystems in the UK, biological recovery (as assessed through surveys of diatoms, plants, macroinvertebrates and fish) so far appears to be much slower and highly variable (Alewell et al., 2000; Evans et al., 2001; Evans & Monteith, 2001; Ormerod & Durance, 2009; Layer et al., 2010; Battarbee et al., 2014;

Evans et al., 2014; Malcolm et al., 2014a, 2014b; Monteith et al., 2014; Murphy et al., 2014; Windsor et al., 2019). It is likely that some land-use practices and episodic releases from mixed sources are limiting the recovery of acid-sensitive freshwater ecosystems (Rose et al., 2004; Malcolm et al., 2014b).

1.1.2. Land use management

Lotic environments and the surrounding riparian zones have long been altered by humans physically and chemically for use by industry, or as a side-effect of development, agriculture and forestry operations (SEPA, 2007, 2009; Natural England and RSPB, 2014). These have extensive direct and indirect impacts on riverine ecosystems, and are detailed by land-use type below.

1.1.2.1. Forestry

Large scale conifer afforestation within the UK and Europe was implemented following the first- and second World Wars respectively in response to changing economic priorities and recognition of the heavily depleted state of the UK forest stock (Weber, 2000; Zanchi et al., 2007). However, lack of knowledge or concern for the environmental impacts of these schemes resulted in significant modification and degradation to both lotic and terrestrial ecosystems. For example, trees were planted in dense stands to maximise use of available land, often on stream and riverbanks (Figure 1.2). This forestry method has since been identified to remove herbaceous vegetation through shading, increase bank erosion, reduce stream productivity (Murgatroyd & Ternan, 1983; Broadmeadow & Nisbet, 2004) and exacerbate acidification through deposition of pollutants on leaf surfaces (Gee & Stoner, 1989; Ormerod, Donald & Brown, 1989; Nisbet, 2001; Evans et al., 2014; Broadmeadow, Nisbet & Forster, 2019). As these plantations reach maturity, felling needs to be managed responsibly to reduce the risk of nutrient leaching, coarse sediment and woody debris deposition in the river channel, or increased water turbidity and brownification (Murgatroyd & Ternan, 1983; Nisbet, 2001; Evans et al., 2014; Forest Research, 2023), all of which will likely affect macroinvertebrate community composition and predator foraging success (Da Prato, 1981; Townsend, Hildrew & Francis, 1983; Abrahams & Kattenfeld, 1997).



Figure 1.2: Example of poor practice in conifer plantation. Trees are planted in dense stands without a 2-20m riparian buffer strip between the plantation and river. Image taken from SEPA, 2009.

While riparian or catchment scale deciduous or mixed woodland would provide fewer impacts to lotic ecosystems, a balance must be struck due to the high demand for timber and wood products. The restoration of native riparian woodland buffers whilst restocking may alleviate some impacts, while bringing benefits for flood management, aquatic and terrestrial biodiversity. As of 2023, forested land cover in the UK has increased to 13.4%, with less than half classed as coniferous woodland (also <50% coniferous for the 35% total forest cover in 2020 for continental Europe; Forest Europe, 2020; Forest Research, 2023). Total forested land cover is likely to continue to rise in the future, driven by current pressure and policy on tree planting to reduce the effects of climate change. If extensive new areas of forested land are established without appropriate and feasible management policies in place, such as a minimum buffer width of 2-20m (SEPA, 2009; Forest Research, 2023), there is a risk that freshwater ecosystems will increasingly be impacted by the forestry sector in the future.

1.1.2.2. Urbanisation and industry

Urban development, infrastructure and industry have the potential to dramatically impact riverine hydrology, ecology and physical structure through point and diffuse source pollution, release of effluent and water abstraction (discussed in section 1.1.2.4 Water management).

Pollutants enter watercourses through surface runoff, drainage systems, groundwater flow or atmospheric deposition, where they can accumulate over stretches of persistent input or be retained in the substrate and cause isolated zones of poor water quality (Pratt, Coler & Godfrey, 1981). Pollutant transfer to watercourses can be significantly exacerbated in urban areas, where the combination of rapid surface run-off due to impervious surfaces and low storage capacity can result in flashy flow regimes, even when managed by drainage systems (Gurnell, Lee & Souch, 2007). Urban or industrial areas contaminated with organic pollutants (e.g. polychlorinated biphenyls [PCBs], polybrominated diphenyl ethers [PBDEs]), light and heavy metals (e.g. cadmium, selenium, mercury) have significantly reduced biodiversity and simplified food-webs, often limited to stress-tolerant species, with consequent impacts on predator body condition and fitness (Maltby et al., 1995; Nedeau, Merritt & Kaufman, 2003; Morrissey et al., 2014; Windsor et al., 2019; Albini et al., 2023). Increased flow conditions at effluent discharge points may create vital riffle habitat, but also cause water temperature to rise with subsequent increases in biological oxygen demand (BOD) from treated sewage effluent (Nedeau, Merritt & Kaufman, 2003). Furthermore, drainage from active and abandoned mining/quarrying operations can release acidic compounds and heavy metal pollution (Figure 1.3), which can impact pollutant- and acid-sensitive macroinvertebrate taxa in the receiving watercourse (Scullion & Edwards, 1980), and leave a pollution legacy by contaminating sediment and groundwater (Jarvis & Younger, 2000).



Figure 1.3: Example of mine drainage evidence in rivers. Water from Junkie's Adit, a pit drain from the retired mine in Bilston (Dalkeith, Midlothian), transported acidic and toxic compounds (e.g. manganese) to the River South Esk in 2021 and 2022. Image taken from Edinburgh Live report (Smith, 2020).

Bridges and culverts that transport water underneath roads and other structures may also modify riverine habitat and increase substrate pollutant retention. If the channel restriction is too narrow for the carrying capacity of the watercourse, particularly under high flow regimes, sediment can accumulate upstream of the structure (Wellman, Combs & Cook, 2000). Downstream of the structure, the river cross-section can be expanded through increased velocity causing substrate and bank erosion, thus removing riffle habitat (Merrill, 2005). This physical modification of the stream or river channel directly affects the freshwater habitat, and has the potential to create accumulation zones for pollutants (Pratt, Coler & Godfrey, 1981; Maltby et al., 1995; Windsor et al., 2019), both of which reduce macroinvertebrate abundance and diversity, simplify food-web structure, and reduce predator foraging efficiency (Da Prato, 1981; Scullion et al., 1982). It should be noted however, that these drainage structures are also commonly used as nest and roost locations by some riverine birds due to their stability compared with natural sites. Hence, these structures may simultaneously support predators whilst either impeding their access to a reliable food source or increasing pollutant exposure.

The addition or retention of riparian vegetation reduces diffuse source pollution through surface runoff and improves macroinvertebrate richness, but the presence of drainage outlets can counteract this effect (Moore & Palmer, 2005; Feld et al., 2018). While there has been widespread improvement in water quality in urban watercourses, anthropogenic pressures can cause localised or episodic falls in water quality (Vaughan & Ormerod, 2012). Furthermore, ongoing

human population growth will increase future demand for urbanisation and industry, and thus intensify pressure on existing infrastructure and lotic ecosystems. For example, Combined Sewer Overflows [CSOs] exist primarily as a ‘safety valve’ on sewerage systems, preventing backflow and flooding of domestic and commercial premises. Permits granted by the Environment Agency (England), SEPA (Scotland) and Natural Resources (Wales) allow water companies to discharge untreated and partially treated sewage into rivers and streams if the system is likely to be overloaded (e.g. under ‘exceptional’ rainfall), with subsequent impacts to water quality and riverine communities (Albini et al., 2023). Increased monitoring has indicated that CSOs discharge more frequently (27% increase in England from 2019 to 2020; Environmental Audit Committee, 2022), sometimes routinely outside rainfall events. This has largely been attributed to failure to update infrastructure in line with urbanisation, population growth, and the increasing frequency and magnitude of rainfall events (Slingo, 2021; Environmental Audit Committee, 2022), all of which are projected to increase in the future. In the absence of strict regulation and improvements to infrastructure (e.g. introduction of green infrastructure such as sustainable urban drainage systems [SUDS]), urbanisation and industry will continue to pose a significant threat to the health and structure of lotic ecosystems.

1.1.2.3. Agriculture

Agriculture is one of the largest sources of pollutants in freshwater bodies in the UK, causing diffuse pollution and eutrophication through nutrient loading (e.g. nitrates, phosphorus), increased turbidity, fine sediment deposition, and modification of river flows and channel structure through sediment runoff (Malmqvist & Rundle, 2002; Moss, 2008; Zhang et al., 2014). Similarly to urban pollution, these processes modify habitat (e.g. reduce the extent of riffle habitat, increase filamentous algal growth), reduce macroinvertebrate diversity and abundance by restricting taxa to pollution-tolerant species, or simplify food-webs with cascading effects on predators, including reductions in foraging success and body condition (Gaufin & Tarzwell, 1952; Abrahams & Kattenfeld, 1997; Malmqvist & Rundle, 2002; Windsor et al., 2019).

The implementation of agri-environment schemes designed to mitigate these impacts can improve macroinvertebrate richness, but many freshwater watercourses within agricultural landscapes remain in poor condition (Moore & Palmer, 2005; Davies et al., 2009). For example, herbaceous and wooded riparian zones are critical in reducing pollution through runoff (Moore & Palmer, 2005; SEPA, 2009; Feld et al., 2018), but are often up to three times narrower than recommended for sufficient ecological protection (Davies et al., 2009), and cannot protect against subsurface drainage of nitrates and high-mobility pesticides where clay-based soils are prevalent (Muscutt et al., 1993).

1.1.2.4. Water management

Artificial modification of surface water levels through abstraction (removal for use in industry, domestic supply or agricultural irrigation) or impoundment (a structure e.g. dam or weir, that raises the upstream water level above the natural state and restricts downstream flow for water supply, hydropower or flood control) can control natural variations in flow and reduce the frequency and magnitude of peak flows (Dewson, James & Death, 2007; Durance & Ormerod, 2007; Matthaei, Piggott & Townsend, 2010; Schmutz & Moog, 2018). However, they impose a broad range of direct and indirect pressures on lotic ecosystems through modifications to habitat, hydrology, and thermal regimes.

Many abstraction and impoundment schemes aim to provide a 'minimum flow' or compensation flow to enable continued use of the watercourse downstream and residual ecological function. This results in lowered downstream flows relative to the natural level and decreased water velocity (Maynard & Lane, 2012), which subsequently reduces dissolved oxygen availability and modifies benthic habitat through changes to temperature regime, sediment, nutrient and metal deposition downstream of the structure (D'Amico et al., 2000; Dewson, James & Death, 2007; Schmutz & Moog, 2018). These processes do not universally affect macroinvertebrates; while conditions may benefit tolerant macroinvertebrate taxa (e.g. Chironomidae larvae, Oligochaeta and Mollusca), losses are generally observed for sensitive taxa associated with high energy conditions (e.g. Plecoptera, Ephemeroptera and Trichoptera; Vaikasas *et al.*, 2013; Krajenbrink *et al.*, 2019; Wu *et al.*, 2019). Lowered flows also reduce wetted channel area, forcing increased densities of macroinvertebrate and vertebrate taxa within more favourable conditions, which can increase predation and competition, and have an overall negative effect on abundance and diversity (Daufresne et al., 2004; Dewson, James & Death, 2007; Matthaei, Piggott & Townsend, 2010; Wu et al., 2019). However, the exposure and retention of marginal river gravels provide essential habitat for gravel-nesting birds (e.g. Common Sandpiper [*Actitis hypoleucos*], Oystercatcher [*Haematopus ostralegus*] and Little Ringed Plover [*Charadrius dubius*]; Laidlaw *et al.*, 2020), and is particularly beneficial when accompanied by colonisation and development of low herbaceous vegetation that aid concealment of nest and young from predators. In the absence of high frequency and magnitude flows, these gravel bars become stabilized over time, enabling a gradual biotic succession to mature woodland and providing similar environmental benefits to riparian and herbaceous buffers, but to the detriment of gravel-nesting birds (Gilvear, 2004; Yabuhara et al., 2015). In some cases, impoundment can also create artificially high-water levels during overspill (Figure 1.4), intentional spate flows or emergency releases at the outlet point (Maynard & Lane, 2012); the impacts of high discharge on the riverine ecosystem are discussed in section 1.1.3 Climate change.



Figure 1.4: Example of varying flow regimes from a hydroelectric dam with stepped spillway. With the spillway active, the downstream environment becomes more oxygenated through turbulence, despite only a modest rise in river level. Dam located on Edgelaw Reservoir, Midlothian. Images taken by R. Steenson (2021).

Depending on the scale of the structure, impoundment can drastically change the ecosystem from lotic to lentic, with significant impacts to river system continuity and biota assemblages, particularly if poorly managed or without appropriate structures in place to alleviate the impacts. For example, without bypass or sluicing procedures, dams and weirs interrupt sediment and nutrient transport through river systems, resulting in accumulation on the upstream side and diminished replacement of eroded substrate on the downstream side, with altered food-webs and predator-prey interactions on both due to changes in water depth and turbidity (Abrahams & Kattenfeld, 1997; D’Amico et al., 2000; Kondolf et al., 2014; Schmutz & Moog, 2018). Furthermore, in the absence of appropriate fish ladders, dams and weirs prevent the upstream migration of taxa such as salmonids and lampreys for breeding, resulting in displaced breeding populations, reduced spawning success, and reduced detritus processing (Mann, 1988; Freeman et al., 2003).

Water temperature is highly influenced by air and groundwater temperatures under low flow conditions or impoundment (Dewson, James & Death, 2007), and is more vulnerable to extremes. For example, cold-water habitat can be heated more efficiently in shallow or unshaded (e.g. riparian tree cover) environments or removed completely via surface (epilimnion) release of stored water from upstream reservoirs. Conversely, release from bottom (hypolimnial) outlets can introduce significantly cooler water that may lower production (Sinokrot et al., 1995; Allan & Castillo, 2007; Maynard & Lane, 2012). As temperature can directly or indirectly regulate reproduction, development and/or emergence across a broad range of invertebrate and

vertebrate taxa, small shifts in temperature can impact lotic community richness and diversity by favouring taxa with higher temperature-tolerance ranges, and their associated predators (Daufresne et al., 2004; Daufresne & Boët, 2007; Durance & Ormerod, 2007; Jonsson, Deleu & Malmqvist, 2013; Jonsson et al., 2015).

Over the last 50 years, it has been widely recognised that ‘minimum’ flows are insufficient to support rivers in good ecological status (GES), particularly as a naturally varying river flow regime supports ecosystem processes (e.g. substrate redistribution and regeneration), and some lotic organisms have varying flow requirements throughout their life cycle (Bragg et al., 2005; Arthington et al., 2006; Schmutz & Moog, 2018). Environmental or Ecological Flows (e-Flows) that seek to provide site-specific natural flow regimes have been widely supported as an alternative to traditional static flows, with the EU recently producing guidance documents for River Basin Planning in the context of the Water Framework Directive (European Commission & Directorate-General for Environment, 2016; Webster et al., 2017). Uptake is not universal nor required by law however, leaving many riverine ecosystems lacking functional processing or good ecological status in the vicinity of impoundment structures or abstraction regimes. Alternatively, the removal of functionally obsolete impoundment structures may alleviate some impacts by restoring habitat connectivity and natural flow regimes, encouraging restoration to GES (Gough, Fernández Garrido & Van Herk, 2018).

1.1.3. Climate change

As previously mentioned, variation in temperature and river flow regimes imposed by land use and management can put significant pressure on riverine ecosystems. These may be amplified, exacerbated or confounded by changes in temperature and precipitation predicted to occur through climate change (Ormerod et al., 2010). The frequency of hard winters is reducing in line with rising average temperatures, but projected rises in temperature and increased frequency and magnitude of spate events will likely impose additional pressures on freshwater ecosystems (Prior & Kendon, 2011; EEA, 2012; Slingo, 2021).

As mentioned in section 1.1.2.4 Water management, small shifts in temperature can affect reproduction, development, emergence, and community structure of aquatic invertebrates (Daufresne et al., 2004; Daufresne & Boët, 2007; Durance & Ormerod, 2007; Jonsson et al., 2015). Research suggests that spring stream macroinvertebrate abundance may decline by 21% per 1°C rise in water temperature, with local extinctions predicted for 5-12% of the scarcest species (Durance & Ormerod, 2007), but it is likely that many core species would persist with a temperature rise of 3°C (Jonsson et al., 2015). Vertebrate predators such as fish and birds may experience direct impacts of warming whereby individuals are forced outside of their physiological tolerance limits (e.g. by hyperthermia, dehydration, body mass loss), resulting in

distributional (i.e. latitudinal or elevational) shifts or increased mortality (McKechnie, 2019). Alternatively, predators may experience indirect effects through altered or reduced prey availability, with consequent impacts to body condition and breeding performance.

Natural drought conditions affect the riverine ecosystem similarly to impoundment and abstraction regimes, but spate conditions or highly variable precipitation impose significant direct effects on all taxa. For example, during high river levels and elevated water velocity, it is energetically costly to maintain position in the water column or to negotiate while searching for prey, whether the predator is a fish or diving bird (e.g. White-throated Dipper; D'Amico and Hémery, 2007); these conditions, in addition to increased turbidity, may force a change in foraging behaviour or activity. Spate flows may also erode and redistribute substrate, reducing the availability of aquatic prey due to bed movement and wash out or temporary redistribution of benthic organisms (Theodoropoulos et al., 2017), and reduce availability, access to and viability of natural spawning points or bankside nest sites (Alder, 1963; Tyler & Ormerod, 1994; Wilson, 1996; Lobón-Cerviá, 1996; Taylor et al., 2019) with subsequent impacts on territory suitability and breeding performance.

While climate-related weather events are difficult to predict, their impacts on riverine ecosystems could be alleviated through appropriate land management. For example, native riparian woodland restoration or creation proposed in multiple land use settings may also moderate stream temperature regimes by providing shade and shelter from climatic conditions, whilst increasing interception and percolation from high intensity rainfall events, with subsequent reduced surface run-off and spate magnitude (Dohet et al., 2015; Johnson & Wilby, 2015; Feld et al., 2018; Turunen et al., 2021).

1.1.4. Brownification

Brownification is the increase of water colour in freshwater, considered to be the combination of high concentrations of dissolved organic matter (DOM) and increased iron content (Figure 1.5). Aside from aquatic primary production, DOM is mainly transported to watercourses from nearby terrestrial (e.g. conifer forest, agricultural land) and wetland sources through surface runoff or drainage (Kritzberg et al., 2019). While wetland environments naturally contain large concentrations of DOM, it is bound to soil under acidic conditions in terrestrial environments; this organic matter can become mobilised alongside iron compounds when the soil pH is neutral or increased through reduced acid deposition or base-rich agricultural supplements (Goulding, 2016; Kritzberg et al., 2019).



Figure 1.5: Example water colour variability due to differences in the concentration of DOM and iron. Water sampled within a 35km area in Jönköping, Sweden, with original image taken by Stefan Löfgren (Kritzberg et al., 2019).

The UK has seen a marked increase in brownification of streams and rivers over the last two decades that coincides with the reduction in acid deposition (Moss, 2014; RoTAP, 2012). While this is potentially a return to pre-acidification conditions, historic data suggests brownification was not as common 30-40 years ago as it is presently (Kritzberg et al., 2019), and that the brownification effects of DOM in freshwater environments are likely exacerbated by trends in temperature and precipitation. DOM production is likely to increase alongside rises in average temperatures, partly through the stimulation of decomposition rates, while increases in annual precipitation and the magnitude of daily heavy rainfall will intensify DOM transport via surface runoff and increases connectivity by raising the water table (EEA, 2012; Kritzberg et al., 2019; Slingo, 2021).

Brownification significantly impacts primary production by limiting light penetration (Kritzberg et al., 2019). In standing freshwater bodies this allows heterotrophic species to dominate, reduces oxygen availability and significantly restricts consumer diversity and abundance. In moving freshwater, however, oxygen concentration is potentially maintained as the water is more readily aerated (Scullion et al., 1982). DOM may replace some primary producers in aquatic food-webs, such as biofilms that experience reduced biomass through a shading effect (Lehmann et al., 2015; Wagner et al., 2015). Since macroinvertebrates can adapt to these conditions effectively, brownification has minimal direct effects on their development and emergence (Jonsson et al., 2015), but top predators that rely on sight to locate prey, such as Three-spined Stickleback, suffer from reduced prey ingestion and increased mortality (Hedström et al., 2017).

1.1.5. Invasive species

Invasive species can be defined as a non-native species that has become established, and imposes significant impacts on the environment, economy and/or human health (Keller et al., 2011). Their presence has increased by 37% over the last 200 years, and is projected to increase by a further 36% by 2050 due to anthropogenically-mediated introduction, transport, and habitat modification (Keller et al., 2011; Mathers, Guareschi & Pattison, 2022). The innate complexity and

integrated dynamics of river systems, alongside difficulties in effective sampling, can mean that a species becomes well established and spreads before being detected (Mathers, Guareschi & Pattison, 2022). Furthermore, habitat modification through impoundment can increase the frequency of invasions in rivers and reservoirs due to regulated flow regimes, high connectivity and homogenised habitat conditions (Johnson, Olden & Vander Zanden, 2008; Mathers, Guareschi & Pattison, 2022).

Invasive species impose a broad range of pressures on riverine ecosystems, particularly on habitat structure and food-webs. Invasive plants such as Himalayan Balsam (*Impatiens glandulifera*), Japanese Knotweed (*Reynoutria japonica*), and Giant Hogweed (*Heracleum mantegazzianum*) can establish quickly along riverbanks and riparian zones, with hydrochorous seed dispersal accelerating further spread (Greenwood et al., 2018). As these species often occur in dense stands, they can displace native vegetation and limit successional development to woodland, with consequent impacts on riverbank stability and erosion (with potential implications for nesting river birds, e.g. Common Kingfisher, *Alcedo atthis*), particularly over winter when live plants are absent (Greenwood et al., 2018; Matte, Boivin & Lavoie, 2022), and can significantly lower stream levels through transpiration (Vanderklein, Galster & Scherr, 2014; Galster & Vanderklein, 2023). Furthermore, invasion of riparian zones by these plants can impact both aquatic invertebrate diversity and composition (primarily through physiochemical factors e.g. channel shading and substrate diversity) and terrestrial invertebrate abundance and diversity (Seeney et al., 2019a, 2019b), with subsequent impacts to both riverine and riparian food webs.

Invasive invertebrates such as Signal Crayfish (*Pacifastacus leniusculus*) quickly establish in rivers with low-magnitude flow (i.e. regulated rivers, or those impacted through climate change), where they impose significant pressures across multiple trophic levels and food-web structures and contribute to alterations in fine sediment dynamics (Mathers et al., 2020a). For example, increased densities of Crayfish have been linked to increased epilithic algal cover (Stenroth & Nyström, 2003), predation of fish embryos and emerging fry (Edmonds, Riley & Maxwell, 2011), and reduced taxonomic and functional richness of native invertebrate communities (Mathers et al., 2020b). Furthermore, burrow excavation in riverbanks may cause or accelerate riverbank instability (Faller et al., 2016) and create diurnal fluctuations in turbidity through contributions of fine sediment (Mathers et al., 2022), which will negatively impact visual predators' foraging efficiency (Da Prato, 1981; Hedström et al., 2017). One final consideration is the presence of invasive predator species, such as American Mink (*Neovison vison*), which been linked to declines in gravel-nesting birds that utilise rivers and riparian habitat (e.g. Common Sandpiper, Oystercatcher) and Water Vole (*Arvicola terrestris*) populations (Rushton et al., 2000; Moore, Roy & Helyar, 2003), but significant trapping and management efforts have supported recovery of impacted native species, including the reintroduced Eurasian Otter (*Lutra lutra*; McDonald et al., 2007).

1.2. Status of riverine communities

Freshwater ecosystems have seen a significantly higher rate of decline in vertebrate taxa than found in terrestrial or marine settings. Since 1970, monitored populations of aquatic mammals, birds, amphibians, reptiles and fish have declined by an average of 83%, with migratory fish species alone declining by 76%, largely due to habitat loss and modifications to the river channel (He et al., 2019; WWF, 2022). However, the status of invertebrate populations is harder to establish, with significant spatial and temporal variability over shorter timescales than observed in vertebrate taxa. Multiple studies have observed overall increases in species richness, functional richness, and abundance of invertebrate communities between 1990 and the early 2000s, but identified the presence of variability within trophic groups, such as a 21.7% decline in decomposer abundance. Furthermore, despite initial improvement from mitigation measures, multiple invertebrate taxa show a decelerating trajectory (Haase et al., 2023; Powell et al., 2023; Qu et al., 2023).

1.2.1. Decline in riverine bird populations

Rivers and streams provide a unique habitat for birds while feeding, socialising, and breeding. Some species use medium- to fast-moving waters in spring and summer for breeding, then spend winter by lakes or coastal waters (e.g. Common Sandpiper, *Actitis hypoleucos*; Grey Wagtail, *Motacilla cinerea*; Goosander, *Mergus merganser*), whereas others are obligately (e.g. White-throated Dipper, *Cinclus cinclus*) or opportunistically (e.g. Common Kingfisher, *Alcedo atthis*) riverine year-round (Everard & Noble, 2008).

1.2.1.1. Population trends across the species' distribution

These five species are broadly distributed across the northern hemisphere, whether permanently resident or utilizing breeding grounds. All are classed as 'Least Concern' under the IUCN Red List criteria due to expansive ranges and sufficiently large population sizes, and despite identifiable downward trends for Dipper and Common Sandpiper, their rates of decline do not cross the threshold for 'Near Threatened' (BirdLife International, 2024). These classifications and trends are consistent within continental Europe, exceptions being the classification of Common Sandpiper as 'near threatened' within the 27 member states of the European Union (EU 27), and Common Kingfisher as Vulnerable within both continental Europe and the EU 27 (European Red List Status; BirdLife International, 2015).

1.2.1.2. Population and geographic range trends in Great Britain

With the exception of Goosander, which has shown a 23% increase in estimated population since 1999, population trends estimated from surveys conducted throughout Great Britain (e.g. the Breeding Bird Survey [BBS], Waterways Breeding Bird Survey [WBBS, previously the Waterways Bird Survey, WBS] and the Atlas of Breeding Birds) indicate widespread population decline and/or changes in geographic range for riverine birds (Table 1.1, Figure 1.6; Balmer et al., 2013; Heywood et al., 2023).

Long-term Atlas trends (1988-91 to 2007-11) suggest widespread declines across the entire geographic range in Great Britain for Dipper, Grey Wagtail and Common Sandpiper, whereas Common Kingfisher have experienced regional declines (Gibbons, Reid & Chapman, 1993; Balmer et al., 2013). When assessed nationally at an annual scale through WBS and WBBS surveys (Figure 1.6), all four species display at least one significant fluctuation, but vary in their overall trend. Dipper and Common Sandpiper populations are both trending downward, with -39% and -28% decrease respectively in UK breeding populations since 1995 (Figure 1.6, panels A and C). In contrast, while Grey Wagtail and Common Kingfisher populations are both classed as stable between 1974 and 2021, both have shown significant downward trends along the monitoring period (Figure 1.6, panels B and F), with the former now classed as ‘amber’ in the Birds of Conservation Concern 5 (BoCC) review (Stanbury et al., 2021).

Table 1.1: Population estimates, conservation status and trends for five bird species commonly associated with riverine habitats in Britain. For each species, the trends are given for the Waterways Breeding Bird Survey (WBBS, top) and Breeding Bird Survey (BBS, bottom). ¹ estimates for Britain in 2016, extrapolated from the 1988–91 Breeding Atlas using WBBS surveys (Gibbons, Reid & Chapman, 1993; Heywood et al., 2023; Massimino et al., 2023). ² assessed in the Birds of Conservation Concern 5 (BoCC) review (Stanbury et al., 2021). ³ extracted from Heywood et al., 2023. ⁴ minimum number of survey squares that the species was encountered. * denotes a trend with a statistically significant change (i.e. 95% confidence intervals do not overlap zero).

Species	Association with riverine habitat	Number of breeding pairs ¹	Conservation status ²	N ⁴	UK population trends (% change) ³			
					26-year (95-21) BBS only	22-year (99-21) WBBS only	10-year (11-21)	1-year (21-22)
White-throated Dipper	Obligate	6,900	Amber	91		-25	-11	4
				67	-47 *		-20	-20
Grey Wagtail	Breeding	37,000	Amber	133		-13	28 *	-1
				240	-4		27 *	14
Common Sandpiper	Breeding	13,000	Amber	69		-38 *	-19 *	7
				77	-27 *		-10	2
Goosander	Breeding	4,800	Green	57		23	14	-1
				46	-13		-8	38
Common Kingfisher	Opportunistic	3,850	Green	72		-16	-2	56 *
				58	-14		24	67 *

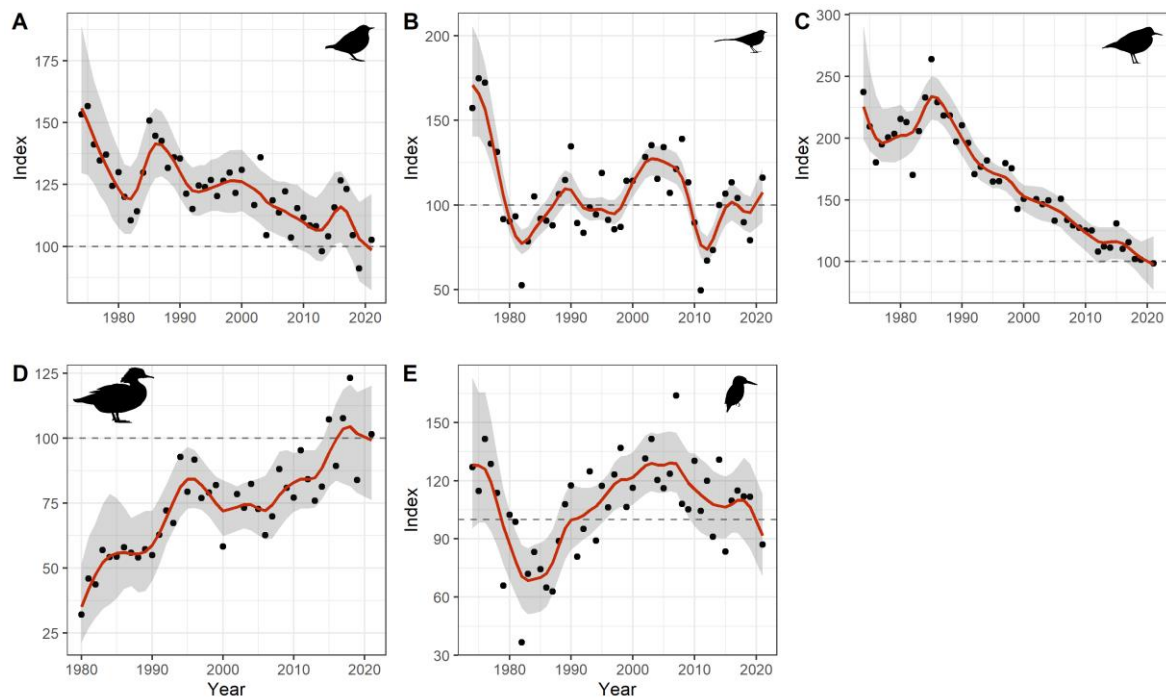


Figure 1.6: Smoothed population trends for five bird species commonly associated with the riverine environment between 1974 and 2021. (A) White-throated Dipper, (B) Grey Wagtail, (C) Common Sandpiper, (D) Goosander, and (E) Common Kingfisher. Trends are estimated from the BTO Waterways Breeding Bird Survey and its precursor, the BTO Waterways Bird Survey (Massimino et al., 2022). Index is set at 100 in the penultimate year (2020). Shaded area shows 85% confidence limits of the trend line (red); dots represent values for individual years. Silhouettes drawn by R. Steenson.

Despite expansion in winter ranges for Dipper and Common Sandpiper (+14.6% and +29.1% respectively), both species have experienced breeding range losses that correspond to declines in abundance (Massimino et al., 2023). While Dipper have only slight losses (-11%) at range margins or in areas of conifer plantation, Common Sandpiper have experienced a -20% constriction in range, concentrated on the southern margins and in lowlands adjacent to upland areas (Balmer et al., 2013). Conversely, Grey wagtail, Goosander and Kingfisher have mostly experienced expansion in both winter (+34.8%, +82.1% and -2.1% respectively) and breeding ranges (+16.5%, +111.9% and +45.7% respectively). While Goosander and Kingfisher are expanding south and north respectively with no detectable losses elsewhere, the range expansion for Grey Wagtail is concerning; despite a distribution that covers that majority of the UK and with recent expansion into the midlands and east England, the decline in abundance suggests overall thinning or an increasingly patchily distributed population (Balmer et al., 2013; Massimino et al., 2023).

1.2.1.3. Indications of population and geographic range trends

Multiple fluctuations along the population trend (e.g. Dipper and Grey Wagtail in Figure 1.6, panels A and B) may reveal a species' susceptibility to episodic or emergent changes to their

environment. Conversely, a consistent downward trend (e.g. Common Sandpiper in Figure 1.6, panel C) may be indicative of a response to persistent changes. While these declining trends can generally be attributed to poor recruitment to breeding populations despite improvements to breeding success, the exact underlying drivers of these patterns are unclear (Dougall, Holland & Yalden, 2010; Eglington & Noble, 2010; Massimino et al., 2023). Alongside range contraction, these trends suggest that riverine habitats have undergone changes that are potentially still ongoing. However, the degree of effect is dependent on the species' ecology, and not all species are equally reliant on a 'healthy' riverine ecosystem. For example, the unique positive trends for Goosander are likely linked to their status as a "new" species in the UK and low population size (Table 1.1), alongside their broad diet and habitat requirements. Similarly, Kingfisher use rivers opportunistically when alternative breeding habitat (e.g. gravel-pits, ponds) are not available (Balmer et al., 2013; Massimino et al., 2023). These factors suggest that Goosander and Kingfisher are not truly representative of the health or resilience of freshwater ecosystems, and thus investigating the drivers of population change in these species is beyond the scope of this project. Conversely, the ecologies of Dipper, Common Sandpiper and Grey Wagtail are more closely tied to riverine ecosystems, and their spatial and temporal trends potentially reflect environmental stressors acting upon the freshwater environment.

1.3. Bioindicators for ecosystem health

1.3.1. What is a bioindicator?

In ecology, a bioindicator is an organism or group of organisms used to assess the state of an environment, often in terms of quality or health, and provide multiple advantages over traditional direct measures (Parmar, Rawtani & Agrawal, 2016; Fierro et al., 2017). Chemical or physical measurements are often either costly, only pertinent to the time of sampling or may overlook episodic pressures, whereas bioindicators add a temporal element associated with length of habitation within a system (Holt & Miller, 2010). Furthermore, biota integrate the effects and degree of disturbance from stressors better than other measures (Fierro et al., 2017), and can alleviate time pressures associated with intensive monitoring of an entire community (Holt & Miller, 2010). However, indicators must be selected carefully to ensure they are fit for purpose.

1.3.2. Common riverine bioindicators

The most commonly used bioindicators for riverine ecosystems worldwide are periphyton, benthic macroinvertebrates and fish (Li, Zheng & Liu, 2010; Fierro et al., 2017). Despite their popularity, there are weaknesses associated with each group. As producers, periphyton cannot be used to identify issues with the larger community of consumers and have relatively short life

cycles, thus they are limited to detection of short-term or sudden impacts. Benthic macroinvertebrates are more representative of the whole community due to their intermediate position within the aquatic food chain and range of diets, but their distribution and abundance may be influenced by factors such as climate or substrate that do not reflect the health of the ecosystem (Li, Zheng & Liu, 2010). Furthermore, the presence of invasive species such as Signal Crayfish may inflate biological indices that are weighted on abundance (e.g. LIFE score, PSI score), complicating their inference (Mathers et al., 2016). Fish maintain a higher position in aquatic food webs and thus represent a large proportion of the ecosystem, but their high mobility and capture difficulty require large teams and/or extended periods for adequate sampling, which can be costly (Fierro et al., 2017).

1.3.3. Evidence of birds as bioindicators

Birds are often used as an indicator of the health of the wider environment (Furness, 1993; Newton, Wyllie & Asher, 1993; Ormerod & Tyler, 1993; Dahlmann et al., 1994; Becker, 2003; Gregory et al., 2008; Gregory & Strien, 2010; Usui, Butchart & Phillimore, 2017; Samplonius et al., 2018; Sinha et al., 2019) or as a proxy for other groups of organisms (Burns et al., 2020) for multiple reasons. Primarily, birds are highly sensitive to both natural and anthropogenic environmental change (Ormerod & Tyler, 1993; Amat & Green, 2010; Gregory & Strien, 2010). For example, climate change has been linked to earlier lay dates and migration timings (Crick & Sparks, 1999; Crick, 2004; Usui, Butchart & Phillimore, 2017; Samplonius et al., 2018), while seabirds are proven indicators of oil pollution and plastics (Furness, 1993; Dahlmann et al., 1994; O'Hanlon et al., 2019). Their mid to high position in food chains allows for identification of changes in producer or prey abundance (e.g. Great Crested Grebe abundance linked to eutrophication in Spain; Fernández et al., 2005) or the presence of toxic compounds that accumulate through trophic levels and have lethal or sub-lethal effects (e.g. pesticide and heavy metal presence in raptors, fish-eating birds and seabirds; Hardy *et al.*, 1987; Becker, 1989; Newton *et al.*, 1993; Becker, 2003; Egwumah *et al.*, 2017). Furthermore, they are conspicuous, relatively long-living, widespread, diverse and mobile, yet easily and cheaply surveyed (Baillie, 1991; Becker, 2003; Egwumah, Egwumah & Edet, 2017). These qualities have led to the development of national (e.g. UK) or continental (e.g. Europe) bird indices, where the annual relative change in abundance of common native bird species are used as a proxy for biodiversity in given landscape types (e.g. UK farmland bird index; Eaton and Noble, 2023).

1.3.4. Dippers as bioindicators

Dippers, a family of aquatic passerines (Cinclidae), possess many traits that are important for a bioindicator (Holt & Miller, 2010), and in theory are an excellent candidate for indicating

freshwater ecosystem health and resilience (Figure 1.1). Since the 1930s, observations of Dippers have provided a depth of understanding to their distribution, highly specialised ecology, behaviour and life history (Serle & Bryson, 1935; Holmes, 1939; Brownlow, 1949; Jones & King, 1952; Alder, 1963; Hewson, 1967, 1969; Shooter, 1970; Shaw, 1978; Da Prato, 1981; Wilson, 1996). Subsequent studies linking their macroinvertebrate prey to water quality (Gauvin & Tarzwell, 1952; Ormerod, 1985) identified how Dippers could act as a bioindicator for acidification (Ormerod, Boilstone & Tyler, 1985; Ormerod, Tyler & Lewis, 1985; Ormerod et al., 1986; Vickery, 1991, 1992). Within the last 20 years, extensive research has reinforced their position as a bioindicator for riverine ecosystem health and quality, whether indirectly where Dipper abundance, behaviour and breeding performance reflects prey abundance and richness (Sorace et al., 2002; Windsor et al., 2019; Sinha et al., 2019), or directly through the uptake of contaminants (e.g. light and heavy metals [cadmium, selenium, mercury], organic pollutants [PCBs, PBDEs], microplastics), as registered in tissue, faeces, regurgitated pellets or eggs (Ormerod & Tyler, 2000; Morrissey et al., 2014; D'Souza et al., 2020; Pedersen, Nybø & Sandercock, 2020). More recently, their populations have also been linked to climate change and hydrology (Nilsson et al., 2011; Royan et al., 2013, 2015; Nilsson et al., 2020b; Balázš et al., 2021), which can exacerbate the impacts of water pollution, habitat degradation or flow modification within aquatic ecosystems. Furthermore, their conspicuous appearance and behaviour alongside use of linear territories make them relatively straightforward to survey, resulting in good representation in national population and distribution surveys throughout their range (e.g. WBBS and Atlas of Breeding Birds in Great Britain; Balmer et al., 2013; Massimino et al., 2022).

1.3.4.1. *Cinclidae family*

Cinclidae contain five recognised species that vary only in their distribution, plumage, size, and some behavioural traits (Figure 1.7). European or White-throated Dipper (*Cinclus cinclus*, henceforth referred to as Dipper throughout this thesis) are the most widespread species, overlapping only slightly in distribution with Brown Dipper (*Cinclus pallasi*), while all other species are geographically distinct (Tyler & Ormerod, 1994). Some species contain races or subspecies; for example, *C. cinclus* contains 14 races (three shown in Figure 1.7; Tyler & Ormerod, 1994), two of which are endemic to Great Britain and are remarkably similar in appearance (*C. c. gularis* and *C. c. hibernicus*), weighing an average of $63.7\text{g} \pm 6.34$.

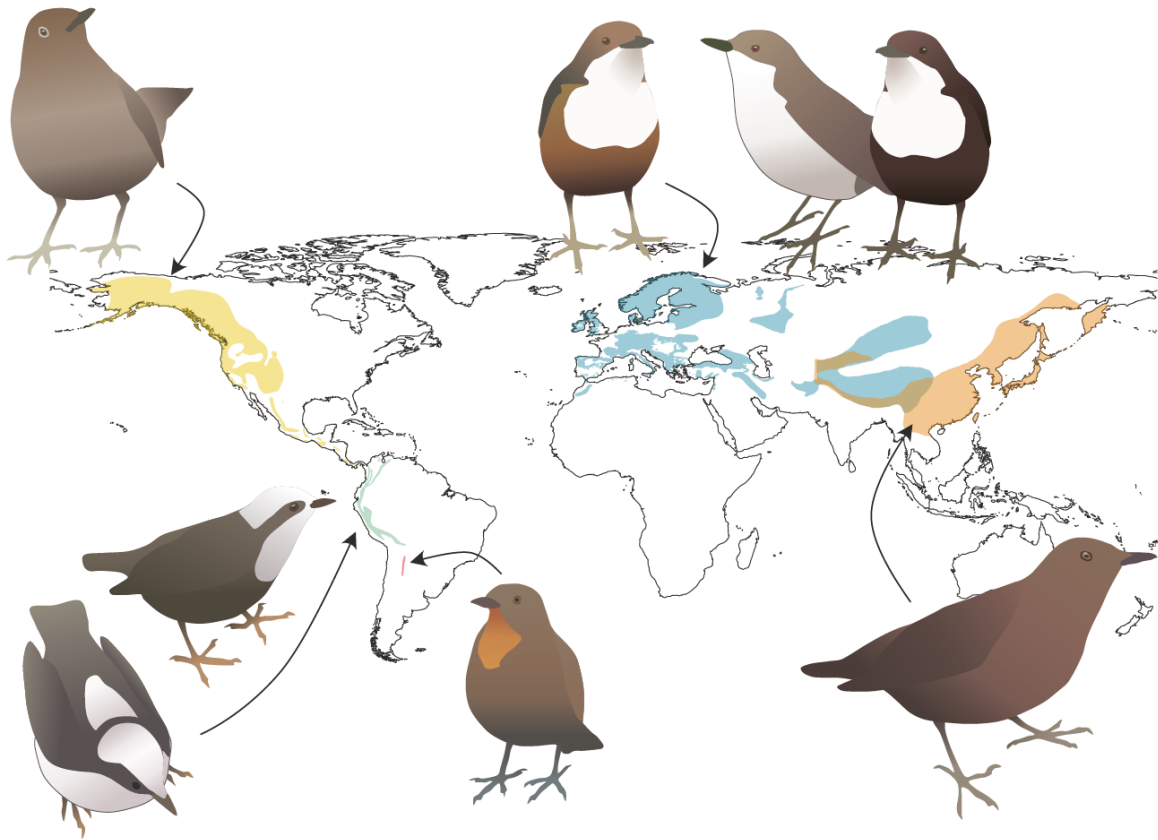


Figure 1.7: Global distribution of Cinclidae species. European or White-throated Dipper (blue; *Cinclus cinclus*, with three races shown, *C. c. gularis* on left, *C. c. leucogaster* in middle, and *C. c. cinclus* on right), Brown Dipper (orange; *Cinclus pallasii*), American Dipper (yellow; *Cinclus mexicanus*), White-capped Dipper (green; *Cinclus leucocephalus*, with two races shown, *C. l. leuconotus* on left, and *C. l. leucocephalus* on right), and Rufous-throated Dipper (red; *Cinclus schulzi*). Species distribution maps produced in R from data provided by Jetz et al., 2012 (R Core Team, 2023); Dipper images adapted by R. Steenson from illustrations by Darren Rees (featured in Tyler & Ormerod, 1994).

1.3.4.2. Association with the riverine environment

The spatial distribution of Dippers in Great Britain is strongly associated with fast-flowing streams and rivers with a coarse substrate, and a shallow pool and riffle bedform. Such features create well oxygenated habitats that support Dippers' preferred macroinvertebrate prey (e.g. insect larvae and nymphs from the orders Ephemeroptera, Plecoptera and Trichoptera; small fish such as Bullhead, *Cottus gobio*; Scullion et al., 1982; Ormerod, 1985; Tyler & Ormerod, 1994). Dippers are highly adapted for hunting prey visually in these habitats, either by walking into riffles and using their strong feet and claws to grip the rocks and substrate, or by diving and using their short powerful wings to manoeuvre and hold themselves underwater. This largely restricts Dipper populations to hilly and mountainous areas, but their range can include lowland waterways with a steeper gradient, or even oligotrophic lake shores, coastal areas or slow-moving rivers outside of the breeding season (Figure 1.8; Ormerod, Boilstone & Tyler, 1985; Tyler & Ormerod, 1994). Further strengthening Dippers close association with rivers is the positioning of their nest directly over moving water, utilising both natural and man-made structures (e.g. ledges

or holes in walls or bridges, behind waterfalls, in riverbanks, in a pipe or culvert) to support the large, dome-shaped nest over one or two breeding attempts a year (Shaw, 1978; Tyler and Ormerod, 1994). Nestlings are altricial, i.e. are incapable of moving independently soon after hatching, and rely heavily on parents for food provision.

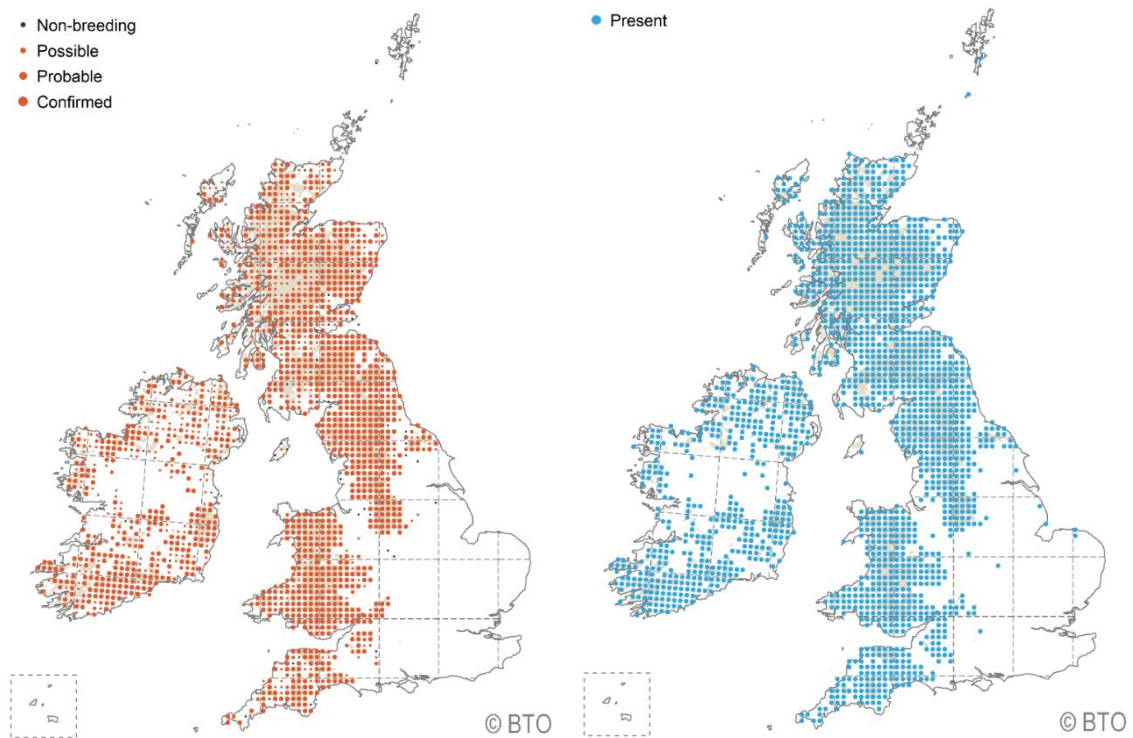


Figure 1.8: Dipper breeding (orange) and winter (blue) distributions in Great Britain. Assessed through surveys conducted between 2008-2011 as part of the Bird Atlas, a partnership project between the British Trust for Ornithology, BirdWatch Ireland and the Scottish Ornithologists Club (Balmer et al., 2013).

1.3.5. Other options for avian bioindicators in riverine ecosystems

Grey Wagtail and Common Sandpiper share multiple characteristics with Dippers, including their use of medium- to fast- flowing watercourses during the breeding season and relatively high positions in food-webs. However, these three species differ in their life history and ecologies (e.g. prey, foraging, nesting, migration), and have varying overlap with riverine, riparian, and terrestrial environments. Thus, Grey Wagtail and Common Sandpiper may be less representative of riverine ecosystem health than Dippers, but may be highly suitable as bioindicators for the broader landscapes that ultimately affect river ecosystem health (i.e. riparian, terrestrial).

1.3.5.1. Grey Wagtail

There are three sub-species of Grey Wagtail: one widespread across the Palearctic region (*Motacilla cinerea cinerea*) and two island forms (*M. c. patriciae* and *M. c. schmitzi*). Grey Wagtail

are a small passerine, weighing an average of $18.1\text{g} \pm 1.32$. They have a more extensive distribution than Dipper, both globally and within Great Britain (Figure 1.9), and are classed as partial migrants with some British birds wintering in continental Europe (Tyler, 1979). Grey Wagtails have a broad diet consisting of insects from both aquatic and terrestrial sources (e.g. Diptera, Plecoptera, Ephemeroptera, Trichoptera, Coleoptera, Arachnida; Ormerod and Tyler, 1987), but will preferentially forage for aquatic prey in wet margins and gravel beds as they lack the ability to dive. This weaker reliance on aquatic prey means that they are poor bioindicators for acidification (Ormerod & Tyler, 1987b, 1991; Vickery, 1991). Grey Wagtail build open cup nests, but position them very similarly to Dipper, utilising natural and manmade sites in close proximity to flowing water for one or two breeding attempts in a year (Tyler, 1972), also with altricial nestlings.

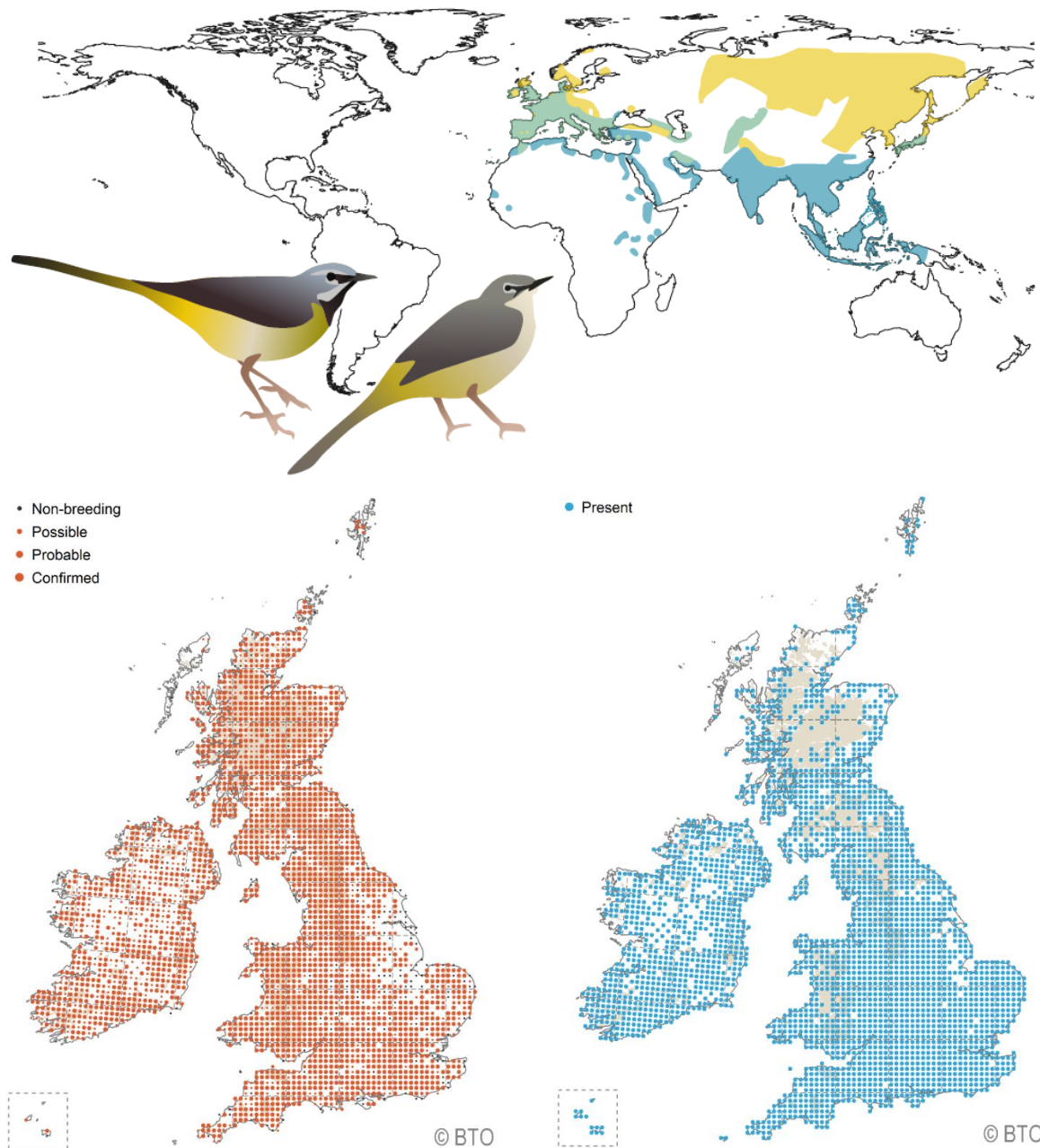


Figure 1.9: Distribution maps for Grey Wagtail. Global distribution (top) with colours denoting status: resident (green), breeding (yellow) and non-breeding (blue); Species distribution maps produced in R from data provided by Jetz et al., 2012 (R Core Team, 2023). Species images drawn by R. Steenson; male (left) and female (right). Distribution in Great Britain shown for breeding (orange) and winter (blue); Assessed through surveys conducted between 2008-2011 as part of the Bird Atlas, a partnership project between the British Trust for Ornithology, BirdWatch Ireland and the Scottish Ornithologists Club (Balmer et al., 2013).

1.3.5.2. Common Sandpiper

Common Sandpiper are a small wader, weighing an average of $58.0g \pm 10.15$. They are monotypic and complete migrants, utilising large areas of the Palearctic region for breeding while wintering in the Southern hemisphere alongside areas of France, Iberia, and Northern Africa (Figure 1.10). In Great Britain, their breeding populations are largely limited to upland regions with sand and

gravel substrate (Holland, Robson & Yalden, 1982), while only a small number remain over winter. Common Sandpiper have a broad diet that varies depending on life stage; while adults preferentially feed on terrestrial invertebrates in adjacent rough grassland habitat (e.g. Diptera, Hymenoptera, Carabidae, Lumbricina) supplemented with aquatic prey (e.g. Trichoptera, Ephemeroptera, Plecoptera, and Chironomidae), they hold linear riverine breeding territories where older chicks (>5 days old) forage along exposed marginal river gravels, targeting primarily aquatic invertebrates supplemented with terrestrial prey (Yalden, 1985, 1986). This overlap between aquatic and terrestrial prey sources likely also makes Common Sandpiper a poor bioindicator for acidification (Vickery, 1991; Buckton & Ormerod, 1997). Common Sandpiper build their nests on the ground within sparse vegetation (Holland, Robson & Yalden, 1982), which presents a failure risk in high-flow conditions (Elas, Rosendal & Meissner, 2023). Unlike Dipper and Grey Wagtail, Common Sandpiper nestlings are precocial and nidifugous, i.e. mobile and able to leave the nest shortly after hatching. From only a few days old, chicks forage and feed themselves independently, while parents provide safety and shelter from weather conditions by alarm calling and brooding respectively. Common Sandpiper have a shorter breeding season than Dipper and Grey Wagtail, focusing on a single breeding attempt unless early failure necessitates a replacement attempt (Holland, Robson & Yalden, 1982).

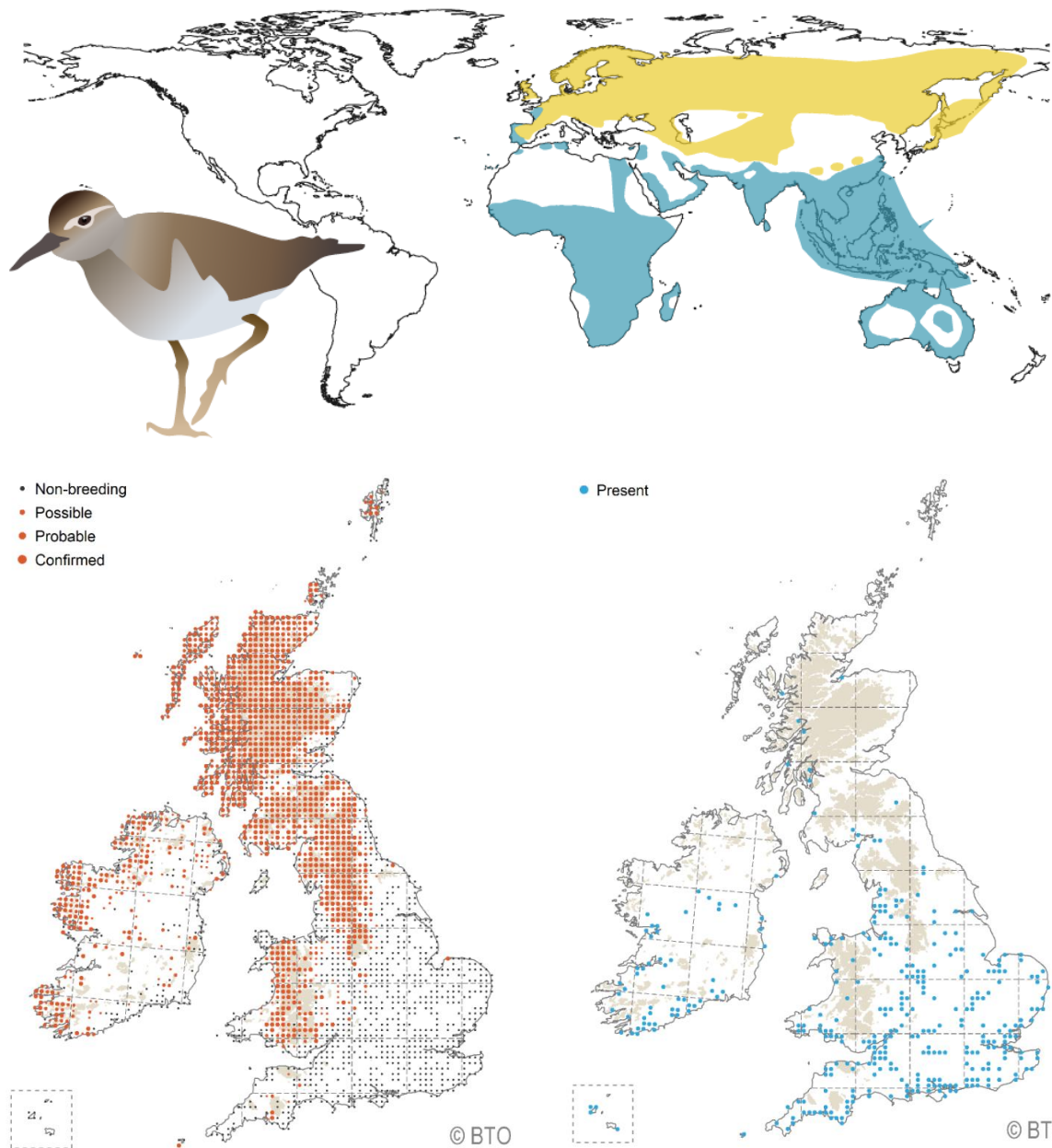


Figure 1.10: Distribution maps for Common Sandpiper. Global distribution (top) with colours denoting status: resident (green), breeding (yellow) and non-breeding (blue); Species distribution maps produced in R from data provided by Jetz et al., 2012 (R Core Team, 2023). Species images drawn by R. Steenson. Distribution in Great Britain shown for breeding (orange) and winter (blue); Assessed through surveys conducted between 2008-2011 as part of the Bird Atlas, a partnership project between the British Trust for Ornithology, BirdWatch Ireland and the Scottish Ornithologists Club (Balmer et al., 2013).

1.4. Research overview

There is a growing importance to effectively and efficiently assess the ecological health and resilience of freshwater ecosystems (Ormerod et al., 2010), particularly to inform management strategies for restoration and conservation, but assessing multiple - often integrated - stressors is challenging. Dippers are an ideal bioindicator for riverine and riparian systems within the UK, particularly as their steady decline (Massimino et al., 2022) aligns with the deterioration in ecological health of UK rivers. Prior research has crucially identified many of the consistent direct and indirect impacts of specific environmental stressors (e.g. acidification, heavy metal) on Dippers through extensive data collection, but these often neglect the complex interactions present in riverine ecosystems. Furthermore, many studies are conducted over a short temporal period (Vickery, 1991, 1992), a relatively small geographic area (Ormerod, 1985; Ormerod, Boilstone & Tyler, 1985; Ormerod et al., 1986; Wilson, 1996; Nilsson et al., 2011, 2020b) or both (D'Amico, Boitier & Marzolin, 2003; D'Amico & Hémery, 2007), which may struggle to fully capture temporal and spatial impacts on riverine ecosystem health or quality. More recently, studies have attempted to assess responses to multiple integrated stressors (Ormerod et al., 2010; Birk et al., 2020), but these frequently use highly specialised datasets that may be spatially or temporally limited (e.g. pollution events, river flow; Royan *et al.*, 2013; Royan *et al.*, 2015), which can restrict their use at national or continental scales.

Other riverine species similarly undergoing population decline or fluctuations, such as Grey Wagtail and Common Sandpiper, share some characteristics with Dipper (i.e. predatory bird of riverine systems within their habitat range and are well-represented in national surveys) that may make them suitable bioindicators for the quality of riverine or riparian habitat more broadly. As these three species vary in their foraging, breeding, and dispersal strategies while utilising rivers, any observed individual or collective change in their populations likely reflects change within the biological communities present. Thus, divergent responses to environmental conditions may indicate the need for bespoke, heterogeneous policies for biodiversity and habitat management, while convergence could necessitate a more targeted approach.

The following chapters in this thesis outline research that examines the responses of riverine bird communities to integrated stressors of riverine and riparian ecosystems in Britain, and investigate their use as broad indicators for riverine ecosystem health, particularly with regards to habitat and biodiversity. Chapter 2 aims to identify how spatial variation in species occupancy and abundance is associated with environmental factors likely to impact riverine birds directly or indirectly at varying scales, and proposes pathways that reflect pressures likely faced by the broader riverine community. This utilises large-scale and open-source datasets to directly compare species' responses to individual environmental variables within a model structure that integrates various characteristics of riverine environments. Chapter 3 makes further use of national open-source data, and aims to explore the response of riverine bird abundance to a set

of temperature and rainfall indices, and assess their suitability to indicate the impacts of local weather conditions on riverine ecosystems. Chapter 4 explores variation in breeding performance of a well-studied Scottish Dipper population, focusing on factors that may be indicative of wider environmental quality and climatic cues. Finally, Chapter 5 integrates these findings to provide clarity on the use of riverine birds as broad indicators of ecological health, and guidance on possible management strategies that may assist with the restoration and conservation of riverine biodiversity.

CHAPTER 2: ENVIRONMENTAL DRIVERS OF SPATIAL VARIATION IN OCCUPANCY AND ABUNDANCE OF THREE DECLINING RIVERINE BIRDS

2.1. Abstract

Freshwater ecosystems are integral to life for a disproportionate number of species, from single-celled organisms to humans, yet are under threat through exposure to a broad range of anthropogenic pressures. As highly dynamic, multiple-stressor environments, it can be challenging to identify ecological degradation within rivers. Traditional bioindicators such as macroinvertebrates or diatoms requires time and skill to quantify ecological status. Predatory riverine birds, already known to be sensitive to acidification and organic pollution, may therefore offer an alternative or complementary approach. This study utilises long-term monitoring data to identify environmental drivers of spatial variation in occupancy and abundance of three declining riverine birds in Britain (White throated Dipper, Grey Wagtail and Common Sandpiper). We demonstrate that occupancy, and to a lesser extent, abundance of these species is governed by underlying physiography (slope, catchment geology, climate), but are also heavily reshaped by land cover at channel, local landscape, and catchment scales. While occupancy in Dipper and Grey Wagtail shared similar environmental controls, divergent responses for abundance imply different controls on bird densities, such as territory length. In contrast, Common Sandpiper showed rather distinct occupancy and abundance responses, suggestive of a weaker association with the riverine environment. These results suggest that multiple direct and indirect pressures (e.g. prey and nest site availability) act on breeding riverine birds, which may reflect stressors experienced by the broader riverine community and supports their value as broad indicators of riverine and riparian ecological health. They also highlight that existing policies and practical initiatives such as buffer strips and restoration of riparian woodland normally advocated for pollution control, climate mitigation or natural flood management, will also benefit declining river birds.

2.2. Introduction

Freshwaters are one of the most important, and at-risk ecosystems in the world. They are a major processing and transport system for solutes from both terrestrial and autochthonous sources, integrate environmental pressures across habitats within their watershed through often vast drainage networks and act as a rapid indicator of ecological degradation both locally and for their wider catchment (Durance & Ormerod, 2007). Freshwaters host a disproportionately high species richness compared with other habitats, supporting 6% of described species despite comprising only 0.8% of Earth's surface (Dudgeon et al., 2006; Miranda, Hermoso & Hassall, 2019), but also

provide food and drinking water, tourism and recreation opportunities, and support industry, agriculture, navigation, waste disposal and electricity generation (Critchlow-Watton et al., 2014). Paradoxically, many of these services impose chemical, biological, or physical pressures that negatively affect freshwater ecological health and long term viability (Miranda, Hermoso & Hassall, 2019).

Acidification is a well-recognised example of anthropogenic pressure on riverine systems, which significantly reduces plant, invertebrate and vertebrate biodiversity compared to pH neutral watercourses of a similar physiography (Vickery, 1991, 1992; Hildrew & Ormerod, 1995; Durance & Ormerod, 2007). In the UK, improved emissions control, reductions in heavy industry and a switch to cleaner fuel sources over the last 40 years have reduced acid deposition and subsequent run-off into catchments, while changes to forestry practices have further mitigated the acidifying impacts of upland conifer plantations (Forestry Commission, 2014, 2019). Monitoring has revealed evidence of chemical recovery of upland freshwaters, but biological recovery has so far proved comparatively slow and highly variable (Ormerod & Durance, 2009; Battarbee et al., 2014; Evans et al., 2014; Malcolm et al., 2014b; Murphy et al., 2014; Windsor et al., 2019). While the risks from acidification may have decreased, freshwater ecosystems are exposed to other persistent and emergent pollutants from industrial, urban and agricultural sources (Reid et al., 2019), including heavy metals (Mohiuddin et al., 2011), PCBs and PBDEs (Nedeau, Merritt & Kaufman, 2003; Morrissey et al., 2014; Windsor et al., 2019), pesticides, sediment and nutrients (e.g. phosphorus [P] and nitrogen [N]) (Zacharia, 2011; Albin et al., 2023). Furthermore, the impact of these pollutants may be further exacerbated by climate change (e.g. drought or spate flows) and land management (e.g. removal or absence of riparian buffers), creating unpredictable multiple stressor combinations that may be additive or synergistic (Reid et al., 2019).

Bioindicators are often used as a cost- and time-effective alternative to traditional direct measures of water quality, particularly in riverine environments. For example, White-throated Dippers (*Cinclus cinclus*) are good bioindicators of acidification (Ormerod, Boilstone & Tyler, 1985; Ormerod et al., 1986; Vickery, 1991, 1992), are sensitive to climate change (Sæther, Sutherland & Engen, 2004; Nilsson et al., 2011; Royan et al., 2014), and have potential utility as a bioindicator for broader riverine ecosystem health due to the high sensitivity of their aquatic macroinvertebrate prey (Windsor et al., 2019; Albin et al., 2023; Sabater et al., 2023). Other riverine birds that are closely reliant on flowing water for breeding, such as Grey Wagtail (*Motacilla cinerea*) and Common Sandpiper (*Actitis hypoleucos*), are possibly less sensitive to water quality issues due to their less specialised diets, but are likely capable of indicating quality and availability of riverine and riparian habitat (Yalden, 1985, 1986; Ormerod & Tyler, 1987b; Massimino et al., 2023).

These three species have undergone population decline over the last few decades, the causes of which remain unclear, but are in line with trends reported for freshwater vertebrates in general (He et al., 2019; WWF, 2022). Within continental Europe, there is considerable evidence that Dipper, Grey Wagtail and Common Sandpiper populations are decreasing, but all remain classified as 'Least Concern' as their rates of decline do not cross the threshold for 'Near Threatened' (European Red List Status; BirdLife International, 2015). Conversely, trends in Great Britain indicate widespread decline and range contraction for Dipper (-39% and -11% respectively) and Common Sandpiper (-28% and -15.3% respectively), alongside regional population declines of Grey Wagtail despite a 16.5% range expansion (Balmer et al., 2013; Heywood et al., 2023; Massimino et al., 2023).

These three species often co-occur during the breeding season, divided by their dietary and nesting preferences. While Dippers prey on benthic macroinvertebrates (e.g. insect nymphs and larvae from the orders Ephemeroptera, Plecoptera and Trichoptera) and occasionally small fish by foraging in shallow areas or diving (Ormerod, 1985; Tyler & Ormerod, 1994), Common Sandpiper and Grey Wagtail have a broader diet that also encompasses terrestrial invertebrates (e.g. carabid beetles, earthworms) and aerial insects (e.g. Diptera) respectively (Yalden, 1985; Ormerod & Tyler, 1987a, 1987b). When nesting, Dippers build their domed nests directly over moving water (Tyler & Ormerod, 1994), while the open nests of Common Sandpiper and Grey Wagtails are positioned on the ground near to water or within rock cavities beside watercourses respectively (Svensson, 2009; Dougall, Holland & Yalden, 2010).

Flowing waters are dynamic, highly complex, multiple-stressor environments, making it difficult to diagnose species responses to persistent and/or emergent factors that operate across contrasting scales. Despite extensive research into their life histories and ecology, the drivers behind the observed decline of these riverine birds remains unclear, yet targeted management to address causes of decline equally relies on such an understanding. Large-scale, long-term monitoring datasets are necessary to estimate bird population distributions and trends, and their use could be extended to explore patterns of association with the environment. By using long-term bird survey data collected throughout Great Britain, this study identifies how spatial variation in species occupancy and abundance is associated with environmental factors likely to impact riverine birds directly or indirectly (i.e. hydromorphology, climate, land cover and influencers of water quality) at local and catchment scales. This information, and any evidence of convergent responses, may be used to guide population recovery within the context of current and developing management agendas for freshwater ecosystems.

2.3. Methods

2.3.1. Bird survey data

Data were obtained from the Waterways Breeding Bird Survey (WBBS), an annual survey of UK breeding birds coordinated by the British Trust for Ornithology (BTO) since 1998, with data collected by experienced citizen scientists. This survey design allows for better detection of riverine specialists over other schemes (e.g. BTO Breeding Bird Survey), particularly those such as Dipper that rarely use the surrounding landscape. Survey sites are located on a single watercourse (river or canal) within a 2x2 km tetrad selected through stratified random sampling, and consist of between one and ten 500m linear transects positioned continuously along the watercourse. Each site is surveyed twice per year during the breeding season (April to mid-May [Early; E] and mid-May to late June [Late; L]). Observers record all adult bird sightings within 100m of each transect and note the number of transects walked, allowing survey effort to be quantified.

Survey data used in this study were limited to a five-year period between 2013 and 2017 within Britain to correspond with sources of spatial data. Sites did not have to be surveyed for all five years to be included. For each species, WBBS survey sites were selected based on the following criteria: (1) site could be geolocated (e.g. vector shapefile of transects or coordinates of survey start and end point); (2) site did not contain a section of canal (identified through visual checks on satellite imagery); and (3) site was located within any of the 100km grid squares that contained at least two 10km squares with 'confirmed' breeding pairs according to the 2007-11 Breeding Birds Atlas, to reduce the risk of false zeros caused by sampling outside each species' known breeding range (Balmer et al., 2013). Furthermore, any sites positioned within 1km of another site on the same river were limited to one representative site by retaining the downstream site (provided this was surveyed between 2013 and 2017). In the case of two rivers (River Derwent/Noe and River Lune, both located in England) that had multiple survey sites positioned consecutively (five and seven respectively), two sites on each were retained: the furthest downstream site, and one upstream site located above a confluence. These selection criteria resulted in 261 sites across the three species, averaging 2.75 km in length (range 0.5 – 5.0 km) that were available for analysis (Figure 2.1, Appendix 2.1).



Figure 2.1: Site locations included in each species' dataset. (A) Dipper, $n=218$, (B) Grey Wagtail, $n=262$, and (C) Common Sandpiper, $n=188$. 100km grid squares containing fewer than two 10km squares with 'confirmed' breeding pairs (Balmer et al., 2013) are shown as hashed grey squares for each species; survey sites excluded by this criterion are shown in dark grey.

2.3.2. Environmental data

Environmental variables were selected based on relevance to riverine ecosystems and likely direct or indirect associations with the focal bird species. Detail on data source, publication date and spatial/temporal scale of available data is given in Table 2.1. Variables were divided into four categories: hydromorphology, climate, local land cover and catchment scale influencers of water quality. Environmental data were extracted for each WBBS site at three spatial scales (Appendix 2.2): (1) the survey reach; (2) within two buffer zones of the survey reach (50m [riparian] and 500m [valley]); and (3) within the upstream catchment area [catchment]. The limits for each WBBS site were identified using the spatial referencing and transformed into the assumed river reach (section) surveyed with the *Shortest Path (Point to Point)* function in QGIS (QGIS Development Team, 2009). Polygons of the upstream catchment area for each WBBS site were generated from the upper survey limit with the Watershed function in ArcGIS. This used two raster datasets from the UK Centre for Ecology & Hydrology (UKCEH) 50m Integrated Hydrological Digital Terrain Model (IHDTM): Cumulative catchment area and Outflow drainage direction (Morris & Flavin, 1990, 1994).

Table 2.1: Detail on datasets used to extract variables for analysis. Publication date refers to the most recent version published at the point of download for use in this thesis. For the stream water pH dataset, sample collection began in 1968 and concluded in 2014, whereby the surface chemistry of the UK was systematically sampled; data is standardised to combined multiple sampling campaigns, but includes little to no repeat measures and should not be classified as having a temporal scale.

	Variable	Dataset name	Data source	Publication date	Spatial scale available	Temporal scale available
Response	Bird counts	Waterways Breeding Bird Survey (WBBS)	BTO	05/06/2020	UK	Annual (1998 – 2019)
Explanatory	Elevation	1:10,000 OS Terrain 5 digital terrain model gridded dataset (DTM)	Ordnance Survey	08/02/2020	UK	NA
	Gradient					
	Bedrock permeability	1:50,000 Permeability dataset	British Geological Society	20/01/2010	GB	NA
	Temperature	Had-UK 1km gridded climate database (daily)	Met Office	24/07/2023	UK	Daily (1960 – 2022)
	Rainfall			24/07/2023		Daily (1891 – 2022)
	Land cover	Land Cover Map 2015 vector data set	UKCEH	12/04/2017	GB	Single year (2015)
	Stream water pH	Geochemistry database	British Geological Society	08/07/2020	UK	NA
	Peat	1:50,000 Geology dataset (superficial drift geology layer) 1:625,000 Geology dataset (superficial drift geology layer)	British Geological Society	30/11/2016	GB	NA

2.3.2.1. *Topography*

Elevation was selected to control for differences in land height between WBBS sites, whereas channel gradient was used as an indicator of channel substrate, water velocity and responsiveness to rainfall events, all of which could affect prey availability, foraging efficiency and nest survival of the focal bird species (Da Prato, 1981; Bryant & Tatner, 1988; Tyler & Ormerod, 1994; Wilson, 1996; Theodoropoulos et al., 2017; Elas, Rosendal & Meissner, 2023). Land height data were extracted from the 1:10,000 OS Terrain 5 digital terrain model gridded dataset (DTM; Ordnance Survey (GB), 2020) at the upper and lower survey limits of each WBBS site. The gradient of the survey reach was calculated as the difference in elevation between the upper and lower survey limits, divided by the surveyed length of stream. Land height in metres was also extracted at the midpoint of each survey reach to indicate site elevation. Two outlying sites with elevations greater than 600m and one site with a gradient of 17.2% were excluded. This gave observed means (and ranges) of 93.2m (0-510.2m) and 0.7% (0-7.1%) respectively across all sites (see Appendix 2.3).

2.3.2.2. *Bedrock permeability*

Bedrock permeability was selected as an indicator of responsiveness to rainfall events, but it may also act as a proxy for stream water pH as permeability is positively correlated with pH (i.e. more permeable geologies such as those containing calcite also have higher acid buffering capacity; Bricker & Rice, 1989), which may affect foraging efficiency of the focal bird species and prey quality/availability respectively. Data were extracted from the BGS 1:50,000 permeability dataset (British Geological Society, 2010). The total proportion of each permeability category within the upstream catchment area of each WBBS site were calculated. Minimum (i.e. minimum, or normal, bulk rate of vertical movement) and maximum (i.e. fastest potential rate of vertical movement) permeability scores were first transformed from categorical (very low, low, moderate, high, very high) to a numeric scale (1 to 5), then averaged, weighted by the proportion of upstream catchment area covered by that permeability type. The final minimum and maximum permeability scores were then averaged to give an overall permeability score for each site (mean = 2.8, range = 1.5-5.0).

2.3.2.3. *Climate*

Air temperature and rainfall data were used as an indicator of site microclimate, which may affect prey availability, foraging efficiency of the focal bird species, access to nest sites or chick growth/survival (Da Prato, 1981; Bryant & Tatner, 1988; Tyler & Ormerod, 1994; Wilson, 1996; Chiu et al., 2013; Theodoropoulos et al., 2017; Finn et al., 2022; Gebert et al., 2022; Elas, Rosendal & Meissner, 2023). Data were extracted from the Met Office Had-UK 1km gridded climate database (Met Office et al., 2018) for the midpoint of each survey reach, and subsetting to cover the same

period as the WBBS surveys (April to June) from 2013 to 2017. The average daily temperature was calculated as the midpoint between the minimum and maximum temperatures; the mean and coefficient of variation (CoV) in temperature were then calculated across all months and years to give temperature measures for the breeding seasons surveyed (average temperature mean = 11.2°C, range = 5.9-13.8°C; CoV temperature mean = 0.3, range = 0.2-0.5). Total daily precipitation was summed for each month, then averaged to give the mean monthly rainfall across the breeding seasons surveyed (mean = 65.9mm, range = 38.4-155.2mm).

2.3.2.4. *Land cover*

Land cover data were used as an indicator of land-use, local habitat quality and potential sources of pollution, which may influence the survey reach water quality and microclimate, affecting prey availability and foraging efficiency of the focal bird species (e.g. through increased turbidity; Da Prato, 1981; Muscutt et al., 1993; Vickery et al., 1999; Soulsby et al., 2002; Nedeau, Merritt & Kaufman, 2003; Brown et al., 2013; Malcolm et al., 2014; Dohet et al., 2015; Johnson & Wilby, 2015; Windsor et al., 2019; Turunen et al., 2021). Data were extracted from the UKCEH Land Cover Map 2015 vector data set (Rowland et al., 2017). Each target cover class was grouped into one of the ten aggregate classes defined by UKCEH (arable and horticulture, broadleaved/mixed woodland, coastal, coniferous woodland, freshwater, improved grassland, mountain, heath and bog, saltwater, semi-natural grassland, urban). Proportional cover of these aggregate classes for each WBBS site were extracted for the two survey reach buffers (50m and 500m) and upstream catchment area in QGIS (QGIS Development Team, 2009). Freshwater and saltwater aggregate classes were omitted to focus on terrestrial land cover classes, while the coastal class was omitted due to low representation across survey sites.

2.3.2.5. *Stream water pH*

Stream water pH was used as a proxy for prey availability and quality, which are known to decline under acidic (pH <5.5) conditions (Vickery, 1991; Ormerod & Durance, 2009). Point data was extracted from the British Geological Society (BGS) geochemistry database (Fordyce et al., 2005; Johnson et al., 2005), and transformed to a raster using inverse distance weighting (IDW) interpolation in QGIS (QGIS Development Team, 2009). pH values were extracted at the midpoint, upper and lower limits of each WBBS site, then averaged to give mean pH across the survey reach (mean = 7.3, range = 5.3-8.2).

2.3.2.6. Peat

The total proportion of peat in the upstream catchment area was used as an additional indicator of survey reach water quality. While natural drainage of peat can reduce water quality (i.e. higher concentrations of dissolved organic carbon, nitrogen and sulphate), this can be intensified by disturbance (e.g. forestry, drainage, muirburn or extraction; Pschenyckyj et al., 2023), which may impact prey availability or foraging efficiency of the focal bird species. Data were extracted from the superficial drift geology layer within the BGS 1:50,000 Geology dataset (British Geological Society, 2016). Five map tiles with no data were infilled with the 1:625,000 data, as recommended by BGS. The data were limited to only include classes that contain peat, then divided by the upstream catchment area to give the total proportion of catchment drift peat for each WBBS site (mean = 0.1, range = 0-0.8).

2.3.3. Modelling approach

All analyses were completed in R (version 4.3.0; R Core Team, 2023). Generalised linear mixed models (GLMMs; *glmmTMB* function; Brooks et al., 2017) were used to assess occupancy and abundance separately for each species. For occupancy, sites were considered occupied (i.e. assumed to be all or part of a breeding territory) in any given year if a bird of that species was observed at least once during both surveys or more than one bird was observed during a single survey, and unoccupied if zero birds were observed across both visits. Sites where only one bird was observed across one or both visits in a single year were considered indeterminate in terms of their occupancy and therefore excluded from this analysis (Table 2.1). Since the response was binary (1= presence, 0= absence), a binomial distribution was used. For abundance, bird counts across all transects at a site were pooled by species to give the total number of birds observed on a given survey. A poisson link function was used to reflect the use of count data. All surveys (Early/Late) were included in the count analysis; survey years with zero observations of a given species at a site were excluded to focus wholly on variation in numbers at sites where birds were detected.

For both occupancy and abundance, species were modelled separately. Site ID was included in all models as a random effect to account for non-independence of repeat surveys at the same location. Year was included in all models as a fixed effect to control for differences in survey years between sites; while five levels is generally considered the minimum to precisely estimate the random-effect variance, fitting year as a fixed effect here reduced the risk of singularity during model fitting with Site ID already included as a random effect (Crawley 2002; Bolker, 2015). Survey timing (E/L) was also included as a fixed effect in the abundance models to control for differences in detection and observed numbers across the survey period (April-June). Both year and survey timing were treated as 'nuisance' fixed effects to focus on spatial variation. The number of 500m

transects were included in both analyses as an offset to control for heterogeneity in survey effort (Appendix 2.4). As the occupancy model used a complementary log-log link function, and the abundance model used a log link function, the offset was log-transformed to ensure proportionality between response variables and the offset.

For each species and land cover aggregate class, bivariate generalised linear models (GLMs; *glm* function; R Core Team, 2023) were first used to identify which buffer size (50/500m) had a higher R^2 value and was therefore most appropriate to include in the full analysis (Appendix 2.5). Land cover in the upstream catchment area was limited to three aggregate classes (arable and horticulture, improved grassland and urban) indicative of pollutant loading via surface run-off (i.e. non-atmospheric sources) that is likely to impact water quality and hence prey availability. All explanatory variables were plotted against response variables to assess their linearity. Elevation and gradient were log-transformed for both Dipper and Grey Wagtail models (using $\log(y+1)$ to account for zeros in the data), while all variables remained untransformed for Common Sandpiper. All explanatory variables were scaled and centred prior to analysis.

Models were checked for multi-collinearity of explanatory variables using variance inflation factors (VIFs; *check_collinearity* function; Lüdecke et al., 2021a) and correlation matrices (Appendix 2.6). Elevation was omitted from analyses due to strong association with temperature and land cover, and CoV temperature was also omitted due to high collinearity with mean temperature. Remaining explanatory variables with a VIF of >5 were removed sequentially to select for the most appropriate occupancy and abundance models for each species (i.e. no VIFs >5 and the highest pseudo R^2 value calculated with the *r2* function; Lüdecke et al., 2021a). No further model selection procedure was used primarily to allow the direct comparison of responses to individual environmental variables between species (e.g. to riparian broadleaved/mixed woodland cover) within a model structure that accounts for other environmental factors, which may better reflect the integrated characteristics present in riverine environments and provides additional context on species' responses. Diagnostics for the final models (Appendix 2.7) were examined using the *DHARMA* package (Hartig, 2022), and no issues were identified once residuals were grouped by site.

Table 2.2: Inclusion of bird survey data in occupancy and abundance models. (a) the number of surveys completed in a given site / year combination (E survey = early April – mid-May; L survey = mid-May – late June; grey block = survey not completed), and the number of birds observed during each survey; (b) inclusion of data in the occupancy analysis where in any given year, ‘occupied’ sites are indicative of a complete/partial breeding territory (i.e. at least one observation across both surveys or more than one observation at a single survey), ‘unoccupied’ if zero birds were observed across both visits, and ‘indeterminate’ if insufficient evidence of at least one breeding territory being present (i.e. only one observation across one or two visits); (c) the number (%) of records (site / year combinations) for each occupancy level by species; (d) inclusion of data in the abundance analysis, which is treated independent of occupancy and includes all count data; (e) the number (%) of records (site / year / visit combinations) for each abundance level by species.

Number of birds observed ^a		Occupancy ^b	Number of records included in occupancy models ^c			Abundance ^d	Number of records included in abundance models ^e		
E Survey	L Survey		Dipper (n=843)	Grey Wagtail (n=1022)	Common Sandpiper (n=722)		Dipper (n=1657)	Grey Wagtail (n=2007)	Common Sandpiper (n=1418)
0	2+	Occupied	372 (44.1%)	455 (44.5%)	255 (35.3%)	Data included	743 (44.8%)	905 (45.1%)	497 (35%)
2+	0								
	2+								
2+									
1+	1+	Indeterminate (data excluded)	107 (12.7%)	150 (14.7%)	69 (9.6%)	Data excluded	914 (55.2%)	1102 (54.9%)	921 (65%)
0	1								
1	0								
	1								
1		Unoccupied	364 (43.2%)	417 (40.8%)	398 (55.1%)	Data excluded	914 (55.2%)	1102 (54.9%)	921 (65%)
	0								
0									
0	0								

2.4. Results

2.4.1. Occupancy

Environmental variables provided a confident predictor for site occupancy of the three focal species (R^2 m: Dipper = 0.663, Grey Wagtail = 0.556, Common Sandpiper = 0.709). Dipper and Grey Wagtail showed largely convergent responses to multiple environmental variables, while Common Sandpiper generally diverged from the other two species (Figures 2.2 and 2.3; Appendix 2.8).

Dipper and Grey Wagtail were most strongly associated with high gradient sites, though the likelihood of Dipper occupancy decreased above gradients of 5%. Conversely, Common Sandpiper were more likely to be present at sites with low gradients, but this variable had lower relative importance for Common Sandpiper occupancy compared with the other species (as assessed by odds ratios in Figure 2.2). Only Grey Wagtail was positively associated with bedrock permeability, with sites of higher permeability more likely to be occupied. Climate had no significant effect on Dipper occupancy. Common Sandpipers were more likely to occupy cooler sites with lower rainfall (i.e. $<9^\circ\text{C}$ and $<60\text{mm/month}$), whereas Grey Wagtail occupancy increased with temperature, albeit only marginally (p -value between <0.1 and >0.05).

Riparian broadleaved/mixed woodland was positively associated with Dipper occupancy, with likelihood of occupancy reaching 100% above 60% cover of riparian woodland, whereas Common Sandpiper were less likely to occupy sites with higher proportions of both woodland types at the riparian scale. Grey Wagtail presence was also positively associated with both broadleaved/mixed and coniferous woodland at a riparian and valley scale respectively, but likelihood of occupancy reached 100% at lower proportions of coniferous than broadleaved/mixed woodland (30% vs. 80% cover). Mountain, heath & bog land cover was associated with lower site occupancy by Dipper and Grey Wagtail at valley and riparian scales respectively; a marginal positive association was identified for Common Sandpiper at the valley scale, but the broad CIs make this association difficult to evaluate. Dipper and Grey Wagtail occupancy had marginal negative associations with valley scale arable and horticulture. Improved grassland, semi-natural grassland and urban land cover had no significant association with site occupancy of the three species at either riparian or valley buffer scales.

For variables likely to impact water quality via surface runoff from the upstream catchment, only arable and horticulture had a consistently negative effect on occupancy of the three species, with the likelihood of occupancy for all three species falling below 50% when arable and horticulture exceeded 20% of the catchment. This was the single most important factor in Common Sandpiper occupancy, but of lesser relative importance for Grey Wagtail. Occupancy of Dipper and Common Sandpiper decreased with higher proportions of upstream peat, but there was a marginal positive association between peat and Grey Wagtail. Only Common Sandpiper occupancy was negatively

associated with upstream Improved grassland. pH and Urban land cover had no significant association with occupancy of any species.

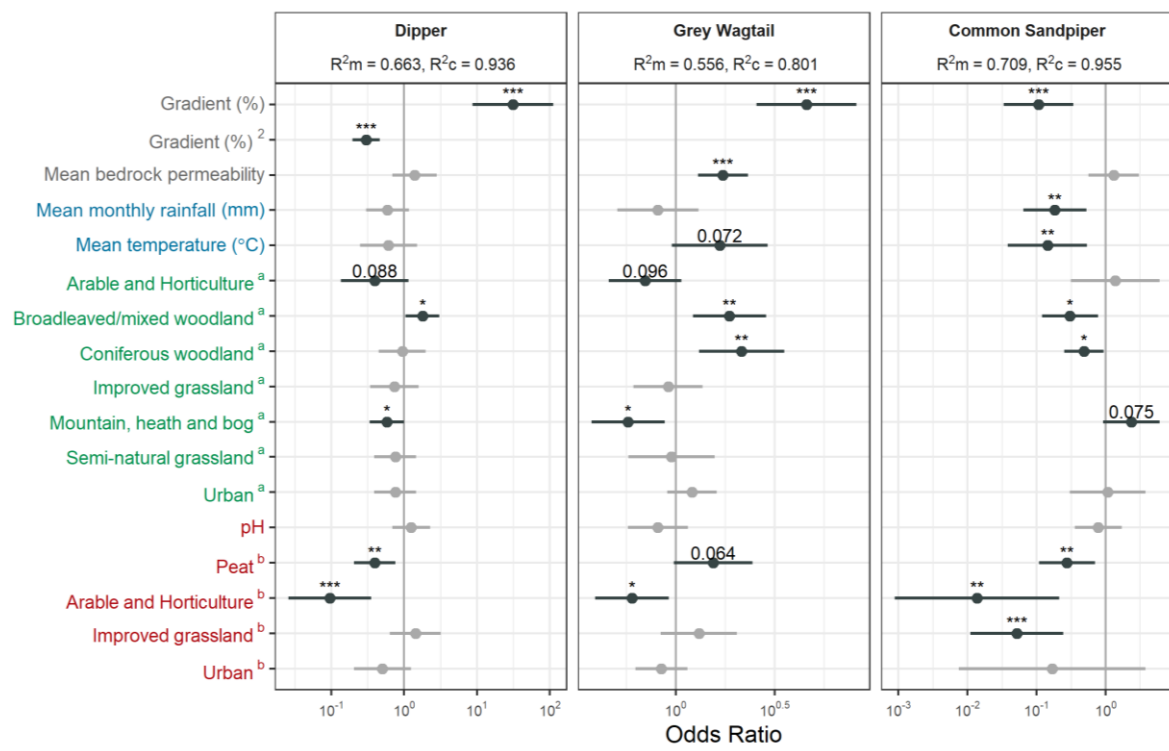


Figure 2.2: Forest plot of GLMM output for Dipper, Common Sandpiper and Grey Wagtail occupancy. Explanatory variables on the y-axis are grouped by hydromorphology indicators (grey), climate (turquoise), local land cover (green) and catchment scale influencers of water quality (red). Pseudo R^2 values are calculated with the performance package (Lüdecke et al., 2021). Risk ratios: >1 = positive effect; <1 = negative effect. ^a proportion of buffer area (50/500m), ^b proportion of upstream catchment area. Marginal p-values (<0.1) are written, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

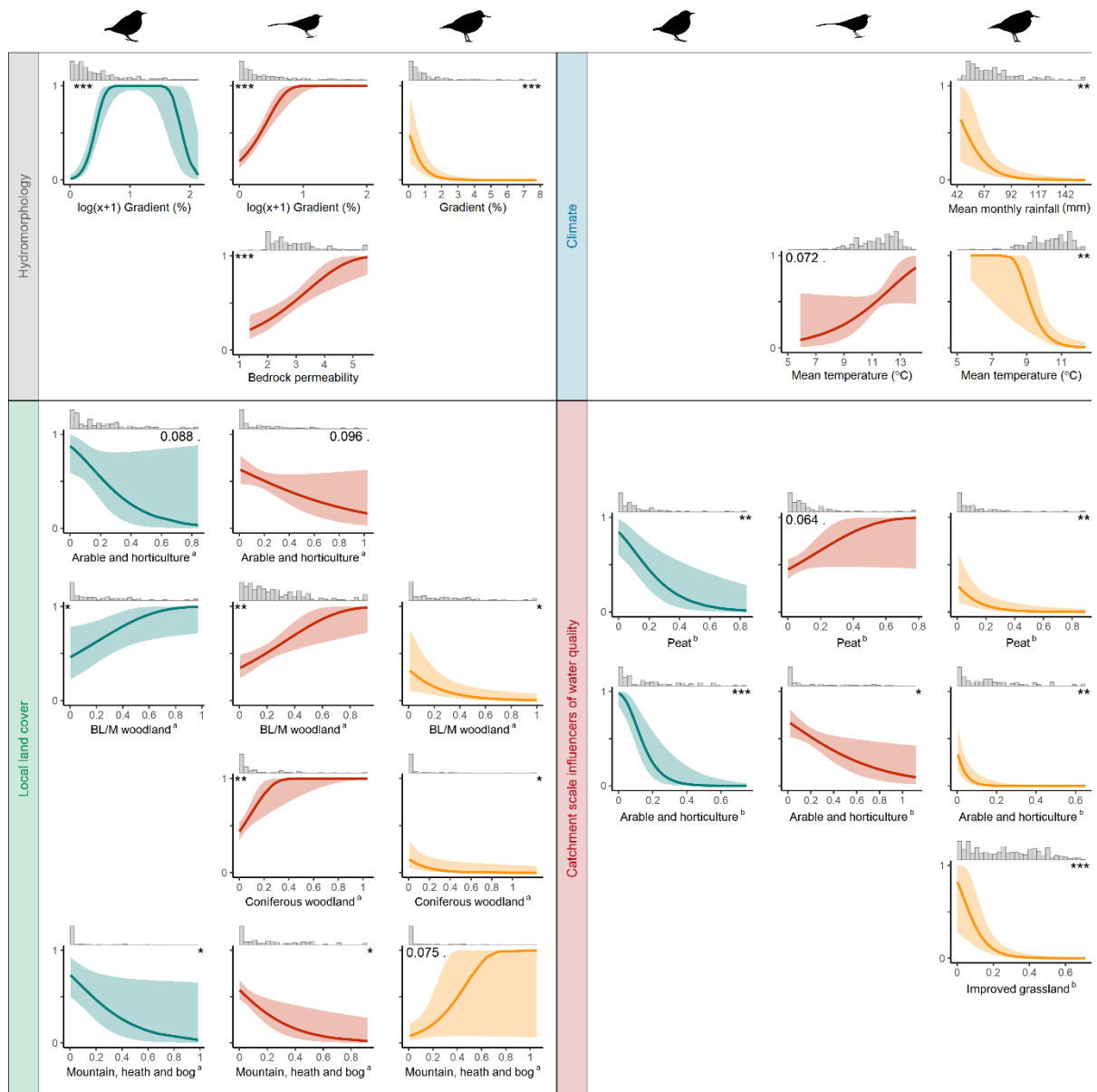


Figure 2.3: Marginal effect plots of species occupancy and histograms of the individual site ranges for significant/marginal explanatory variables. Dipper (blue); Grey Wagtail (red); Common Sandpiper (orange). The number of transects (offset in model) is held constant at the mean value by species (6.6, 6.5 and 6.7 respectively). ^a proportion of buffer area (50/500m), ^b proportion of upstream catchment area. Marginal p-values (<0.1) are written, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

2.4.2. Abundance

Environmental variables were less effective for predicting focal species abundance (R^2 m: Dipper = 0.048, Grey Wagtail = 0.059, Common Sandpiper = 0.114), with fewer significant variables and lower effect magnitudes (odds ratios) than observed in the occupancy models. Dipper and Grey Wagtail showed convergent responses to some variables, as did Grey Wagtail and Common Sandpiper, but no associations were shared between Dipper and Common Sandpiper (Figures 2.4 and 2.5; Appendix 2.8).

Similar to the occupancy models, Common Sandpiper were more abundant at low stream gradients, whereas Dipper had a marginally positive association with gradient. Climate had almost no effect on the focal species, with only Common Sandpiper abundance halving as mean monthly rainfall increased from 40 to 140mm/month. Both Dipper and Grey Wagtail abundance increased under higher proportions of riparian and valley scale broadleaved/mixed woodland respectively, with at least 1 bird/km present where woodland exceeds 50% of the buffer land cover. While only of marginal significance, Grey Wagtail numbers also increased with coniferous woodland at the valley scale. Dipper and Common Sandpiper abundance marginally declined with increasing proportions of valley scale mountain, heath and bog and urban land cover respectively. Arable and horticulture, improved grassland and semi-natural grassland land cover at local scales were unrelated to variation in abundance for any of the three species.

Similar to the occupancy models, stream pH and catchment scale urban land cover had no association with abundance for any of the three species. Dipper numbers had a marginally negative association with upstream peat. Catchment scale arable and horticulture was the most important driver of abundance for Common Sandpiper and Grey Wagtail (in terms of effect size), with numbers for both decreasing with as little as 10% agricultural land in the catchment area. Common Sandpiper were also marginally less abundant at sites with more catchment scale improved grassland.

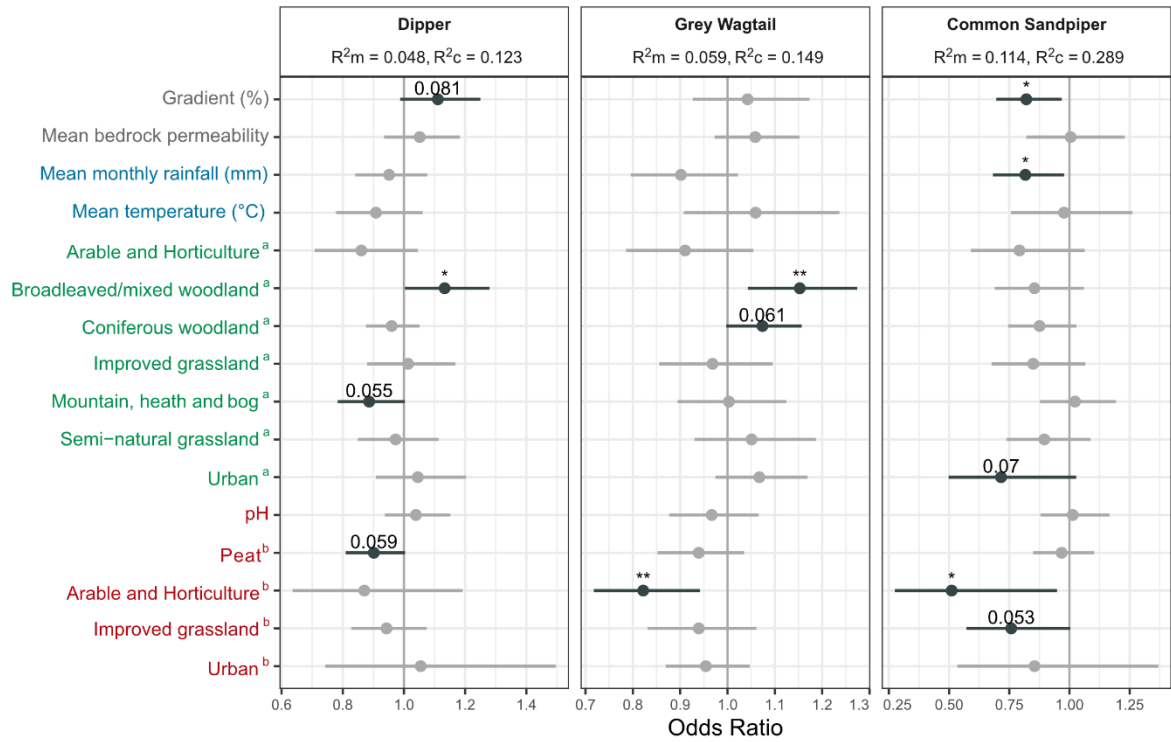


Figure 2.4: Forest plot of GLMM output for Dipper, Common Sandpiper and Grey Wagtail abundance. Explanatory variables on the y-axis are grouped by hydromorphology indicators (grey), climate (turquoise), local land cover (green) and catchment scale influencers of water quality (red). Pseudo R^2 values are calculated with the performance package (Lüdecke et al., 2021). Risk ratios: >1 = positive effect; <1 = negative effect. ^a proportion of buffer area (50/500m), ^b proportion of upstream catchment area. Marginal p-values (<0.1) are written, * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

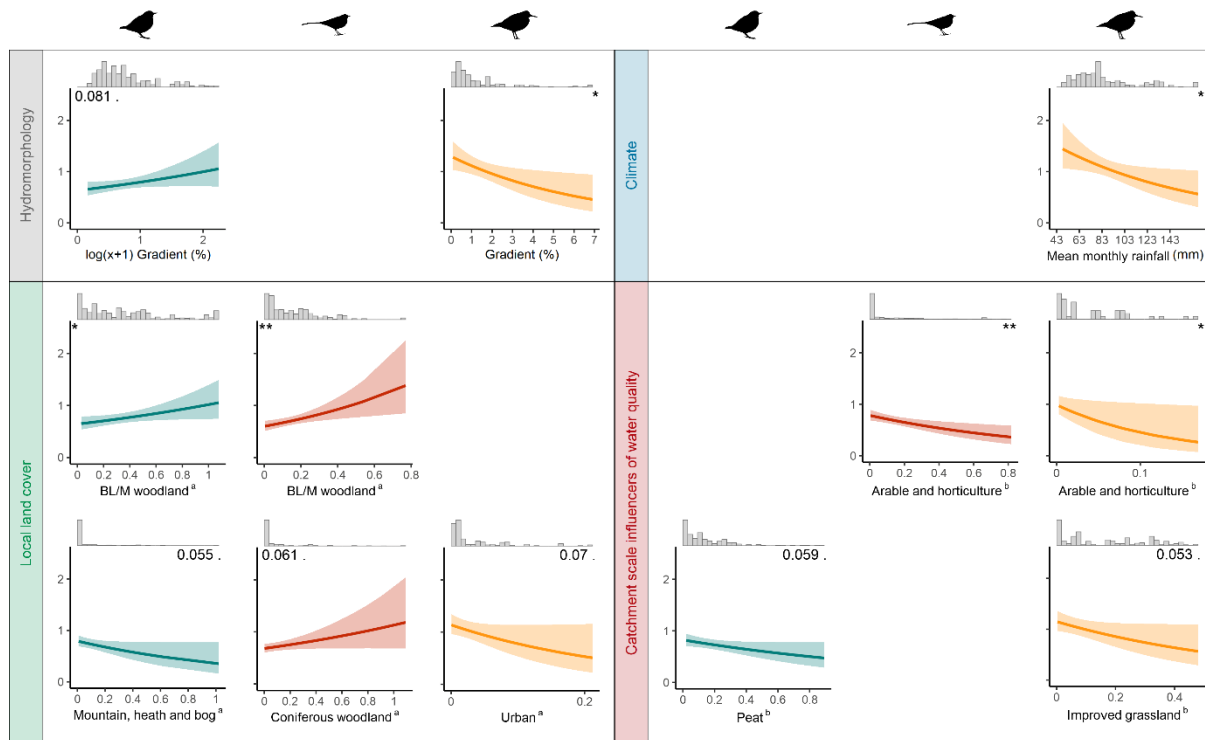


Figure 2.5: Marginal effect plots of species abundance (birds/km) and histograms of the individual site ranges for significant/marginal explanatory variables. Dipper (blue); Grey Wagtail (red); Common Sandpiper (orange). Number of transects (offset in model) is held constant at 2 (equivalent to 1km), year at 2015, and visit at "E". ^a proportion of buffer area (50/500m), ^b proportion of upstream catchment area. Marginal p-values (<0.1) are written, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

2.5. Discussion

This study demonstrates that occupancy and, to a much lesser extent, abundance of Dipper, Grey Wagtail and Common Sandpiper recorded in 0.5-5km river reaches across Great Britain respond to a subset of environmental variables at channel, local landscape, and catchment scales. Dipper and Grey Wagtail occupancy responded similarly, suggesting a high degree of niche overlap. These two species however were divergent in their abundance response, which may reflect different controls on bird densities such as the territory length required to raise young to fledging. Conversely, Common Sandpiper showed rather distinct occupancy and abundance responses to the environmental variables considered, suggestive of a weaker association with the riverine environment. Due to the timing of the WBBS bird surveys (April–June), it is likely that many of the environmental associations identified in our results reflect direct or indirect controls on breeding, including prey and nest site availability or other attributes of territory quality, which supports their utility as broad indicators of riverine and riparian ecological health, but not necessarily water quality or ecosystem resilience.

The design of the WBBS scheme makes it highly suitable for identifying how species occupancy is linked to environmental factors at multiple scales. However, there are potentially issues with inference of environmental predictors of abundance due to the maximum survey length of 5km. All three focal species hold linear river territories, averaging between 1.2km to 3.5km in length (Tyler, 1972; Holland, Robson & Yalden, 1982; Ormerod & Tyler, 1987b; Vickery, 1991). As the median number of transects in both analyses in this study was six (equating to 3km), it is likely that surveyors at shorter survey sites observed only one breeding pair. We attempted to account for variation in survey effort in this study by including a model offset for survey length, but a lower likelihood of detection of birds at shorter sites (Appendix 2.5) may still mask any relationships present. Furthermore, the typically small number of birds observed per site likely contributes to the low amount of variance explained in the abundance models (Figure 2.4; Appendices 2.1 and 2.8; R^2_c for Dipper=0.123, Grey Wagtail=0.149, and Common Sandpiper=0.289) compared with the occupancy models (Figure 2.2; R^2_c for Dipper = 0.936, Grey Wagtail=0.801, and Common Sandpiper=0.955).

The use of national open-source datasets in this study allows for greater spatial coverage than is possible with specialised regional datasets or focused field studies. However, the high diversity in scale of appropriate datasets (Table 2.1) and resulting range of values for analysis (Appendix 2.3) presents multiple challenges. For example, while some environmental variables lack a temporal range and correspond to the bird survey data by site alone (e.g. reach gradient), other temporally disparate datasets were standardised to allow modelling to focus wholly on environmental differences between sites. UKCEH land cover data products were irregularly produced prior to 2017, thus all temporal data in this study were limited to a short time-period over which any

significant land cover change from a single data product was unlikely (2013-2017), such as the 5-year average computed for daily temperature and rainfall data. Furthermore, some variables exhibited a low range of values across the sites. For example, the observed range in pH across sites in this study (5.3 - 8.2) is reduced from the full range available (0.4 - 9.95; Fordyce et al., 2005; Johnson et al., 2005). While the subset in this study is perhaps representative of the majority of rivers in Britain, any relationships that might be present across the full range may be masked by the lack of extremes, and necessitates careful inference of results.

2.5.1. Species responses to environmental variables

Dipper and Grey Wagtail shared a strong positive association with gradient. Moderate gradients (4-9%) and fast-flowing water with coarse bedloads are conducive to the formation of well-oxygenated riffles. These habitats are ideal for the benthic larvae or nymphs of insects such as Ephemeroptera, Plecoptera and Trichoptera that are intolerant of lower water quality (Gauvin & Tarzwell, 1952; Vickery, 1991; Nedeau, Merritt & Kaufman, 2003; Windsor et al., 2019). Dippers preferentially feed on these aquatic life stages (Ormerod, 1985; Tyler & Ormerod, 1994), while Grey Wagtails target the emerged adults to supplement their broader diet of aerial insects (Ormerod & Tyler, 1987a, 1987b). The decrease in Dipper occupancy above an average reach gradient of 5% is likely due to higher water velocities, which can reduce the availability of aquatic food resources through bed movement (Theodoropoulos et al., 2017) and increase the foraging costs associated with diving for prey (Da Prato, 1981; Bryant & Tatner, 1988). In contrast, Common Sandpiper preferred low gradients with low monthly rainfall, which aligns well with their utilisation of exposed riverine gravels while foraging (Yalden, 1985, 1986). These features form in wider channels when bedload is deposited as velocity slows, and thus occur less consistently at sites with high gradients, high rainfall, or low bedrock permeability.

Only Grey Wagtail occupancy had a positive association with bedrock permeability. Bedrock is strongly linked to stream chemistry (Bricker & Rice, 1989) and there is a strong likelihood that permeability is positively correlated with pH, but since Grey Wagtail are less sensitive to acidic conditions than Dipper (Ormerod & Tyler, 1987b), the observed association more likely reflects the superior ability of permeable catchments to moderate river response to rainfall events. This results in a more stable flow regime with slower rates of rise and to a lower peak level compared with catchments dominated by impermeable bedrock, which often experience flashy flows. Such flow regimes may reduce the availability of aquatic food resources (Theodoropoulos et al., 2017), reduce efficiency or increase cost of foraging (Da Prato, 1981; Bryant & Tatner, 1988), reduce the availability of natural nest sites or wash out active nests (Tyler & Ormerod, 1994; Wilson, 1996; Elas, Rosendal & Meissner, 2023), or increase mortality, particularly of fledglings (Chiu et al., 2013). Considering the foraging and nesting behaviour of the focal species, they would therefore

likely all benefit from a stable flow regime. The lack of association with catchment permeability for Dipper and Common Sandpiper might suggest that these species tolerate variable flows better than Grey Wagtail (Royan et al., 2013), but may also be an artefact of the low number of sites with high permeability included in analysis for these species (Appendix 2.3).

None of our focal species had an association with stream pH, which is particularly perplexing given the historical negative association between Dippers and acidified watercourses (Ormerod, Boilstone & Tyler, 1985; Ormerod et al., 1986; Vickery, 1991, 1992). The mean stream pH values included in our analysis range from moderately acidic to weakly basic (pH 5.3-8.2; Appendix 2.3), but very few sites could be classed as 'acidic' (6 sites with pH < 6.0). This is likely too narrow a range of values to identify a relationship between stream pH and riverine bird occupancy or abundance, but more positively may be indicative of chemical recovery as multiple WBBS sites are located in areas of historic acidification (i.e. mid-Wales, north England, south-west Scotland; Battarbee et al., 2014; Evans et al., 2014) that are otherwise suitable sites for breeding Dipper.

Grey Wagtail occupancy increased with average air temperature, in contrast to the negative association for Common Sandpiper. Insects of both terrestrial and aquatic origin are affected by temperatures, but the relationship between temperature and phenology (the timing of biological events) is highly complex. In general, many insect groups in temperate regions respond plastically to warming temperatures with increased development rates and a shift towards earlier emergence, though many species may also extend their activity period (Forrest, 2016). Thus, warmer sites may contain higher insect abundance and richness, but this could favour warm-adapted taxa (Gebert et al., 2022), particularly in open habitats. While no association with temperature was identified for Dipper, their invertebrate prey are likely still affected by temperature (Finn et al., 2022), which may be masked by other factors at occupied sites (e.g. riparian woodland shading).

Both Dipper and Grey Wagtail preferred wooded stream reaches, consistent with previous research (Buckton and Ormerod, 1997). Broadleaved tree-shading may alleviate warming effects on thermo-sensitive species by moderating stream temperatures and providing essential habitat, with riparian planting being increasingly advocated to mitigate climate change impacts on streams (Gurnell, Gregory & Petts, 1995; Dohet et al., 2015; Johnson & Wilby, 2015; Turunen et al., 2021). Riparian woodland also contributes a large proportion of aerial insects to the riparian environment (Mason & Macdonald, 1982; Dineen, Harrison & Giller, 2007), and increases aquatic insect habitat complexity and production through the addition of coarse woody debris and leaf litter (Gurnell, Gregory & Petts, 1995; Schneider & Winemiller, 2008). Furthermore, woody vegetation provides materials (e.g. mosses, leaves) and sites (e.g. tree hollows, exposed roots) for nest building, and can buffer diffuse inputs of nutrients from agricultural and urban areas (Muscutt et al., 1993; Gurnell, Gregory & Petts, 1995; Turunen et al., 2021). Historic associations

between coniferous plantations and reduced water quality through acidification are likely still present in catchments with reduced buffering capacity, and evidence suggests that afforestation can further delay chemical and biological recovery (Gee & Stoner, 1989; Battarbee et al., 2014; Evans et al., 2014; Malcolm et al., 2014b). However, some of the direct and indirect benefits present in riparian broadleaved woodland may extend to coniferous plantation (e.g. insect provision, shade, nesting sites), providing an appropriate buffer of 2-20m between the stand and river edge is maintained (Forestry Commission, 2014, 2019).

Conversely, Common Sandpiper occupancy was lower in wooded reaches, suggesting that restoring riparian woodland is not a ubiquitous management solution for riverine bird species, even in upland settings. A previous study identified that adult Common Sandpiper have remarkably broad, unspecialized diets (Yalden, 1985), and will preferentially feed in semi-natural or even agriculturally improved grassland, despite negative associations between management practices (e.g. grazing, fertilising, cutting) and water quality, invertebrate diversity and abundance in improved grassland (Vickery et al., 1999). Grassland however is rarely targeted or defended as part of Common Sandpiper territories, with pairs prioritizing river reaches with exposed gravel beds that are the favoured foraging habitat of juveniles (>5 days old; Yalden, 1986a, 1986b). This is consistent with the lack of association between abundance and grassland we observed. Another study using standardised habitat surveys indicated a preference of Common Sandpiper for mixed rough pasture and wetlands, but highlighted that they are likely more influenced by channel and flow characters than riparian character (Buckton & Ormerod, 1997). This, alongside the lack of a significant positive association with any single land cover type in our study, suggests that habitat heterogeneity (i.e. a mixture of grassland and other habitat types) with limited tree cover is preferred by breeding Common Sandpiper over any specific habitat type.

Habitat surveys have previously indicated that Dipper and Grey Wagtail avoid habitat dominated by low-height vegetation, particularly moorland (Buckton & Ormerod, 1997), which generally supports higher water quality due to limited pollutant loading. However, in the absence of natural tree cover, water quality may still be reduced through abstraction, release of nitrates, sulphates and dissolved organic carbon (DOC) via upstream afforestation and deforestation, grazing, and peat drainage and burning (Gee & Stoner, 1989; Soulsby et al., 2002; Brown et al., 2013; Evans et al., 2014; Malcolm et al., 2014b). Despite this, the reduction in Dipper occupancy and abundance at sites with montane habitat we observed may also link more directly and simply to watercourse width. Narrow upland streams will require Dippers to defend a longer territory in order to adequately provision their offspring to independence (Wilson, 1996). Fewer birds would therefore be expected as the proportion of montane habitat increases. Longer than average territories (i.e. >1.5km) within this habitat may also explain the lower occupancy, as the short

survey lengths utilised in the WBBS scheme (between 0.5 - 5km) may reduce the likelihood of detection (Appendix 2.5), an effect that is potentially exacerbated if Dippers breeding at higher elevations use multiple low-order streams within a single territory. As water quality likely impacts Grey Wagtail less than Dipper due to use of both aquatic and terrestrial resources, the observed decline in Grey Wagtail occupancy as montane land cover increases may be due to conflation with other factors such as elevation, which is negatively correlated with temperature (Appendix 2.6). Additionally, the lack of woodland in montane habitat may reduce availability of non-aquatic prey (Mason & Macdonald, 1982; Ormerod & Tyler, 1987a).

Considering that urban areas can be a point-source of multiple pollutants, and often lack riparian woodland, the lack of a significant relationship between all three species and riparian or valley scale urban landcover is unexpected. There are multiple possibilities; firstly, water quality in urbanised catchments has improved considerably since 1990, but localised deterioration or delayed improvement introduces variation among sites (Vaughan & Ormerod, 2012), thus increasing urban land cover may not necessarily correlate with poor quality water. Secondly, it may reflect a willingness of birds to nest within or near urban areas when a high population density or shortage of nest sites increases competition for territories. While unlikely for Common Sandpiper, Dipper and Grey Wagtail both readily utilise man-made structures for nesting (e.g. bridges, culverts; Tyler, 1972; Tyler & Ormerod, 1994). This may partially mask an expected negative effect of common urban pollutants such as polychlorinated biphenyls (PCBs) and polybrominated diphenyl ethers (PBDEs), which have the potential to reduce aquatic prey richness (Nedeau, Merritt & Kaufman, 2003; Windsor et al., 2019) and impair nestling development (Morrissey et al., 2014). Thirdly, the low number of urban sites within the random sampling design may obscure detection of any relationships present (only 9-12% of sites had >25% urban land at riparian or valley scale for the focal species).

All focal species displayed one or more negative associations to the proportion of arable and horticulture, improved grassland, and peat in the upstream catchment area. Occupancy was significantly lower at sites with >20% of these land cover types upstream, and occupied sites displayed reduced abundance. This is likely reflective of an overall reduction in breeding density, whereby breeding pairs require a longer territory to yield sufficient aquatic, and possibly terrestrial, prey resources (Vickery, 1991) as upstream pollutant sources may impact stream quality through indirect effects on prey richness and density (Zacharia, 2011; Albin et al., 2023), and/or directly on foraging efficiency (e.g. via effects of DOC or suspended sediment on visual predation; Da Prato, 1981). Thus, while Dippers are the iconic bioindicator for riverine ecosystem health, it is likely that Grey Wagtail and Common Sandpiper are also responding to influencers of water, or riparian habitat quality.

2.5.2. Managing rivers for the benefit of river birds

While it would be inappropriate to manage rivers solely for the benefit of riverine birds, the associations identified here suggest that there are several existing policies and related practical initiatives that are likely to act in their favour. There is significant evidence that these promote aquatic and riparian biodiversity in general, but have rarely been highlighted as specifically supporting river bird populations. For example, our results suggest that the introduction or restoration of riparian broadleaved/mixed woodland would benefit both Dippers and Grey Wagtails, while vegetated buffer strips (>10m wide) may be more beneficial for Common Sandpiper. These habitats provide significant landscape-scale benefits such as diffuse pollution management, natural flood management and climate mitigation (Muscutt et al., 1993; Forestry Commission, 2014, 2019; Thomas, Griffiths & Ormerod, 2016; Cooper et al., 2021; Turunen et al., 2021), which filter down to improve invertebrate diversity and abundance (e.g. via improved water quality, water velocity moderation, temperature regulation, habitat complexity and litter inputs; Gurnell, Gregory & Petts, 1995; Nedeau, Merritt & Kaufman, 2003; Schneider & Winemiller, 2008; Dohet et al., 2015; Johnson & Wilby, 2015; Thomas, Griffiths & Ormerod, 2016; Theodoropoulos et al., 2017; Windsor et al., 2019; Turunen et al., 2021), predator foraging efficiency (e.g. via improved water clarity; Da Prato, 1981; Hedström et al., 2017) and spawning point/nest site availability (e.g. associated with trees, woody debris or gravel substrate; Tyler & Ormerod, 1994; Taylor et al., 2019). Collectively, these actions may also improve riverine bird abundance and breeding performance through larger clutches, improved provisioning and increased fledgling survival (Tyler & Ormerod, 1994; Wilson, 1996; Chiu et al., 2013; Elas, Rosendal & Meissner, 2023).

2.6. Appendix

Appendix 2.1: BTO WBBS data

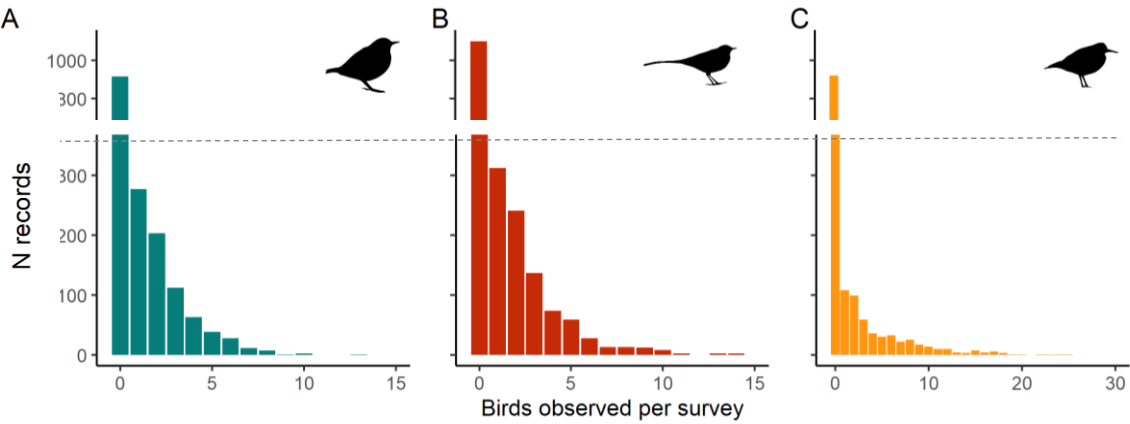


Figure A2.1-1: Histograms of the relative number of each species included in data. (A) Dipper; (B) Grey Wagtail and (C) Common Sandpiper. Records equate to a site / year / visit / species combination (where a survey was completed in a given year). The y-axis is split at the dashed line to account for the large number of records with zero birds observed.

Appendix 2.2: Description and use of spatial scale for each environmental variable

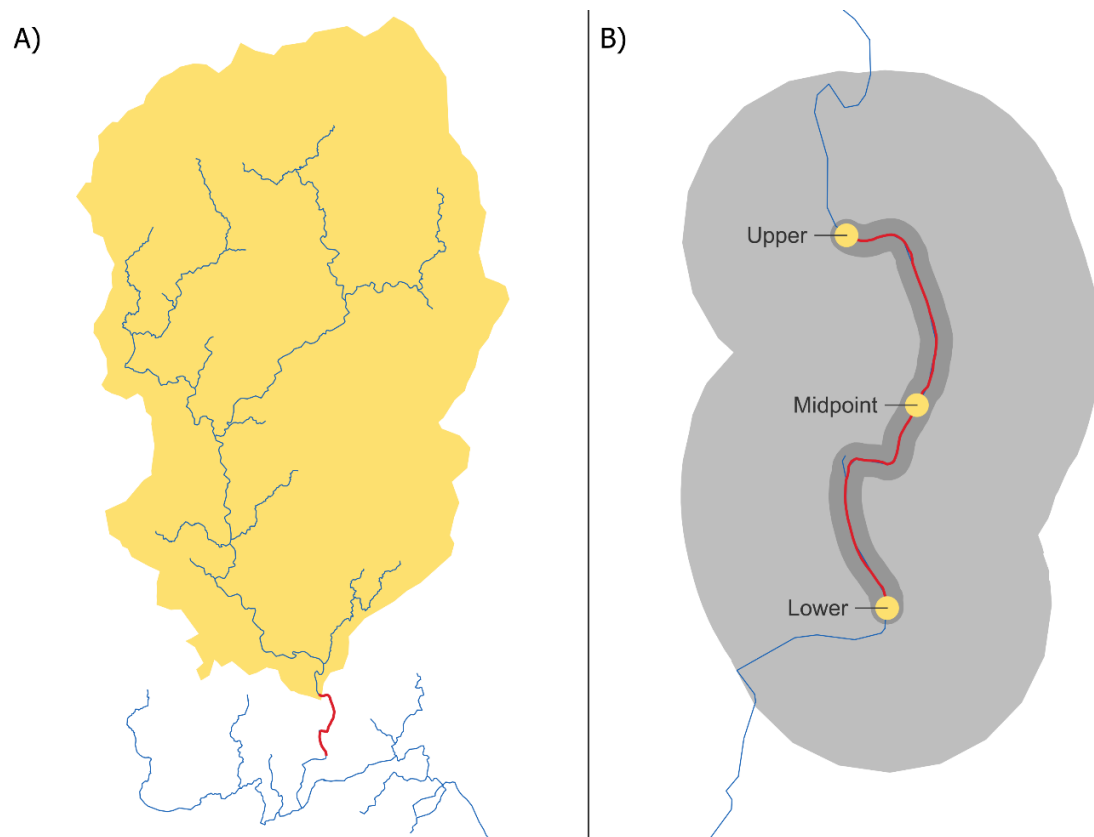


Figure A2.2-1: Description of data extraction areas for each WBBS survey site. The upstream catchment area (A) consists of the total land area (yellow) that theoretically drains into the survey reach (red line) via surface watercourses (blue lines). The survey reach (B) includes three points of data extraction (the survey midpoint, upper and lower limits; shown in yellow) and two buffer areas (50m buffer shown in dark grey; 500m buffer shown in light grey).

Table A2.2-1: Summary of spatial scales for environmental variables used in analysis. Spatial scales (described in Figure A2.2-1) include survey reach, buffer and upstream catchment area. Hyphen (-) denotes data not extracted at that spatial scale.

Explanatory variable	Reach	Buffer	Upstream catchment
Elevation	Midpoint	-	-
Gradient	Whole reach	-	-
Bedrock permeability	-	-	Weighted average of UC area
Temperature	Midpoint	-	-
Rainfall	Midpoint	-	-
Land cover	-	50/500m	Proportion of UC area
Stream water pH	Average of upper, midpoint and lower	-	-
Peat	-	-	Proportion of UC area

Appendix 2.3: Value range of environmental variables by species



Figure A2.3-1: Histograms of explanatory variable values for Dipper. Both un-transformed and log-transformed plots are included for elevation and gradient. ^a proportion of 50m buffer area, ^b proportion of 500m buffer area, ^c proportion of upstream catchment area.

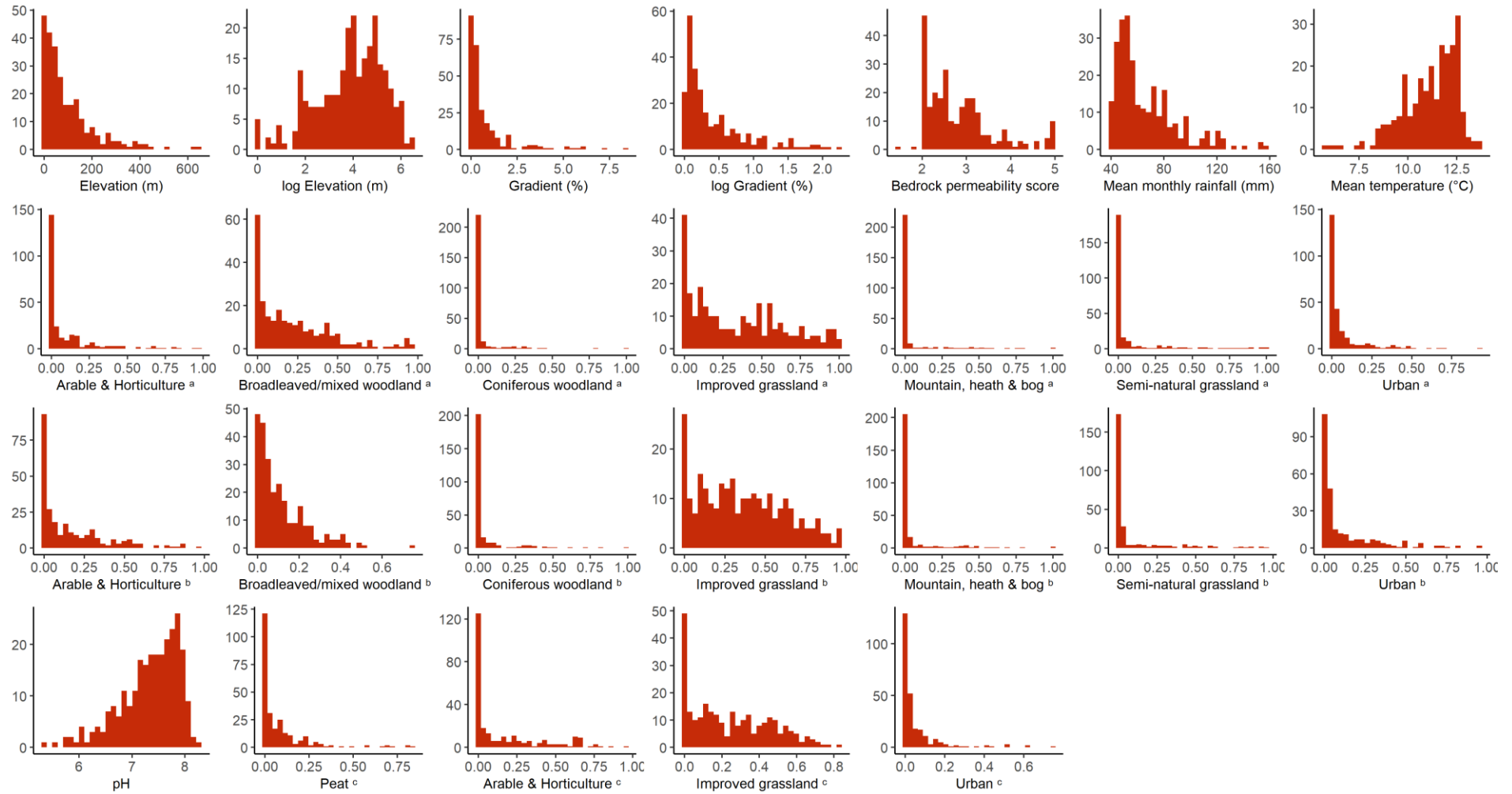


Figure A2.3-2: Histograms of explanatory variable values for Grey Wagtail. Both un-transformed and log-transformed plots are included for elevation and gradient. ^a proportion of 50m buffer area, ^b proportion of 500m buffer area, ^c proportion of upstream catchment area.

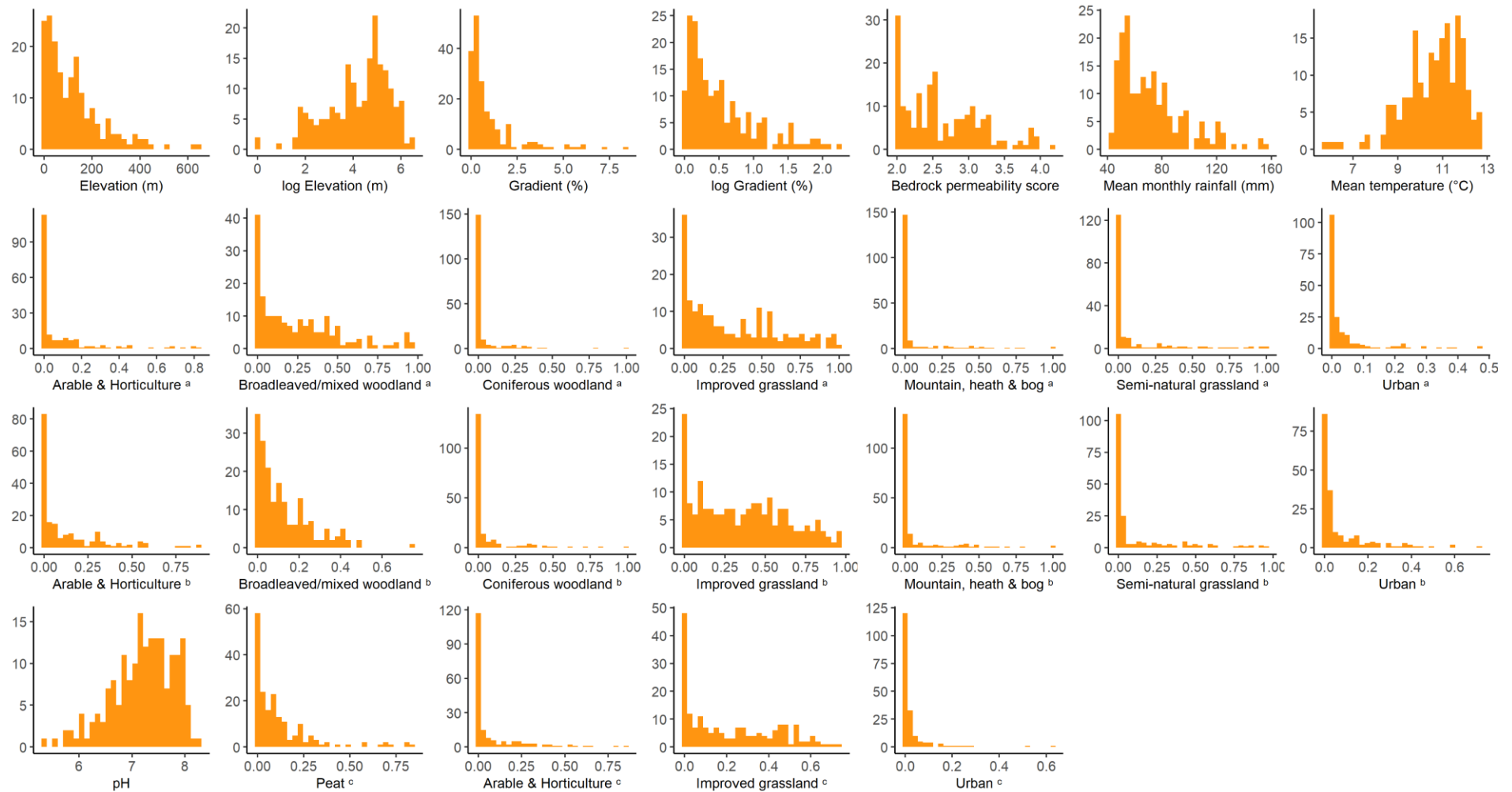


Figure A2.3-3: Histograms of explanatory variable values for Common Sandpiper. Both un-transformed and log-transformed plots are included for elevation and gradient. ^a proportion of 50m buffer area, ^b proportion of 500m buffer area, ^c proportion of upstream catchment area.

Appendix 2.4: Effect of survey effort on occupancy and abundance

Linear models were used to explore how both response variables (occupancy and abundance) were associated with survey effort (number of transects). Both models indicate that increased survey effort results in increased likelihood of observing a bird (Figure A2.4-1A and Table A2.4-1) and of observing more birds (Figure A2.4-1B and Table A2.4-2).

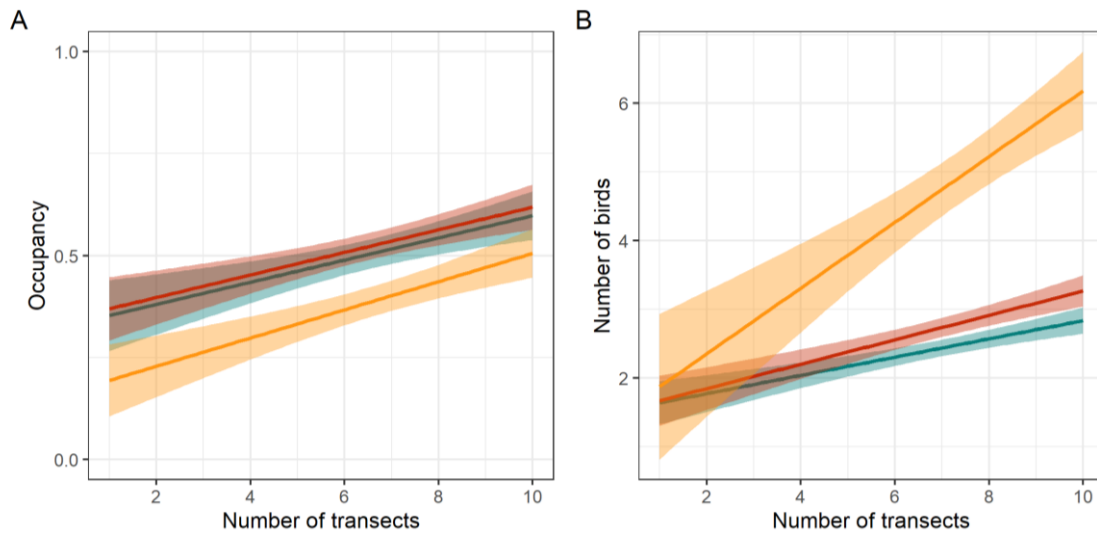


Figure A2.4-1: Linear association between survey effort and (A) occupancy and (B) abundance. Blue = Dipper; red = Grey Wagtail; orange = Common Sandpiper.

Table A2.4-1: LM output for occupancy and survey effort of the three species. SE = Std. Error. RMSE = Root Mean Squared Error.

	Dipper				Grey Wagtail				Common Sandpiper			
Predictors	Estimate	SE	z	p	Estimate	SE	z	p	Estimate	SE	z	p
(Intercept)	0.326	0.051	6.424	<0.001	0.342	0.045	7.516	<0.001	0.159	0.052	3.092	<0.01
N transects	0.027	0.007	3.802	<0.001	0.028	0.007	4.260	<0.001	0.035	0.007	4.818	<0.001
Observations	736				850				649			
R ² (adjusted)	0.019 (0.018)				0.020 (0.019)				0.034 (0.033)			
RMSE	0.495				0.494				0.479			

Table A2.4-2: LM output for abundance and survey effort of the three species. SE = Std. Error. RMSE = Root Mean Squared Error.

	Dipper				Grey Wagtail				Common Sandpiper			
Predictors	Estimate	SE	z	p	Estimate	SE	z	p	Estimate	SE	z	p
(Intercept)	1.506	0.183	8.245	<0.001	1.490	0.212	7.013	<0.001	1.394	0.615	2.268	<0.05
N transects	0.133	0.025	5.356	<0.001	0.178	0.029	6.086	<0.001	0.479	0.080	6.014	<0.001
Observations	743				905				497			
R ² (adjusted)	0.037 (0.036)				0.039 (0.038)				0.068 (0.066)			
RMSE	1.657				2.109				4.369			

Appendix 2.5: Buffer sizes for land cover variables by species

Table A2.5-1: Details of reach level land cover buffer sizes for each species. Spatial scales (50/500m) for each land cover type and species were selected based on the highest R^2 value from univariate models. Variables with the same R^2 for both buffer sizes were both tested in the appropriate multivariate model, then selected based on highest pseudo- R^2 if all VIFs were <5 .

Land cover type	Dipper	Grey Wagtail	Common Sandpiper
Occupancy model			
Arable and horticulture	500m	500m	500m
Broadleaved/mixed woodland	50m	50m	50m
Coniferous woodland	50m	500m	50m
Improved grassland	50m	50m	500m
Mountain, heath and Bog	500m	50m	500m
Semi-natural grassland	500m	500m	500m
Urban	500m	50m	500m
Abundance model			
Arable and horticulture	50m	500m	500m
Broadleaved/mixed woodland	50m	500m	500m
Coniferous woodland	500m	500m	50m
Improved grassland	50m	50m	500m
Mountain, heath and Bog	500m	500m	500m
Semi-natural grassland	500m	50m	50m
Urban	500m	50m	500m

Appendix 2.6: Correlation test results

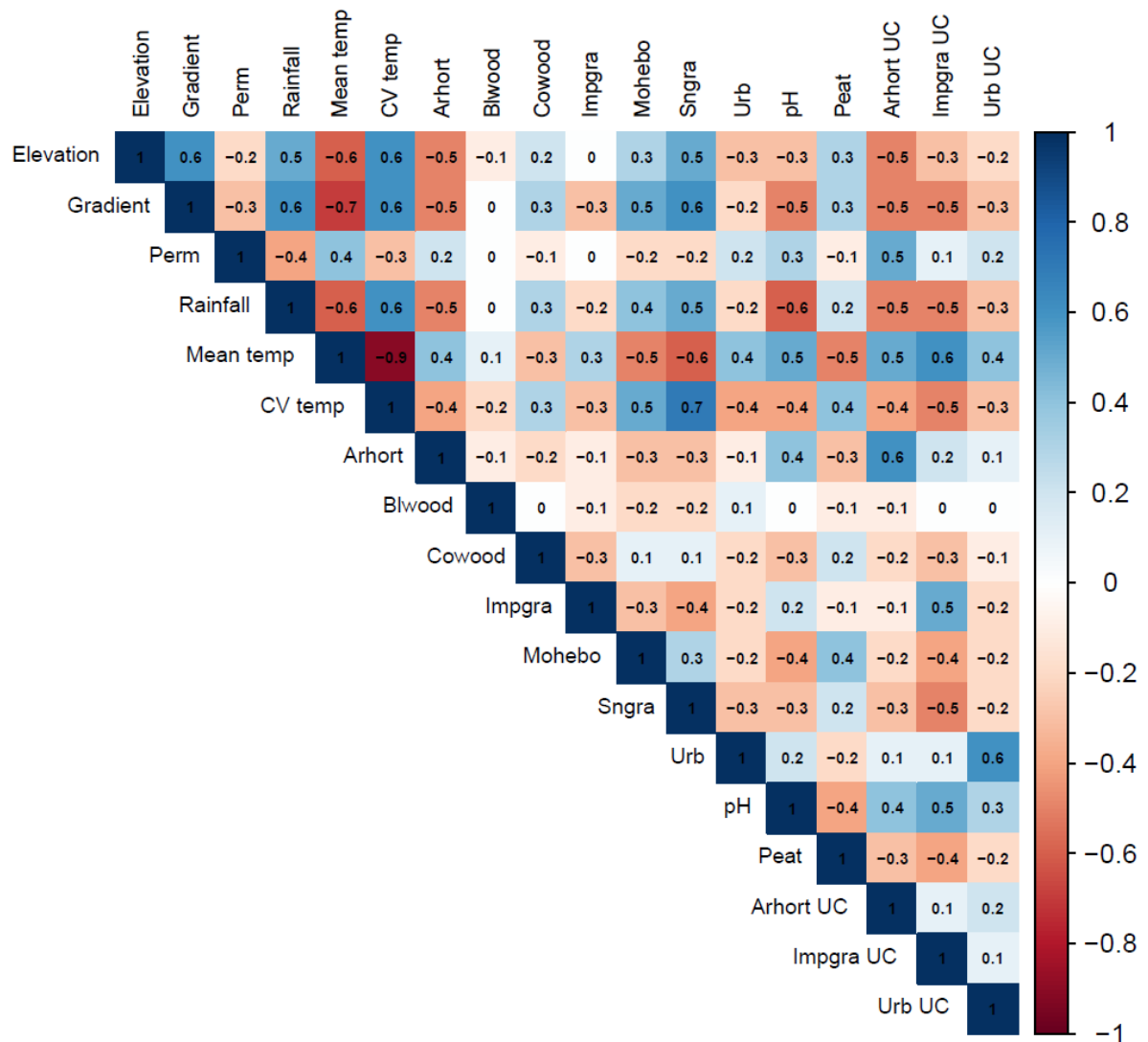


Figure A2.6-1: Correlation plot of explanatory variables at sites in the bird survey data. Perm = bedrock permeability, CV temp = coefficient of variation in temperature, Arhort = arable & horticulture, Blwood = broadleaved/mixed woodland, Cowood = coniferous woodland, Impgra = improved grassland, Mohebo = mountain, heath & bog, Sngra = semi-natural grassland, Urb = urban.

Appendix 2.7: Model structures

Table A2.7-1: Final multivariate occupancy model structures. Variables are shown in *italics*: *perm* = bedrock permeability, *temp* = temperature, *rain* = precipitation, *arhort* = arable & horticulture, *blwood* = broadleaved/mixed woodland, *cowood* = coniferous woodland, *impgra* = improved grassland, *mohebo* = mountain, heath & bog, *sngra* = semi-natural grassland, *urb* = urban. Models produced using *glmmTMB* (Brooks et al., 2017).

Dipper	Occupancy ~	offset(log(<i>n transects</i>) + year + poly(log <i>slope</i> , 2, raw=T) + <i>perm</i> + <i>temp</i> + <i>rain</i> + <i>arhort</i> + <i>blwood</i> + <i>cowood</i> + <i>impgra</i> + <i>mohebo</i> + <i>sngra</i> + <i>urb</i> + <i>pH</i> + <i>peat</i> + <i>arhort UC</i> + <i>impgra UC</i> + <i>urb UC</i> + (1 <i>site</i>), family = binomial(link = "cloglog")
Grey Wagtail	Occupancy ~	offset(log(<i>n transects</i>) + year + log <i>slope</i> + <i>perm</i> + <i>temp</i> + <i>rain</i> + <i>arhort</i> + <i>blwood</i> + <i>cowood</i> + <i>impgra</i> + <i>mohebo</i> + <i>sngra</i> + <i>urb</i> + <i>pH</i> + <i>peat</i> + <i>arhort UC</i> + <i>impgra UC</i> + <i>urb UC</i> + (1 <i>site</i>), family = binomial(link = "cloglog")
Common Sandpiper	Occupancy ~	offset(log(<i>n transects</i>) + year + <i>slope</i> + <i>perm</i> + <i>temp</i> + <i>rain</i> + <i>arhort</i> + <i>blwood</i> + <i>cowood</i> + <i>mohebo</i> + <i>urb</i> + <i>pH</i> + <i>peat</i> + <i>arhort UC</i> + <i>impgra UC</i> + <i>urb UC</i> + (1 <i>site</i>), family = binomial(link = "cloglog")

Table A2.7-2: Final multivariate abundance model structures. Variables are shown in *italics*: *perm* = bedrock permeability, *temp* = temperature, *rain* = precipitation, *arhort* = arable & horticulture, *blwood* = broadleaved/mixed woodland, *cowood* = coniferous woodland, *impgra* = improved grassland, *mohebo* = mountain, heath & bog, *sngra* = semi-natural grassland, *urb* = urban. Models produced using *glmmTMB* (Brooks et al., 2017).

Dipper	<i>N birds</i> ~	offset(log(<i>n transects</i>) + year + survey + log <i>slope</i> + <i>perm</i> + <i>temp</i> + <i>rain</i> + <i>arhort</i> + <i>blwood</i> + <i>cowood</i> + <i>impgra</i> + <i>mohebo</i> + <i>sngra</i> + <i>urb</i> + <i>pH</i> + <i>peat</i> + <i>arhort UC</i> + <i>impgra UC</i> + <i>urb UC</i> + (1 <i>site</i>), family = poisson(link = "log")
Grey Wagtail	<i>N birds</i> ~	offset(log(<i>n transects</i>) + year + survey + log <i>slope</i> + <i>perm</i> + <i>temp</i> + <i>rain</i> + <i>arhort</i> + <i>blwood</i> + <i>cowood</i> + <i>impgra</i> + <i>mohebo</i> + <i>sngra</i> + <i>urb</i> + <i>pH</i> + <i>peat</i> + <i>arhort UC</i> + <i>impgra UC</i> + <i>urb UC</i> + (1 <i>site</i>), family = poisson (link = "log")
Common Sandpiper	<i>N birds</i> ~	offset(log(<i>n transects</i>) + year + survey + <i>slope</i> + <i>perm</i> + <i>temp</i> + <i>rain</i> + <i>arhort</i> + <i>blwood</i> + <i>cowood</i> + <i>impgra</i> + <i>mohebo</i> + <i>sngra</i> + <i>urb</i> + <i>pH</i> + <i>peat</i> + <i>arhort UC</i> + <i>impgra UC</i> + <i>urb UC</i> + (1 <i>site</i>), family = poisson (link = "log")

Appendix 2.8: Model outputs

Table A2.8-1: GLMM output for occupancy by species. Risk ratios: >1 = positive effect; <1 = negative effect; ^a proportion of buffer area (50/500m), ^b proportion of upstream catchment area. Nuisance fixed effects (year) are shown in italics. Intraclass correlation coefficient (ICC) and pseudo R^2 values are calculated with the performance package (Lüdtke et al., 2021).

Predictors	Dipper				Grey Wagtail				Common Sandpiper			
	Risk Ratios	std. Error	z	p	Risk Ratios	std. Error	z	p	Risk Ratios	std. Error	z	p
Intercept	0.09	0.04	-5.66	<0.001	0.11	0.03	-9.70	<0.001	0.004	0.004	-6.53	<0.001
<i>Year [2014]</i>	<i>2.43</i>	<i>0.88</i>	<i>2.46</i>	<i><0.05</i>	<i>1.15</i>	<i>0.30</i>	<i>0.55</i>	<i>0.581</i>	<i>2.13</i>	<i>0.97</i>	<i>1.66</i>	<i>0.096</i>
<i>Year [2015]</i>	<i>2.21</i>	<i>0.80</i>	<i>2.19</i>	<i><0.05</i>	<i>1.50</i>	<i>0.38</i>	<i>1.60</i>	<i>0.110</i>	<i>1.45</i>	<i>0.69</i>	<i>0.79</i>	<i>0.430</i>
<i>Year [2016]</i>	<i>1.49</i>	<i>0.53</i>	<i>1.12</i>	<i>0.262</i>	<i>1.37</i>	<i>0.33</i>	<i>1.29</i>	<i>0.196</i>	<i>0.76</i>	<i>0.33</i>	<i>-0.63</i>	<i>0.529</i>
<i>Year [2017]</i>	<i>1.34</i>	<i>0.49</i>	<i>0.82</i>	<i>0.415</i>	<i>1.42</i>	<i>0.35</i>	<i>1.42</i>	<i>0.155</i>	<i>1.23</i>	<i>0.56</i>	<i>0.45</i>	<i>0.656</i>
Gradient	31.05	20.30	5.26	<0.001	4.60	1.36	5.14	<0.001	0.11	0.06	-3.77	<0.001
Gradient ²	0.30	0.07	-5.53	<0.001								
Bedrock permeability	1.39	0.50	0.91	0.361	1.73	0.26	3.71	<0.001	1.31	0.57	0.63	0.527
Mean monthly rainfall (mm)	0.59	0.20	-1.54	0.124	0.81	0.20	-0.87	0.384	0.18	0.10	-3.13	<0.01
Mean temperature (°C)	0.61	0.28	-1.08	0.279	1.67	0.48	1.80	0.072	0.14	0.10	-2.88	<0.01
Arable and Horticulture ^a	0.39	0.22	-1.71	0.088	0.70	0.15	-1.66	0.096	1.38	1.04	0.42	0.674
Broadleaved/mixed woodland ^a	1.79	0.49	2.13	<0.05	1.87	0.41	2.88	<0.01	0.30	0.15	-2.50	<0.05
Coniferous woodland ^a	0.94	0.36	-0.15	0.878	2.15	0.54	3.03	<0.01	0.48	0.16	-2.17	<0.05
Improved grassland ^a	0.74	0.29	-0.78	0.434	0.91	0.19	-0.44	0.661				
Mountain, heath and bog ^a	0.58	0.16	-2.00	<0.05	0.57	0.13	-2.55	<0.05	2.36	1.14	1.78	0.075
Semi-natural grassland ^a	0.76	0.26	-0.83	0.407	0.95	0.24	-0.20	0.843				
Urban ^a	0.75	0.25	-0.84	0.400	1.21	0.18	1.30	0.194	1.07	0.69	0.11	0.914
pH	1.25	0.38	0.73	0.469	0.81	0.15	-1.18	0.238	0.78	0.32	-0.61	0.543
Peat (UC) ^b	0.40	0.13	-2.79	<0.01	1.54	0.36	1.85	0.064	0.27	0.13	-2.71	<0.01
Arable and Horticulture ^b	0.10	0.06	-3.53	<0.001	0.60	0.13	-2.33	<0.05	0.01	0.02	-3.07	<0.01
Improved grassland ^b	1.42	0.58	0.87	0.387	1.31	0.30	1.19	0.234	0.05	0.04	-3.74	<0.001
Urban ^b	0.50	0.23	-1.49	0.137	0.85	0.13	-1.09	0.276	0.17	0.27	-1.12	0.262
Random Effects												
σ^2		1.65				1.65				1.65		
τ_{00}		6.94 _{site}				2.02 _{site}				9.09 _{site}		
ICC		0.81				0.55				0.85		
N		210 _{site}				251 _{site}				181 _{site}		
Observations		736				872				653		
R^2 (marginal/conditional)		0.663/0.936				0.556/0.801				0.709/0.955		
RMSE		0.203				0.271				0.177		

Table A2.8-2: GLMM output for abundance by species. Risk ratios: >1 = positive effect; <1 = negative effect; ^a proportion of buffer area (50/500m), ^b proportion of upstream catchment area. Nuisance fixed effects are shown in *italics*. Intraclass correlation coefficient (ICC) and pseudo R² values are calculated with the performance package (Lüdtke et al., 2021).

Predictors	Dipper				Grey Wagtail				Common Sandpiper			
	Risk Ratios	std. Error	z	p	Risk Ratios	std. Error	z	p	Risk Ratios	std. Error	z	p
Intercept	0.28	0.03	-12.81	<0.001	0.26	0.02	-19.14	<0.001	0.23	0.04	-9.27	<0.001
<i>Year [2014]</i>	1.08	0.09	0.98	0.328	1.08	0.08	1.03	0.303	1.00	0.07	-0.07	0.945
<i>Year [2015]</i>	1.16	0.09	1.92	0.054	1.23	0.09	2.89	<0.01	1.13	0.08	1.85	0.065
<i>Year [2016]</i>	1.06	0.08	0.70	0.487	1.28	0.09	3.44	<0.01	1.04	0.07	0.54	0.589
<i>Year [2017]</i>	1.14	0.09	1.65	0.099	1.24	0.09	3.00	<0.01	1.04	0.07	0.54	0.591
<i>Visit (L)</i>	0.88	0.04	-2.64	<0.01	1.16	0.05	3.66	<0.001	1.00	0.04	-0.06	0.956
Gradient	1.11	0.07	1.75	0.081	1.04	0.06	0.69	0.491	0.82	0.07	-2.35	<0.05
Bedrock permeability	1.05	0.06	0.84	0.402	1.06	0.05	1.32	0.187	1.01	0.10	0.05	0.963
Mean monthly rainfall (mm)	0.95	0.06	-0.79	0.427	0.90	0.06	-1.62	0.105	0.82	0.08	-2.21	<0.05
Mean temperature (°C)	0.91	0.07	-1.21	0.225	1.06	0.08	0.73	0.465	0.98	0.13	-0.18	0.861
Arable & Horticulture ^a	0.86	0.09	-1.51	0.131	0.91	0.07	-1.25	0.211	0.79	0.12	-1.55	0.121
Broadleaved/mixed woodland ^a	1.13	0.07	2.01	<0.05	1.15	0.06	2.79	<0.01	0.86	0.09	-1.43	0.152
Coniferous woodland ^a	0.96	0.05	-0.88	0.38	1.07	0.04	1.87	0.061	0.88	0.07	-1.61	0.107
Improved grassland ^a	1.01	0.07	0.19	0.851	0.97	0.06	-0.51	0.609	0.85	0.10	-1.41	0.159
Mountain, heath & bog ^a	0.89	0.06	-1.92	0.055	1.00	0.06	0.05	0.960	1.02	0.08	0.29	0.771
Semi-natural grassland ^a	0.97	0.07	-0.40	0.688	1.05	0.07	0.80	0.425	0.90	0.09	-1.11	0.266
Urban ^a	1.05	0.08	0.62	0.537	1.07	0.05	1.40	0.162	0.72	0.13	-1.81	0.070
pH	1.04	0.06	0.73	0.466	0.97	0.05	-0.68	0.496	1.01	0.07	0.19	0.853
Peat (UC) ^b	0.90	0.05	-1.89	0.059	0.94	0.05	-1.27	0.206	0.97	0.07	-0.50	0.620
Arable and Horticulture (UC) ^b	0.87	0.14	-0.87	0.386	0.82	0.06	-2.83	<0.01	0.51	0.16	-2.13	<0.05
Improved grassland (UC) ^b	0.94	0.06	-0.88	0.379	0.94	0.06	-1.01	0.314	0.76	0.11	-1.93	0.053
Urban (UC) ^b	1.06	0.19	0.30	0.765	0.95	0.05	-0.99	0.322	0.86	0.21	-0.65	0.515
Random Effects												
σ ²	1.403				1.345				1.198			
τ ₀₀	0.120 _{site}				0.142 _{site}				0.294 _{site}			
ICC	0.079				0.096				0.197			
N	140 _{site}				201 _{site}				105 _{site}			
Observations	743				905				497			
R ² (marginal/conditional)	0.048/0.123				0.059/0.149				0.114/0.289			
RMSE	1.294				1.485				2.313			

CHAPTER 3: IS THE ABUNDANCE OF RIVERINE BIRDS INFLUENCED BY WEATHER CONDITIONS?

3.1. Abstract

Climate change and abnormal or extreme weather conditions have the potential to impose temporary or long-term pressures on populations across multiple trophic levels. High temperatures and heavy rainfall events are projected to rise in frequency, duration and/or magnitude in the future, raising additional concerns for biodiversity and conservation, particularly in riverine ecosystems. As predators, riverine birds are significantly exposed to climate and weather effects, whether through direct impacts on behaviour, condition, reproductive success, or mortality, or indirectly via effects on their prey and habitat. This study utilises long-term (1998-2019) monitoring data collected throughout Britain to compare the sensitivity of three declining riverine species (White-throated Dipper, Grey Wagtail and Common Sandpiper) to a selection of temperature and rainfall indices at their breeding sites and identify the species-specific weather-based drivers of abundance. All three species displayed some sensitivity to weather conditions, particularly events in the winter preceding the breeding season, even when some birds are yet to arrive at their breeding site. Grey Wagtail displayed the greatest overall sensitivity, responding negatively to both hard or warm ($>15^{\circ}\text{C}$) winters and wet breeding seasons. Common Sandpiper were sensitive to implied flow conditions, their abundance benefitting from wet winters preceding the breeding season and wet conditions during breeding. Dipper proved the least weather-sensitive, but breeding abundance was significantly reduced following cold and/or very wet winters. These results suggest that weather conditions impose direct and indirect pressures on breeding riverine bird populations, and that the focal species suitably indicate some impacts of varying weather conditions on riverine ecosystems, with potential extension to abnormal or extreme events and climate change. Weather and climate extremes are inherently difficult to predict, but management strategies such as the restoration and expansion of riparian zones may help alleviate their impacts on multiple trophic levels in rivers.

3.2. Introduction

Climate is a well-recognised driver of riverine ecosystem processes through its influence on thermal and hydrological regimes (Pletterbauer, Melcher & Graf, 2018). Both changes in long-term average climate or incidence of abnormal/extreme weather events (i.e. abnormal departures in magnitude or duration of rainfall or temperature) have the potential to disrupt processes by shifting local conditions outside their typical range for, with consequences for exposed biota.

Annual average temperatures in Europe have warmed more than the global average since 1950, alongside increased frequency in high temperature extremes (e.g. hot days, heat waves) and reduced frequency of hard winters (Prior & Kendon, 2011; EEA, 2012). Over the same period, annual precipitation has increased by up to 70mm/decade in Northern Europe, with increased variability and magnitude (EEA, 2012). Similar patterns of warming and increased frequency of high temperature extremes have been observed for the UK, alongside regional increases in annual mean rainfall and extreme heavy daily rainfall (Slingo, 2021). While research indicates significant impacts of climate change on riverine ecosystems, there is evidence that abnormal or extreme events may have greater consequences for population performance than change in long-term average climate conditions (Sabater et al., 2023).

As predators with relatively high positions in aquatic food webs, variation in weather and climate conditions will likely affect riverine birds, whether as direct impacts on behaviour, condition, reproductive success, or mortality, or via indirect effects on their prey and habitat. Warming temperatures or heat waves may cause acute impacts (e.g. hyperthermia, dehydration, body mass loss; McKechnie, 2019) whereby individuals are forced outside their tolerance limits, but many responses are sub-acute and medium-to-long term, expressed as distributional (i.e. latitudinal or elevational) and phenological shifts (e.g. earlier lay dates) where birds attempt to maximise access to available resources. Any miscuing (inappropriate/lack of response) or disjunction (asynchrony with the environment) has consequences for breeding, such as more variable clutch and brood sizes, reduced provisioning and growth rates of nestlings, and highly variable survival of fledglings (Crick & Sparks, 1999; Crick, 2004; Sauve, Friesen & Charmantier, 2021). While freezing conditions may reverse or cause similar impacts to those of warming (Cohen, Fink & Zuckerberg, 2021), they also reduce body condition and survival rates in river birds by limiting access to aquatic food resources due to ice formation (e.g. White-throated Dipper [henceforth Dipper], *Cinclus cinclus*, and Common Kingfisher, *Alcedo atthis*; Nilsson et al., 2011; Rubáčová et al., 2021). Furthermore, temporary or prolonged spate flows may reduce foraging efficiency through increasing water depth, velocity, turbidity and colour (e.g. Dipper; Da Prato, 1981; D'Amico & Hémery, 2007), force a change in foraging behaviour (e.g. switch from river shallows to aerial prey in Grey Wagtail, *Motacilla cinerea*), and reduce survival, particularly of first-year Dippers (Chiu et al., 2008).

The indirect effects of weather and climate on riverine birds are no less consequential for survival and breeding. Rainfall that translates into spate flows may reduce the availability of aquatic prey due to bed movement and wash out or temporary redistribution of benthic organisms (Theodoropoulos et al., 2017), reduce access to foraging habitat (e.g. exposed gravel beds for Common Sandpiper, *Actitis hypoleucos*; Yalden, 1985, 1986), and reduce availability, access to and viability of natural or manmade nest sites (Alder, 1963; Tyler & Ormerod, 1994; Wilson, 1996; Elas, Rosendal & Meissner, 2023). Conversely, drought conditions reduce the wetted channel area,

which lowers dissolved oxygen whilst increasing aquatic prey competition, predation, and vulnerability to temperature extremes (Dewson, James & Death, 2007). As temperature regulates development, reproduction, emergence and community structure of both aquatic and terrestrial invertebrates, small shifts in temperature may have significant effects on prey abundance and richness (Daufresne et al., 2004; Durance & Ormerod, 2007; Forrest, 2016; Finn et al., 2022; Gebert et al., 2022), which in turn will likely impact site choice, timing and breeding success in riverine birds.

As extremes in temperature and rainfall are predicted to increase in both frequency and magnitude (IPCC, 2023), there is an urgent need to understand how birds respond to temporary or prolonged changes in weather conditions, particularly for those species that may act as indicators of riverine ecosystem health or quality. Species such as Dipper, Grey Wagtail and Common Sandpiper have undergone population declines over the last few decades (Heywood et al., 2023). Similar trends have been reported in other freshwater vertebrate taxa (He et al., 2019; WWF, 2022), suggesting an ecosystem level decline, but it is not clear to what extent observed declines are the result of gradual pressure (i.e. long-term change in average climate), abrupt disturbances (i.e. extreme events), or both. Previous studies have identified changes in population dynamics (Sæther et al., 2000; Pearce-Higgins et al., 2009; Nilsson et al., 2011; Chiu et al., 2013) and distributions (Royan et al., 2013, 2014, 2015) of these focal species in response to local or large-scale variation in climatic conditions. However, little is known about the effects of local weather conditions on their breeding populations. This study uses long-term monitoring data to (1) compare the sensitivity of breeding abundance of three riverine species (Dipper, Grey Wagtail and Common Sandpiper) to a selection of temperature and rainfall indices at breeding sites, and (2) identify the significant species-specific weather-based drivers of abundance. As these species represent different foraging, nesting, and development (i.e. altricial vs. precocial) strategies for utilising rivers during the breeding season, convergent responses to conditions may guide management approaches that alleviate the impacts of abnormal/extreme weather events on riverine biodiversity, with potential extension to moderate against longer-term impacts of climate change.

3.3. Methods

3.3.1. Bird survey data

Data were obtained from the Waterways Breeding Bird Survey (WBBS), an annual survey of UK birds conducted by experienced citizen scientists since 1998 and coordinated by the British Trust for Ornithology (BTO). Survey sites consist of between one and ten 500m linear transects positioned along a single watercourse (river or canal) within a 2x2 km tetrad selected through stratified random sampling. Observers record all adult bird sightings within 100m of each transect

and note the number of transects walked, allowing survey effort to be quantified. Each site is surveyed twice per year during the breeding season (April to mid-May [Early; E] and mid-May to late June [Late: L]).

Data were extracted for Britain from 1998 to 2019, with the exception of 2001; this was excluded from analysis due to the livestock foot-and-mouth epidemic, which restricted countryside access and survey completion that year. For each species, WBBS survey sites were selected based on the following criteria: (1) site could be geolocated (e.g. vector shapefile of transects or coordinates of survey start and end point); (2) site did not contain a section of canal (identified through visual checks on satellite imagery); and (3) site was located within any of the 100km grid squares that contained at least two 'confirmed' breeding pairs according to the 2007-11 Breeding Birds Atlas, to reduce the risk of false zeros caused by sampling outside each species' known breeding range (Balmer et al., 2013). Furthermore, any sites positioned within 1km of another site on the same river were limited to one representative site by retaining the most downstream site. In the case of two rivers (River Derwent/Noe and River Lune, both located in England) that had multiple survey sites positioned consecutively (five and seven respectively), two sites on each were retained: the furthest downstream site, and one upstream site located above a confluence.

Sites were considered occupied by the focal species (and therefore included in analysis) if one or more birds were observed there in at least three years over the 21-year period. Zero counts were included at occupied sites to allow for detection of potential short- or long-term absence due to climatic conditions. To determine the response variable (abundance), bird counts across all transects at a site were pooled by species to give the total number of birds observed on a given survey. Individual visits at each site for each year and species were treated separately, totalling 12,848 records. Any site survey years based on only a single transect (500m; $n = 101$) were excluded from analysis to reduce the risk of false zeros created by surveying only a small proportion of the average territory length of the focal species (1.2 - 3.5km; Tyler, 1972; Vickery, 1991). Across the data, this resulted in 262 sites available for analysis (median length 3.5 km, range 1.0 – 5.0 km; Figure 3.1).

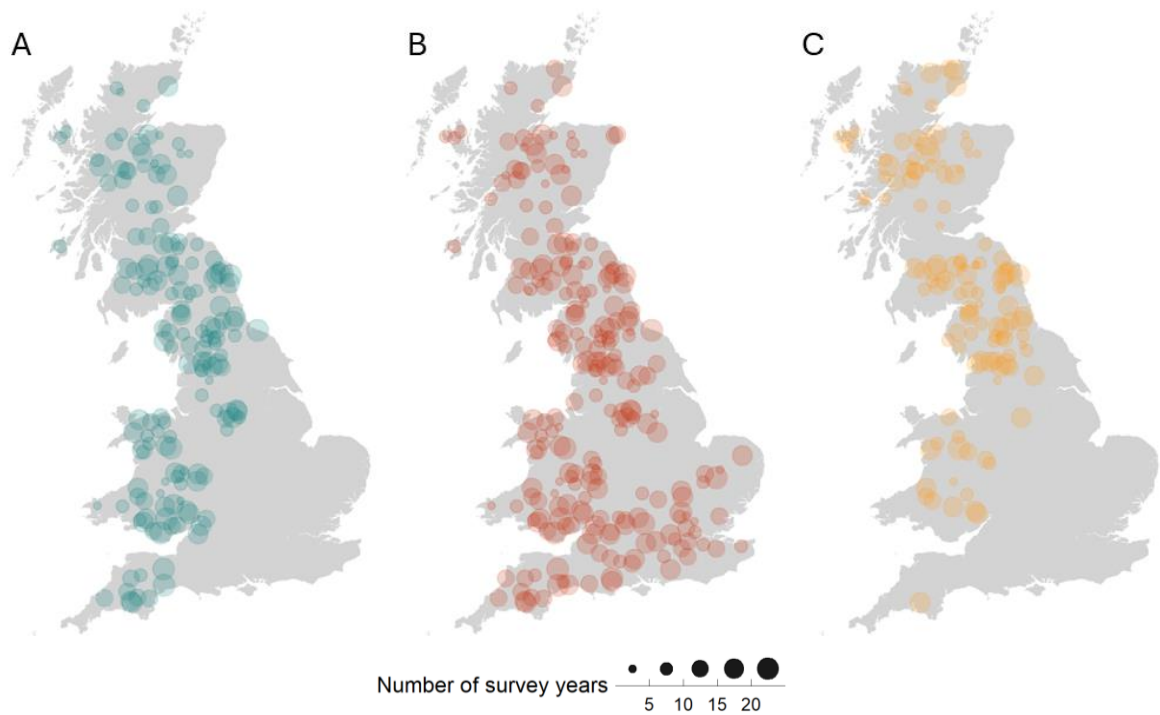


Figure 3.1: Maps showing the site locations that are included in each species' dataset. (A) Dipper, $n=165$ sites, (B) Grey Wagtail, $n=232$, and (C) Common Sandpiper, $n=121$. Points are scaled by the number of years in which each individual site was surveyed.

3.3.2. Weather data

Temperature and rainfall variables were considered *a priori* as likely to have an impact on riverine birds both directly and indirectly, then selected from the candidate set of indices developed by the Expert Team on Climate Change Detection and Indices (ETCCDI; Klein Tank, Zwiers & Zhang, 2009). Daily total rainfall (mm), minimum and maximum temperatures were extracted from the Met Office Had-UK 1km gridded climate database (Appendix 3.1; Met Office et al., 2018) for each site midpoint using the *tidync* package in R (Sumner, 2022; R Core Team, 2023). Five variables for both temperature and rainfall (Table 3.1) were calculated for the preceding winter (December to March inclusive) and for the months covering the bird survey period (April to June inclusive) for each of the individual years surveyed. Indices used as proxies for winter conditions may affect populations of Dipper and Grey Wagtail both directly and indirectly as birds are potentially present at survey sites year-round (though both species are recognised as partial migrants, particularly along elevational gradients; Sharrock, 1969; Tyler & Ormerod, 1994; Sikora & Neubauer, 2018). In contrast, it is expected that winter conditions extracted at the site level will only affect Common Sandpiper indirectly through changes to the riverine ecosystem, as this species migrates to Britain to breed after over-wintering in Southern Europe and Africa (Dougall, Holland & Yalden, 2010; Summers et al., 2019).

Table 3.1: Temperature and rainfall variables considered for analysis. Variables were selected from the candidate set of indices developed by the Expert Team on Climate Change Detection and Indices (ETCCDI; Klein Tank, Zwiers & Zhang, 2009). Variables are calculated by site and year, divided into four groups: winter rainfall, winter temperature, breeding rainfall and breeding temperature.

Variable	Variable name	Description	Winter (December - March)		Breeding (April – June)	
			Mean (range)	Ecological significance	Mean (range)	Ecological significance
Rainfall						
Rx1day	Max 1-day rainfall	Maximum rainfall (mm) in any single day over the season.	28.9 mm (5 - 147)	Spate flows in the winter preceding a given breeding season could reduce aquatic prey availability in the spring, or have other relevant effects (e.g. loss of aquatic mosses, increased sediment transport, creation of bare sediment etc; Yalden, 1985; Theodoropoulos et al., 2017). They may also reduce foraging efficiency and recruitment in Dipper populations (Da Prato, 1981; D’Amico & Hémery, 2007; Chiu et al., 2013).	24.9mm (6 - 116)	Spates or excessive rain during breeding may affect foraging ability (and thus nestling provision; (Da Prato, 1981; Bures, 1995; D’Amico & Hémery, 2007), adjust channel substrate (sediment transport; Lake, 2000) or remove nests positioned close to the normal flow for all focal species (Tyler, 1972; Nilsson et al., 2020b; Elas, Rosendal & Meissner, 2023).
DD	Dry days	Number of days in the season with < 1mm rainfall.	65.3 days (14 - 101)		56.7 days (25 - 79)	
CDD	Consecutive dry days	Maximum number of consecutive days in the season with <1mm rainfall.	14 days (3 - 35)		14.8 days (5 - 37)	
R10mm	Days >10mm rainfall	Number of days in the season where daily rainfall exceeded 10mm.	12.5 days (0 - 67)		5.9 days (0 - 27)	
CWD	Consecutive wet days	Maximum number of consecutive days in the season with ≥1mm rainfall.	10.6 days (2 - 44)		7.3 days (2 - 28)	
Temperature						
Tx	Absolute maximum temperature	Maximum observed temperature (°C) across the season.	15.5°C (6.8 – 22.7)	Temperature may affect availability and quality of prey, mainly through timing of emergence in both aquatic and terrestrial prey (Daufresne et al., 2004; Durance & Ormerod, 2007; Forrest, 2016; Finn et al., 2022; Gebert et al., 2022). Freezing temperatures may prevent access to aquatic prey (due to ice) and reduce aerial prey activity, consequently reducing survival rates in Dipper (Nilsson et al., 2011) and Grey Wagtail (Tyler & Ormerod, 1991; Bures, 1995) respectively.	25.4°C (15.9 – 33.3)	See winter temperature.
Tn	Absolute minimum temperature	Minimum observed temperature (°C) across the season.	-6.7°C (-15.9 – 0.6)		-1.8°C (-9.5 – 3.7)	
DTR	Mean diurnal temperature range	Mean difference between the maximum and minimum daily temperature in the season.	6.4°C (4.1 – 8.9)		9.0°C (4.9 – 13.1)	Temperature may also affect breeding performance, with warmer temperatures resulting in earlier lay dates, more variable clutch and brood sizes, and highly variable survival (Crick & Sparks, 1999; Crick, 2004; Sauve, Friesen & Charmantier, 2021).
HD	Hot days	Number of days in the season with a maximum temperature of >15°C (winter) or >25°C (breeding).	2.3 days (0 - 16)		1.9 days (0 - 19)	
FD	Frost days	Number of days in the season with a minimum temperature of <=0°C.	40 days (0 – 113)		4.7 days (0 - 42)	

3.3.3. Modelling approach

All analyses were completed in R (version 4.3.0; R Core Team, 2023).

3.3.3.1. Species abundance trend models

Due to complexity in the WBBS data (heterogeneity in survey effort, high frequency of zeros), an initial analysis was completed to identify the presence of trends in species abundance over time, which utilised bivariate Generalized Additive Models for Location, Scale and Shape (GAMLSS; Rigby & Stasinopoulos, 2005; Rigby et al., 2017). This framework can flexibly combine linear, smoothed, and random terms in the same model, whilst utilising a broad range of model distributions not available in other GAM packages (e.g. *mgcv*; Wood, 2017). While a poisson and negative binomial distribution were considered for analysis, a zero-inflated poisson (ZIP) distribution was more appropriate as it accounts for the high number of zero-value observations in the WBBS data. Individual GAMLSS models were run for each species. In all models, year was defined with cubic smoothing splines with fixed degrees of freedom depending on a manual GAIC (Generalized Akaike Information Criterion) minimization technique (see Appendix 3.2). Survey timing (E/L) was included as a nuisance fixed linear effect to control for differences in detection and observed numbers across the survey period (April-June). The number of 500m transects was included as an offset to control for heterogeneity in survey effort (Appendix 3.3). Site was included as a random effect to account for non-independence of repeat surveys at the same location.

3.3.3.2. Detrending models

All temperature and rainfall variables were scaled and centred prior to analysis, then visually assessed for the presence of trends over the 21-year study period (Appendix 3.4). To reduce the risk of spurious associations between species abundance and weather indices due to observed underlying trends caused by temporal autocorrelation, we removed the linear trend from both response and predictor variables, then used yearly residuals for analysis (process described in Appendix 3.5). The inclusion of the offset (number of 500m transects) in the abundance detrending model standardises the data on both year and survey effort, resulting in non-zero bounded continuous response variable. This allows the use of Generalised Additive Mixed Models (GAMMs; *mgcv* package; Wood, 2017) for all subsequent analyses.

3.3.3.3. Weather models

All GAMMs were defined with cubic splines, with additional penalisation on the smoothing process via the shrinkage method (Wood, 2017); this allows both the range (wiggly) and null (smoothed) spaces to be penalised, allowing identification of terms that do not affect the model

(0 effective degrees of freedom). To ensure reasonable interpretation, the effective degrees of freedom (edf) were set at a maximum of four for each variable, with smoothing parameter estimation allowed via the Restricted Maximum Likelihood (REML) method. Survey timing (E/L) was included as a nuisance fixed linear effect to control for differences in detection and observed numbers across the survey period (April-June). Site and year were included as random effects to account for non-independence of repeat surveys at the same location and differences in survey years between sites respectively.

An initial set of univariate GAMMs were run between every weather variable and bird abundance by species to assess associations independent of the other indices (Appendix 3.6). Based on these models, species sensitivity to each weather index was categorised as having a predominantly positive or negative impact on breeding abundance based on the region of response showing the least uncertainty. Non-significant values were omitted to focus solely on significant or marginal (<0.1) relationships.

Multivariate GAMMs were then used to identify the species-specific responses to weather indices. Using the univariate model results as a guide, two indices from each variable group (i.e. winter rainfall, winter temperature, breeding rainfall, breeding temperature) were selected for inclusion in the multivariate model, provided they had a positive edf value (i.e. $\text{edf} > 0$, which indicates a measurable response, even if non-significant). Selection was allowed to vary between species. In variable groups where only one index had a positive edf, no second index was selected. In variable groups where more than two indices had a positive edf, the two indices with biggest reduction in AIC relative to the null model were selected, providing that they did not display a correlation coefficient of > 0.7 or < -0.7 (Appendix 3.7; Dormann et al., 2013). The only exception to this rule was for winter rainfall in Grey Wagtail; all five indices had a positive edf, three of which were significant. To avoid using two indices of dry conditions (number of dry days [DD], number of consecutive dry days [CDD]), the index with the lowest AIC (DD) was omitted, with CDD and R10mm selected for inclusion in the multivariate model. A final model selection step involved stepwise removal of terms that displayed an edf of zero, starting with the variable with the highest p -value (Appendix 3.8). The final multivariate GAMMs (Appendix 3.9) were checked for concurvity (i.e. an indicator of collinearity in smoothed terms; *mgcv* package; Wood, 2017; Appendix 3.10); all models displayed pairwise values below the recommended threshold of 0.5 (He, 2004), indicating no concurvity.

3.4. Results

3.4.1. Abundance trends for focal species

Both Dipper and Common Sandpiper breeding abundances declined over the survey period (Figure 3.2), falling by 19% and 38% respectively relative to 1998 figures. While this decline was relatively continuous for Dipper (with only a brief increase in 2015), Common Sandpiper displayed multiple recovery periods in 2002, 2010 and 2015, all of which were followed by an immediate small decline. Grey Wagtail abundance experienced only a minor decline over the 21-year period (9%), but their trend included pronounced fluctuations; after an initial increase from 1998 to 2004 (1.8 to 2.4 birds/km), the breeding abundance almost halved between 2008 and 2012 (2.2 to 1.3 birds/km), followed by a brief recovery peaking in 2016 (2.1 birds/km) before further decline.

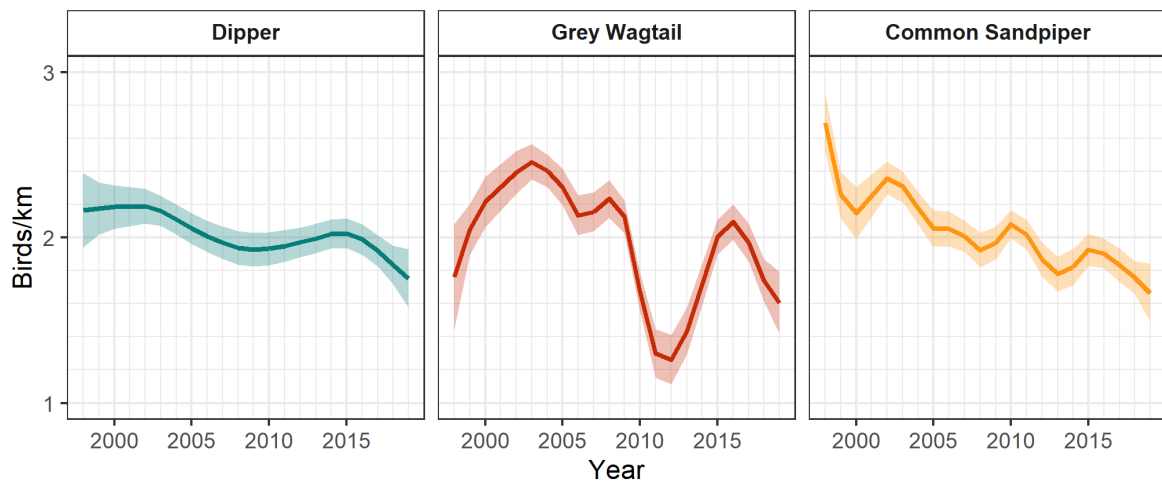


Figure 3.2: Trends for species abundance (birds/km) from 1998 to 2019. Dipper (blue); Grey Wagtail (red); Common Sandpiper (orange). Results are estimated by species from a zero-inflated poisson GAMLSS defined with cubic-splines (Rigby & Stasinopoulos, 2005; Rigby et al., 2017). Degrees of freedom are fixed at 4, 10 and 10 for Dipper, Grey Wagtail and Common Sandpiper respectively. The number of transects is included as an offset, visit (E/L) as a nuisance fixed effect, and site as a random effect. All trends are significant at $P < 0.001$ (***).

3.4.2. Comparative species' sensitivity to weather indices

All three species displayed varying sensitivity (i.e. significant response to one or more variables) to weather (Figure 3.3; Appendix 3.6), with no consistency between positive or negative response for a given index. All three species shared an overall greater sensitivity to winter climate indices, with only Grey Wagtail displaying a significant response to those falling in the breeding season. Dipper displayed the least sensitivity of the three species, with only three significant/marginal indices, all of which were associated with winter; these correspond to negative responses to high maximum daily rainfall and frost days, while a broader diurnal temperature range was associated with higher abundance in the subsequent breeding season. While Common Sandpiper were

sensitive to four indices, these were spread equally over winter and the breeding season. Consistently wet winters were associated with high numbers of Common Sandpipers the following breeding season, but this number fell with a low absolute minimum winter temperature. Grey Wagtail were highly sensitive to weather conditions, showing associations with eight winter indices, but only two indices for breeding rainfall. These corresponded to negative responses to dry winters with unusually warm or prolonged low temperatures, or extensive heavy rainfall during breeding. However, wet, cool winters resulted in higher abundance in the subsequent breeding season, particularly when accompanied by dry conditions between April and June.

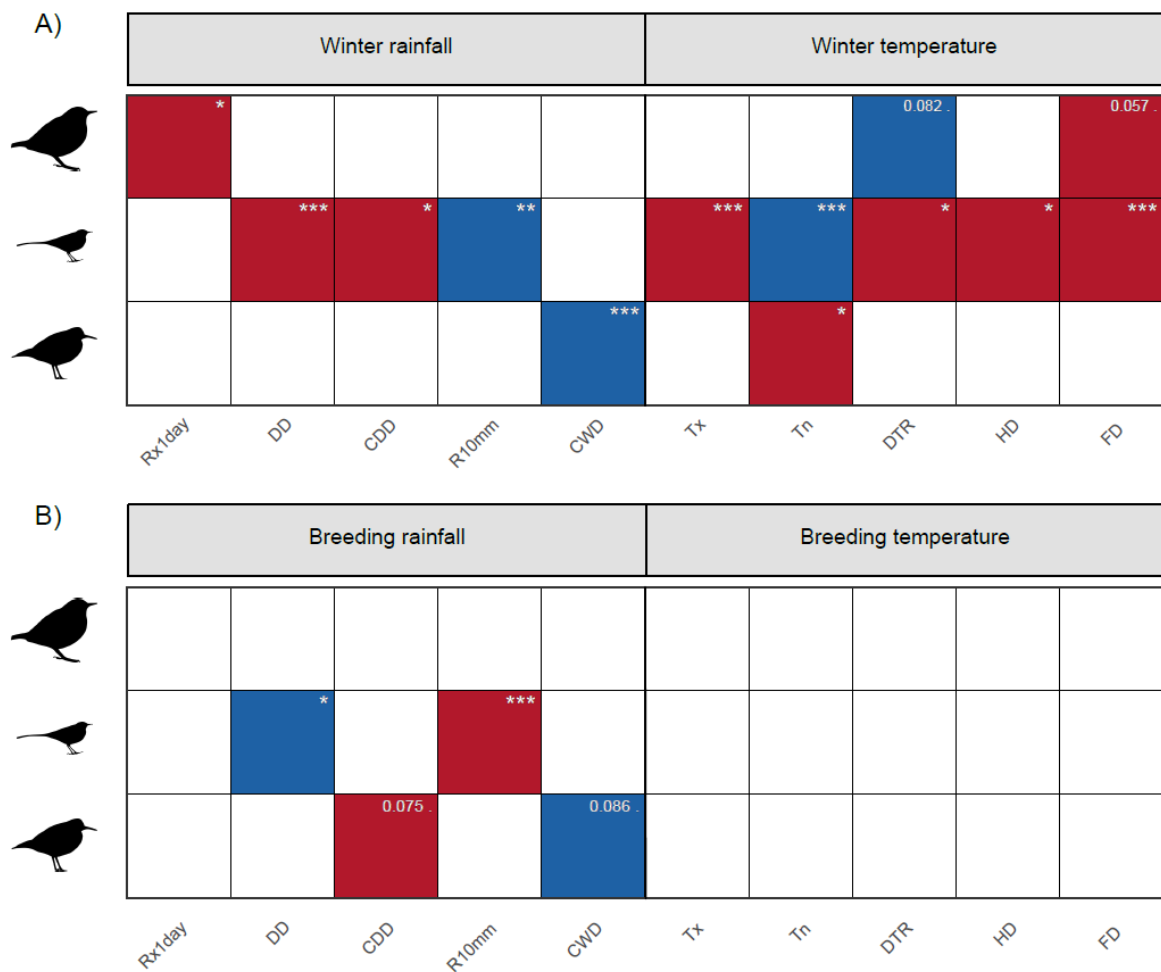


Figure 3.3: Diagram summarising species sensitivity to length of Winter (A) and Breeding (B) weather indices. Results are summarised as having a predominantly positive (blue), n.s. (non-significant, white) or negative (red) impact on breeding abundance based on the region of response showing the least uncertainty. Species: Dipper (top), Grey Wagtail (middle), Common Sandpiper (bottom). Weather indices: Rx1day = max 1-day rainfall, DD = dry days, CDD = consecutive dry days, R10mm = days over 10mm rainfall, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, DTR = diurnal temperature range, HD = hot days, FD = frost days. P-values: marginal p-values ($P < 0.1$) are written, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

3.4.3. Full species-level responses to weather conditions

All three focal species displayed multiple significant associations between abundance and weather, whether corresponding to the preceding winter or the breeding season itself (Figure 3.4, Table 3.2). These were largely linear associations, with Grey Wagtail and Common Sandpiper exhibiting at least one non-linear relationship. While there was limited consistency between species for specific indices, Dipper and Grey Wagtail shared similar responses over winter and the breeding season, whereas Common Sandpiper frequently benefitted from contrasting conditions.

Dipper and Grey Wagtail were both impacted by winter conditions that are likely to yield high stream flows. For Dipper, this is indicated by a steady decline in abundance with high maximum daily rainfall, whereas Grey Wagtail displayed an initial increase with the number of winter days with >10mm rainfall before declining. In contrast, Common Sandpiper abundance in the subsequent breeding season benefitted from significant consistent rainfall over winter. This association was particularly pronounced relative to the other modelled indices and species because the trend is sufficiently distinct that the pattern is carried through the detrending process. Dipper and Grey Wagtail both experienced negative responses to indices that indicate hard winters, reflected in declines with increasing frost days and lower absolute minimum temperatures respectively. However, while Dipper abundance marginally benefitted from wider ranging daily temperatures in winter, Grey Wagtail displayed marginal declines with absolute maximum temperatures of >10°C. In contrast, Common Sandpiper breeding abundance benefitted from colder minimum temperatures in the preceding winter.

All three species displayed very limited responses to variation in breeding season indices, with multiple associations being only marginal in effect. While Grey Wagtail were impacted by multiple days of heavy rainfall between April and June, Common Sandpiper displayed marginal benefits from consistent wet conditions (>1mm rainfall per day), with drought resulting a reduction in abundance. Dipper had no significant response towards rainfall conditions between April and June. During the breeding season, Dipper abundance was higher at cooler sites, reflected by a decline with an increasing absolute minimum temperature and number of days above 20°C (though the latter response was marginal). In contrast, Grey Wagtail preferred warmer sites, with higher breeding abundance alongside higher absolute maximum temperatures.

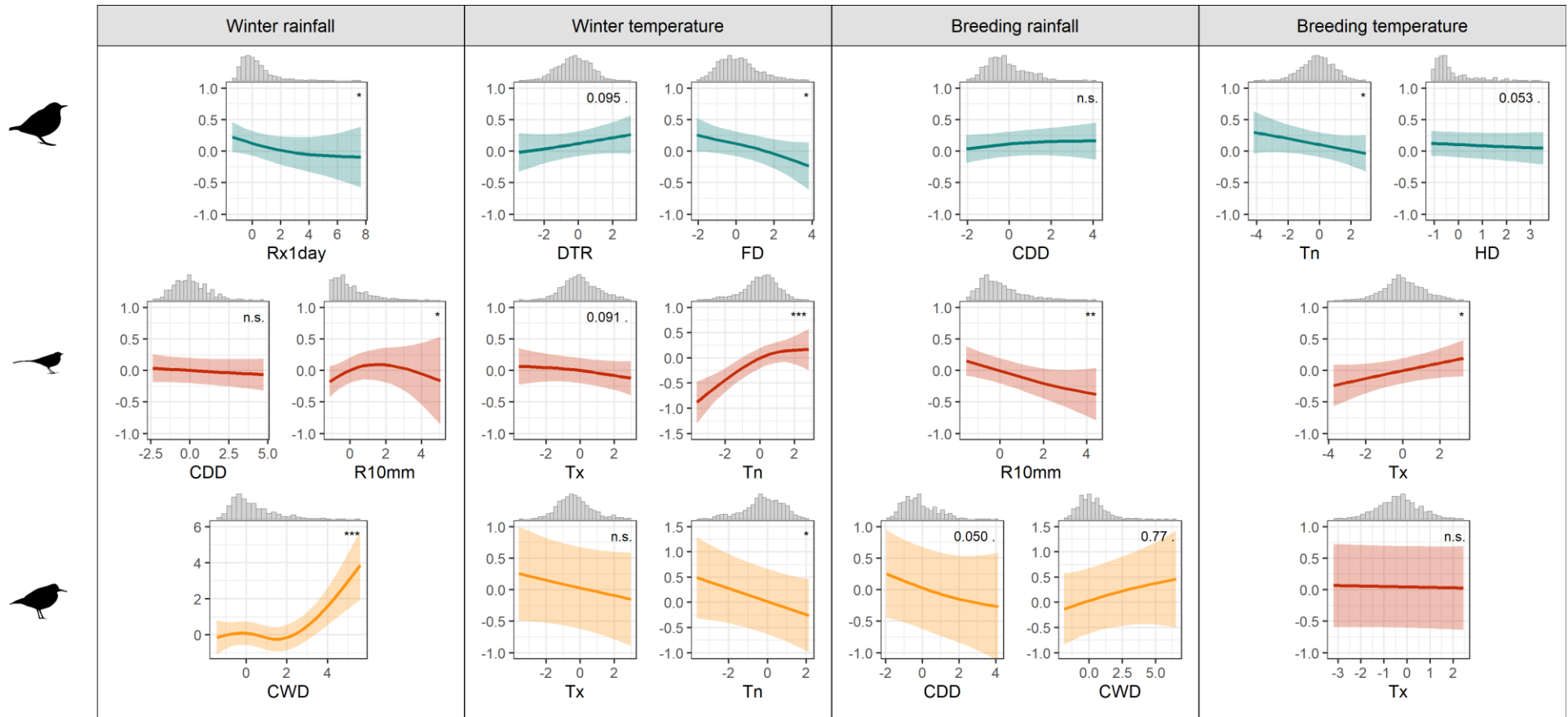


Figure 3.4: Partial effect plots of species abundance for species-specific responses to weather indices. Dipper (blue); Grey Wagtail (red); Common Sandpiper (orange). Residuals of both abundance and weather variables are used. Histograms show the distribution of observations for each variable. Weather variables: Rx1day = max 1-day rainfall, CDD = consecutive dry days, R10mm = days over 10mm rainfall, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, DTR = diurnal temperature range, FD = frost days. Season: W = winter, B = breeding. P-values: n.s. non-significant, marginal p-values ($P < 0.1$) are written, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3.2: Multivariate Generalised additive mixed model (GAMM) output by species. Smoothed terms are listed individually by species due to the varying model structures. Concurvity test results calculated in the *mgcv* package (Wood, 2017), with range given in table.

Component	Dipper					Grey Wagtail					Common Sandpiper				
	Term	Est.	Std Error	t-value	p-value	Term	Est.	Std Error	t-value	p-value	Term	Est.	Std Error	t-value	p-value
Parametric coefficients	<i>(Intercept)</i>	0.107	0.098	1.097	0.2728	<i>(Intercept)</i>	-0.071	0.096	-0.741	0.459	<i>(Intercept)</i>	0.036	0.319	0.113	0.91
	<i>Visit (L)</i>	-0.158	0.039	-4.018	<0.001	<i>Visit (L)</i>	0.324	0.037	8.684	<0.001	<i>Visit (L)</i>	-0.01	0.084	-0.119	0.906
Component	Term	edf	Ref. df	F-value	p-value	Term	edf	Ref. df	F-value	p-value	Term	edf	Ref. df	F-value	p-value
Smooth terms	<i>Rx1day (W)</i>	0.941	4	0.829	<0.05	<i>CDD (W)</i>	0.463	4	0.198	0.183	<i>CWD (W)</i>	3.011	4	4.685	<0.001
	<i>DTR (W)</i>	0.723	4	0.469	0.095	<i>R10mm (W)</i>	1.61	4	1.185	<0.05	<i>Tx (W)</i>	0.588	4	0.321	0.132
	<i>FD (W)</i>	1.223	4	1.36	< 0.05	<i>Tx (W)</i>	0.807	4	0.51	0.091	<i>Tn (W)</i>	0.875	4	1	<0.05
	<i>CDD (B)</i>	0.767	4	0.42	0.124	<i>Tn (W)</i>	2.12	4	9.653	<0.001	<i>CDD (B)</i>	0.833	4	0.707	0.051
	<i>Tn (B)</i>	0.842	4	0.676	0.055	<i>R10mm (B)</i>	1.193	4	2.301	<0.01	<i>CWD (B)</i>	0.778	4	0.536	0.078
	<i>HD (B)</i>	0.422	4	0.158	0.205	<i>Tx (B)</i>	0.882	4	1.01	<0.05	<i>Tx (B)</i>	0.08	4	0.022	0.295
Observations	4140					5822					2785				
R ² (adjusted)	0.003					0.018					0.017				
AIC	15080.06					22637.97					13711.1				
Concurvity test	0.02 - 0.39					0.02 - 0.30					0.03 - 0.30				

3.5. Discussion

This study demonstrates that the breeding abundance of Dipper, Grey Wagtail and Common Sandpiper is sensitive to weather conditions in terms of abnormal departures in magnitude or duration of rainfall or temperature that occur during both the breeding season and the preceding winter, even when, as in the case of Common Sandpiper, birds are not actually present at the time to experience this directly. Declines were observed across all three species between 1998 and 2019, consistent with national population trends reported by the BTO, which are estimated from data contributed by eight monitoring schemes (including the Waterways Breeding Bird Survey used in this study; Harris et al., 2022). Prior research indicates that climate change or weather events may be partially responsible for the observed trends, particularly conditions that affect over-winter survival (Dipper and Grey Wagtail; Sharrock, 1969; Nilsson et al., 2011; Chiu et al., 2013) or adults during migration (Common Sandpiper; Summers et al., 2019). This study supports these findings and identifies potential weather-based drivers of population decline.

All three species displayed greater sensitivity (i.e. significant response to one or more indices) towards winter extremes, but responses differed in terms of direction, effect size and specific weather index, which is likely reflective of their contrasting foraging, nesting, and development strategies. Grey Wagtail were overall the most sensitive of the three, with negative responses towards hard or warm winters (multiple days over 15°C), and wet springs. Common Sandpiper were intermediate, associated most strongly with enhanced flow conditions whereby wet winters and springs were both beneficial for breeding abundance, while low winter temperatures could reduce numbers. Dipper were the least sensitive, being affected primarily by either cold or very wet winters.

While some associations identified here had relatively small, yet significant effect sizes (e.g. Grey Wagtail abundance residuals increased by <0.1 per unit change in absolute maximum temperature during breeding [Tx B]), others resulted in a substantial increase or reduction in abundance (e.g. Common Sandpiper abundance residuals increased by up to 1.39 per unit change in consecutive wet days over winter [CWD W]). The small but significant effects are often linear responses that do not deviate far outside of the normal range of breeding densities, and are likely reflective of adaptation to natural temporal variation in the riverine environment (0.2–4.7 pairs/km, depending on species and geography; Tyler, 1972; Ormerod & Tyler, 1987; Vickery, 1991), whereas the larger effects are indicative of conditions either corresponding to niche requirements (increase) or exceeding the tolerance limits (reduction) of that species. These demonstrate that the WBBS data is effective for capturing patterns between riverine bird abundance and variation in weather conditions.

However, the low R^2 values observed in both the sensitivity (R^2 [adjusted] range for Dipper = -0.001 – 0.003, Grey Wagtail = 0.002 – 0.016, and Common Sandpiper = -0.001 – 0.005; Appendix

3.6) and species-specific (R^2 [adjusted] for Dipper = 0.003, Grey Wagtail = 0.018, and Common Sandpiper = 0.017; Table 3.2) analyses here suggest that weather conditions may be a poor predictor for overall species abundance. This is similarly observed in Chapter 2, and is likely due to the maximum survey length of 5km within the WBBS scheme. As all three focal species hold linear river territories, averaging between 1.2km to 3.5km in length (Tyler, 1972; Holland, Robson & Yalden, 1982; Ormerod & Tyler, 1987b; Vickery, 1991), the typically small number of birds observed per site visit (median birds observed when present = 2, range = 1 – 32), likely reduces the variance explained when assessing abundance.

Furthermore, these findings should be interpreted with care, as bird counts during the breeding season are subject to detection bias, particularly when avian behaviour changes to reflect nest development stage (e.g. incubation), weather or river flow conditions. For example, Dippers may remain stationary during spate flows rather than engaging in energetically costly diving for food (D'Amico & Hémery, 2007); if positioned amongst vegetation or under an overhang, an observer may overlook them during the count. Thus, our investigation of breeding season weather indices against bird abundance in the same year (t) may simply describe behaviour or detectability. We attempted to account for seasonal variation in detection or numbers by including survey (E/L) as a nuisance fixed effect in all models. It may also be beneficial to include a lagged phase in future analyses, whereby abundance in year t are associated with weather indices for the breeding season in year $t-1$, which may revise the picture of sensitivity towards weather conditions over the breeding season.

3.5.1. Species' responses towards weather conditions

These findings indicate that Dipper are less sensitive to variation in weather conditions than Grey Wagtail and Common Sandpiper, yet similarly respond more negatively to winter extremes than those occurring over the breeding season. Dippers are the most aquatic of the three species, being physiologically and anatomically well adapted to the riverine environment (Tyler & Ormerod, 1994), allowing them to better cope with extended periods of abnormally wet or dry conditions, for example by temporarily modifying foraging rates, behaviour or target prey, or by relocating to alternative nearby watercourses (e.g. smaller tributaries) or waterbodies (e.g. upland lake shores) with more favourable conditions (Da Prato, 1981; Taylor & O'Halloran, 2001; Chiu et al., 2013). However, our analysis of species-specific responses indicated a decline in Dipper abundance in site-years with a high winter maximum daily rainfall, suggesting that high magnitude flow events over winter can impact their breeding populations. Extreme winter floods have been observed to reduce survival of both adult and juvenile Dippers in the UK (Wilson, 1996). However, it is not clear whether this is driven by the reduction in abundance, biomass and richness of invertebrate prey (indirect mechanism; Taylor & O'Halloran, 2001), a reduction in foraging activity through

inability to feed or due to the higher energetic costs of diving (D'Amico & Hémery, 2007) or inefficiency of visual foraging in turbid water (Da Prato, 1981), none of which are mutually exclusive. Reduced survival of Brown Dippers (*Cinclus pallasii*) in sub-tropical systems were similarly attributed to winter extreme flooding (Chiu et al., 2013).

Both analyses in this study indicated that Dipper abundance is favoured by milder winters and cooler breeding seasons. Hard winters have previously been linked to diminished breeding populations of Dipper in Norway (Nilsson et al., 2011), where rivers and lakes freeze annually for a prolonged period, which in turn limits access for foraging birds. As rivers at most WBBS sites are unlikely to freeze completely, the reduced abundance of Dipper in hard winters may, in Britain, be due to birds acclimatizing over time to typically milder winters, resulting in reduced capacity to adapt their physiology to infrequent extreme cold when these conditions arise. A common adaptation in temperate birds is to maintain lipid reserves as a buffer against starvation (Laplante et al., 2019). While Dippers are well adapted to foraging in cold water and will rely on communal roosts to conserve energy overnight, freezing conditions may still result in mortality. The last decade has seen more extreme winters than the previous (2010-2019 vs. 2000-2009; Appendix 3.4); if this pattern continues, breeding Dipper populations may fluctuate in response to extreme low temperatures, leading towards continued decline.

Grey Wagtail displayed significant sensitivity to winter weather conditions, with a negative response to eight of the ten indices. Indices reflecting rainfall duration were more important drivers of Grey Wagtail abundance than rainfall magnitude, but both duration and magnitude indices produced significant responses to temperature. As with Dippers, breeding populations were higher following a mild winter. Grey Wagtail have experienced heavy losses in breeding populations following a hard winter, as observed following the winter of 1962/63 (Dobinson & Richards, 1964; Sharrock, 1969; Tyler, 1979), and this pattern is clearly replicated for the severe winters of 1981/82 and 2010/11 (Figure 1.6 and Appendix 3.4; Massimino et al., 2022). While Grey Wagtail are partial migrants, it appears to be rare for birds to emigrate to mainland Europe in winter (Sharrock, 1969), suggesting that few British breeding birds will escape extreme winters through passage. Adults attain their greatest weight in winter, but first-year birds on average fail to add mass and fat reserves for December, and consequently have increased mortality (Tyler & Ormerod, 1991). However, in extreme cold, there is also potential for increased mortality in adults (Dobinson & Richards, 1964; Sharrock, 1969) as aerial prey density drops significantly in cold conditions, and birds may be unable to forage for alternative aquatic prey in shallow marginal habitat if this is frozen (Bures, 1995).

In contrast, Grey Wagtail were tolerant of a broad range of conditions during the breeding season, which is reflected in expansion of their breeding range by 19% over a 40-year period (Balmer et al., 2013). The single limiting factor was multiple days with heavy rainfall (>10mm). Grey Wagtails

are capable of both aerial and aquatic foraging, but both are affected by heavy rainfall. Rises in river level will restrict access to aquatic invertebrate prey as Grey Wagtail primarily forage on exposed gravels and in shallow water (Ormerod & Tyler, 1991; Bures, 1995), while aerial prey density drops during rain (Bures, 1995). As access to prey is essential for brood provisioning and will directly impact breeding success, failed breeding attempts due to heavy rainfall may result in territory abandonment and reduced observation of birds during WBBS surveys, whether due to a true reduction in numbers or reduced activity and detection because of reduced brood provisioning.

In the case of Common Sandpiper, despite their migratory status, moving from wintering grounds in Africa, mainland Europe and southern England to arrive in British breeding grounds between April and May (Dougall, Holland & Yalden, 2010; Summers et al., 2019), abundance was most strongly linked to cool and wet preceding winters. These associations are likely indirect and driven by influences on invertebrate prey and habitat quality. For example, consistent rainfall resulting in sustained high river discharge can redistribute coarse bedload materials, scour the channel, remove plants and displace biota, which may recover once low flow conditions have returned (Lake, 2000). This process likely promotes the renewal of exposed and sparsely vegetated shingle habitat favoured by foraging juvenile Common Sandpiper (Yalden, 1985), accounting for the significant increase in abundance of birds observed following consecutive days of winter rainfall. As temperature regulates development and emergence of both aquatic and terrestrial invertebrates (Daufresne et al., 2004; Durance & Ormerod, 2007; Forrest, 2016; Finn et al., 2022; Gebert et al., 2022), warm winters are likely to reduce density of cold-adapted invertebrate species (Durance & Ormerod, 2007), or accelerate their emergence and thus cause asynchrony between Common Sandpiper and their prey in the following season, with impacts on reproductive success. Adult birds are therefore likely to favour upland sites exposed to relatively harsh winter temperatures (Yalden, 1986).

Common Sandpiper displayed limited sensitivity to weather conditions over the breeding season, with only marginal responses to rainfall, specifically declines under extended drought conditions and increases with consecutive days of >1mm of rainfall. It is likely that consistent rainfall during the breeding season is only beneficial when low in magnitude, as heavy rain may reduce the availability of aquatic prey due to bed movement and wash out of benthic organisms (Theodoropoulos et al., 2017), or limits foraging access to exposed shingle due to inundation (Yalden, 1985, 1986), and risks flooding low-lying nests (Elas, Rosendal & Meissner, 2023). Drought conditions may similarly impact aquatic invertebrate prey richness and diversity through reduced wetted channel area, increased competition and predation, and elevated heat stress (Dewson, James & Death, 2007). Drought flows may also drive interstitial invertebrates deeper into the hyporheic zone, thus reducing access to foraging birds (Stubbington, 2012; Stubbington & Datry, 2013). Common Sandpiper may therefore be particularly vulnerable to flow regulation

(e.g. abstraction, impoundment, flow diversion). While adult Common Sandpiper diet comprises mainly invertebrates of terrestrial origin, juveniles are reliant on wet margins and exposed gravels, which adults will prioritize within their breeding territories (Yalden, 1985). Thus, sites in years with limited food resources for offspring are likely to have reduced abundance of breeding adults.

3.5.2. Management strategies

Weather and climate extremes are, by their very nature, difficult to predict, and therefore reducing their impact on riverine ecosystems presents significant challenges, both for the organisms affected and practitioners. However, management strategies such as the restoration and expansion of riparian zones may alleviate the impacts of abnormal or extreme weather conditions on multiple trophic levels (including riverine birds), whilst providing additional benefits.

For example, riparian woodland and vegetated buffer strips (>10m wide) are widely advocated methods to moderate stream temperature regimes by providing shade and shelter, and act as a flow buffer by increasing interception and percolation, thereby reducing or delaying surface run-off from high intensity rainfall events and lowering spate magnitude (Dohet et al., 2015; Johnson & Wilby, 2015; Thomas, Griffiths & Ormerod, 2016; Turunen et al., 2021). Bankside vegetation also reduces bank and channel erosion, and increases habitat complexity and invertebrate production via the addition of coarse woody debris and leaf litter (Gurnell, Gregory & Petts, 1995; Schneider & Winemiller, 2008; Cooper et al., 2021), which may also provide refugia for aquatic invertebrates and increase their retention during high flows. These management strategies will likely benefit Dipper and Grey Wagtail populations, both directly through reduced temperature-associated mortality and improved foraging conditions, and indirectly through conservation of invertebrate prey communities.

Another habitat management strategy that would alleviate pressures imposed by drought conditions is the transition from 'minimum' to environmental or ecological flows (e-flows) in abstraction or impoundment schemes. These seek to replicate site-specific natural flow regimes, which supports the sustenance of key ecosystem processes (e.g. substrate redistribution and regeneration) and meets the varying flow requirements of lotic organisms (Bragg et al., 2005; Arthington et al., 2006; Dudgeon et al., 2006; European Commission & Directorate-General for Environment, 2016; Webster et al., 2017; Schmutz & Moog, 2018). This transition would likely benefit breeding Common Sandpiper by maintaining wetted channel habitat for prey, and thereby increasing prey availability and foraging habitat for juvenile birds (Yalden, 1985; Stubbington, 2012; Stubbington & Datry, 2013).

3.6. Appendix

Appendix 3.1: Example of HAD-UK climate data

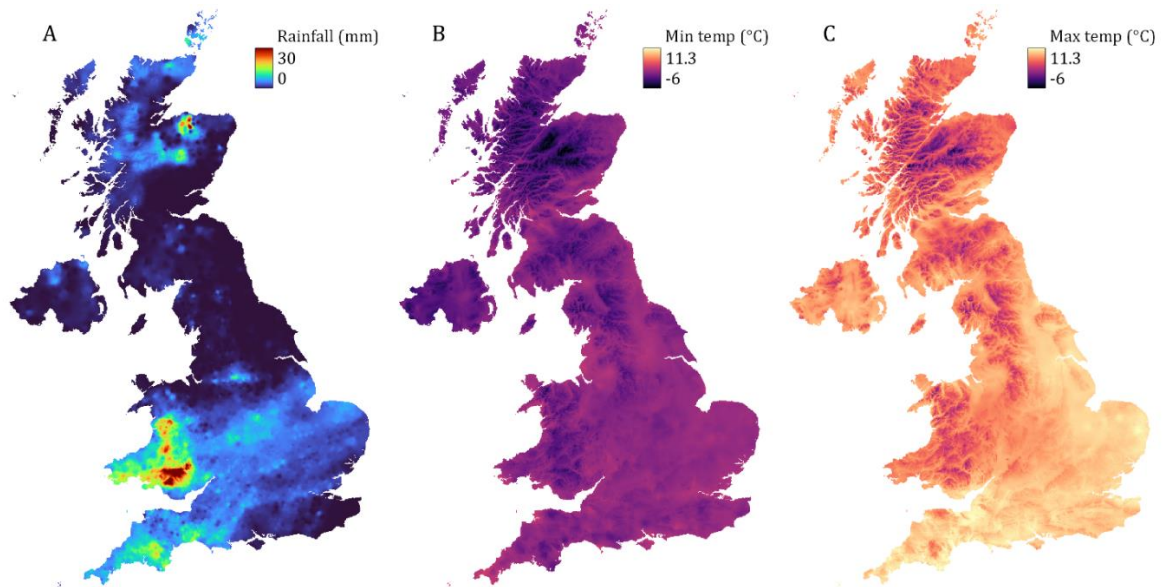


Figure A3.1-1: Example raw temperature and rainfall data. Maps show (A) Daily rainfall (mm), (B) Daily minimum temperature (°C), and (C) Daily maximum temperature (°C) for the UK on 1st April 2010. Data is downloaded from Met Office Had-UK 1km gridded climate database (Met Office et al., 2018).

Appendix 3.2: Model selection for species abundance trends

Smoothing parameters can be defined in multiple ways. Due to the relatively short time series (1998 to 2019), there is a risk of overfitting the smoothing parameters. Three methods were compared to identify the most appropriate for analysis (Figure A3.2-1; Table A3.2-1):

1. Cross validation: the automatic selection of smoothing parameters, utilising P-splines.
2. GAIC minimalization: manual selection of the degrees of freedom using cubic splines, based on multiple model runs varying the df from 0-10 to reduce the risk of overfitting (Table A3.2-2).
3. Fixed GAIC across species = manual selection of 5 df using cubic splines.

Each method was tested with species-specific zero-inflated poisson GAMLSS (Rigby et al., 2017), which model abundance against year. The number of transects is included as an offset, visit (E/L) as a nuisance fixed effect, and site as a random effect. Method two (GAIC minimalization) was selected for full analysis as it balances reduction of the GAIC whilst minimising the risk of overfitting.

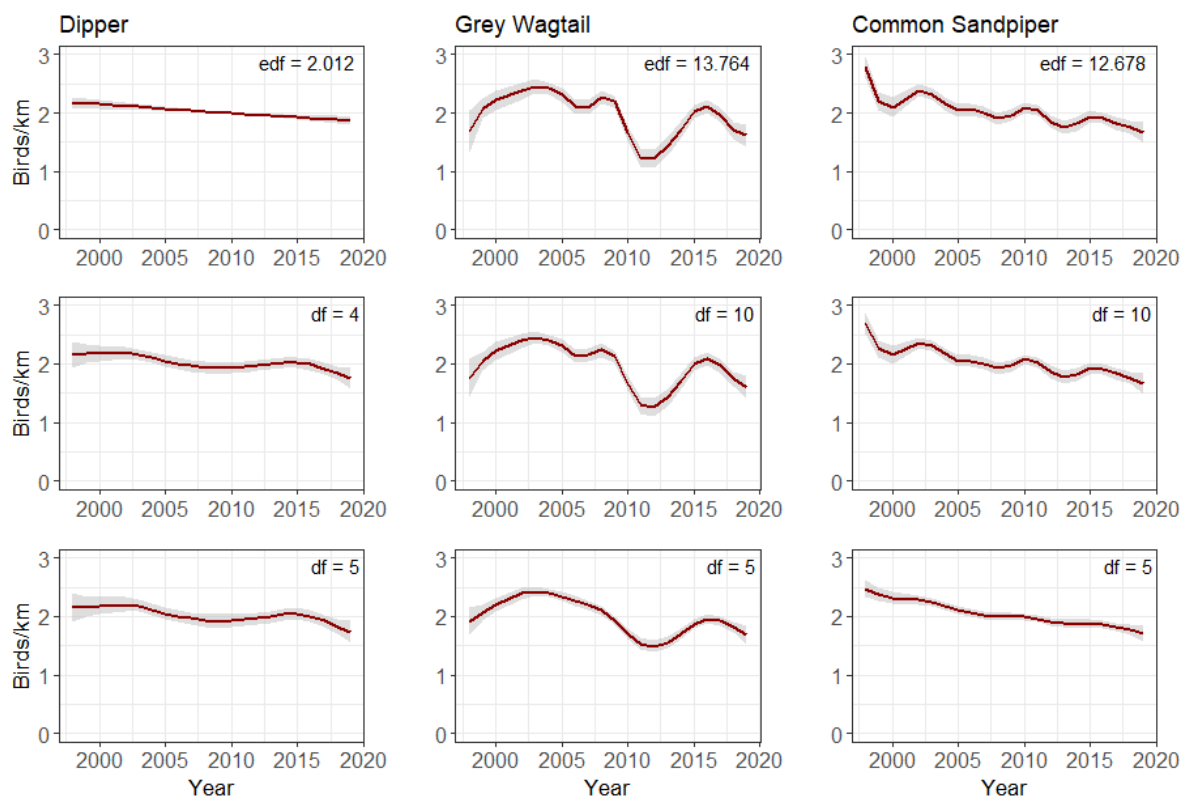


Figure A3.2-1: GAMs of species abundance trends. (top) Penalized cross validation (automatic selection of appropriate smoothing); (middle) manually set df (degrees of freedom), based on lowest GAIC score (Table A3.2-2); (bottom) fixed degrees of freedom. P-values remain at <0.001 for all models. Edf (effective degrees of freedom) or df are given at the top-right of each plot. Grey shading shows the 95% confidence intervals.

Table A3.2-1: Comparison of GAIC values of the three smoothing methods. Cross validation = automatic selection of smoothing parameters, utilising P-splines; GAIC minimalization = manual selection of the degrees of freedom using cubic-splines, based on multiple model runs varying the df from 0-10 to reduce the risk of overfitting (Table A3.2-2); Fixed GAIC across species = manual selection of 5 df using cubic-splines.

Smoothing method	Dipper	Grey Wagtail	Common Sandpiper
Cross validation	12422.5	17385.34	10576.91
GAIC minimalization	12419.53	17389.91	10581.11
Fixed GAIC across species	12419.99	17440.29	10600.81

Table A3.2-2: Generalized Akaike information criterion (GAIC) for species abundance trend model comparison. Bold highlights the lowest GAIC value.

Df	GAIC		
	Dipper	Grey Wagtail	Common Sandpiper
0	12422.79	17590.90	10603.02
1	12422.98	17569.13	10604.51
2	12421.15	17531.10	10604.80
3	12419.86	17496.62	10605.33
4	12419.53	17465.69	10603.53
5	12419.99	17440.29	10600.81
6	12420.21	17421.78	10597.05
7	12420.66	17415.46	10592.75
8	12421.33	17400.27	10588.43
9	12421.61	17394.19	10584.73
10	12421.67	17389.91	10581.11

Appendix 3.3: Effect of survey effort on occupancy and abundance

Linear models were used to explore how abundance was associated with survey effort (number of transects). Results indicate that increased survey effort results in increased likelihood of observing more birds (Figure A3.3-1 and Table A3.3-1).

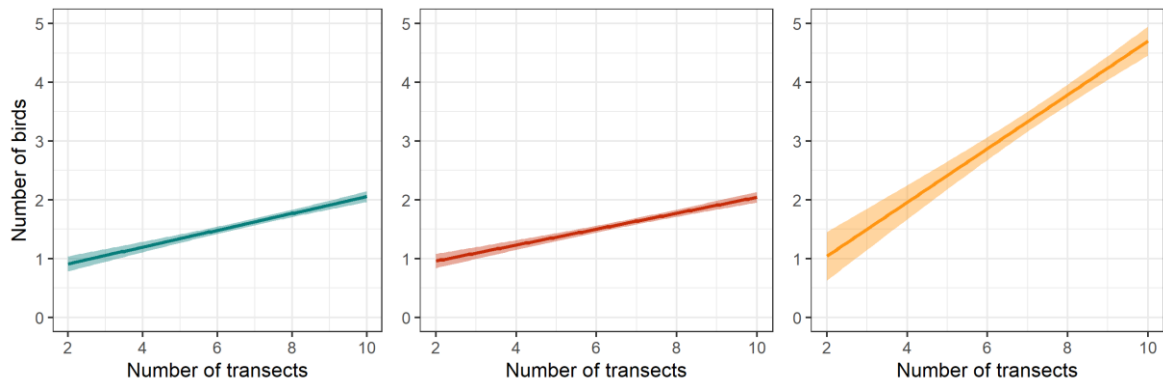


Figure A3.3-1: Linear association between survey effort and abundance, including zero counts. Blue = Dipper; red = Grey Wagtail; orange = Common Sandpiper.

Table A3.3-1: LM output for occupancy and survey effort of the three species. SE = Std. Error. RMSE = Root Mean Squared Error.

	Dipper				Grey Wagtail				Common Sandpiper			
Predictors	Estimate	SE	z	p	Estimate	SE	z	p	Estimate	SE	z	p
(Intercept)	0.624	0.087	7.139	<0.001	0.688	0.083	8.31	<0.001	0.126	0.277	0.453	0.65
N transects	0.143	0.012	12.02	<0.001	0.136	0.012	11.75	<0.001	0.458	0.036	12.80	<0.001
Observations	4140				5822				2785			
R ² (adjusted)	0.034 (0.033)				0.023 (0.023)				0.056 (0.056)			

Appendix 3.4: Annual variation in weather indices

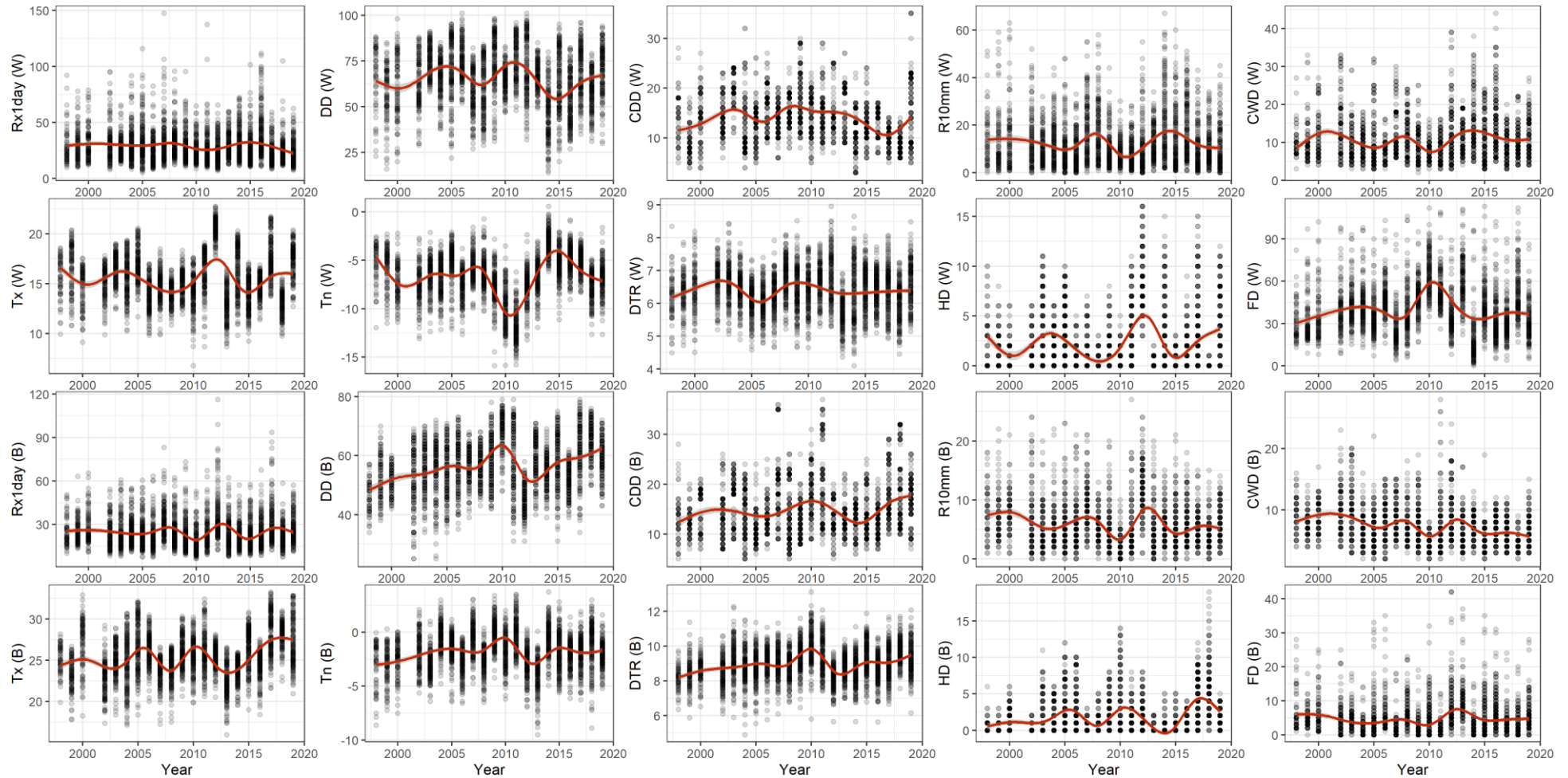


Figure A3.4-1: Annual variation in weather variables. Trend line is shown in red. Weather vars: Rx1day = max 1-day rainfall, DD = dry days, CDD = consecutive dry days, R10mm = days over 10mm rainfall, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, DTR = diurnal temperature range, HD = hot days, FD = frost days. Season is given in brackets after each variable: W = winter, B = breeding.

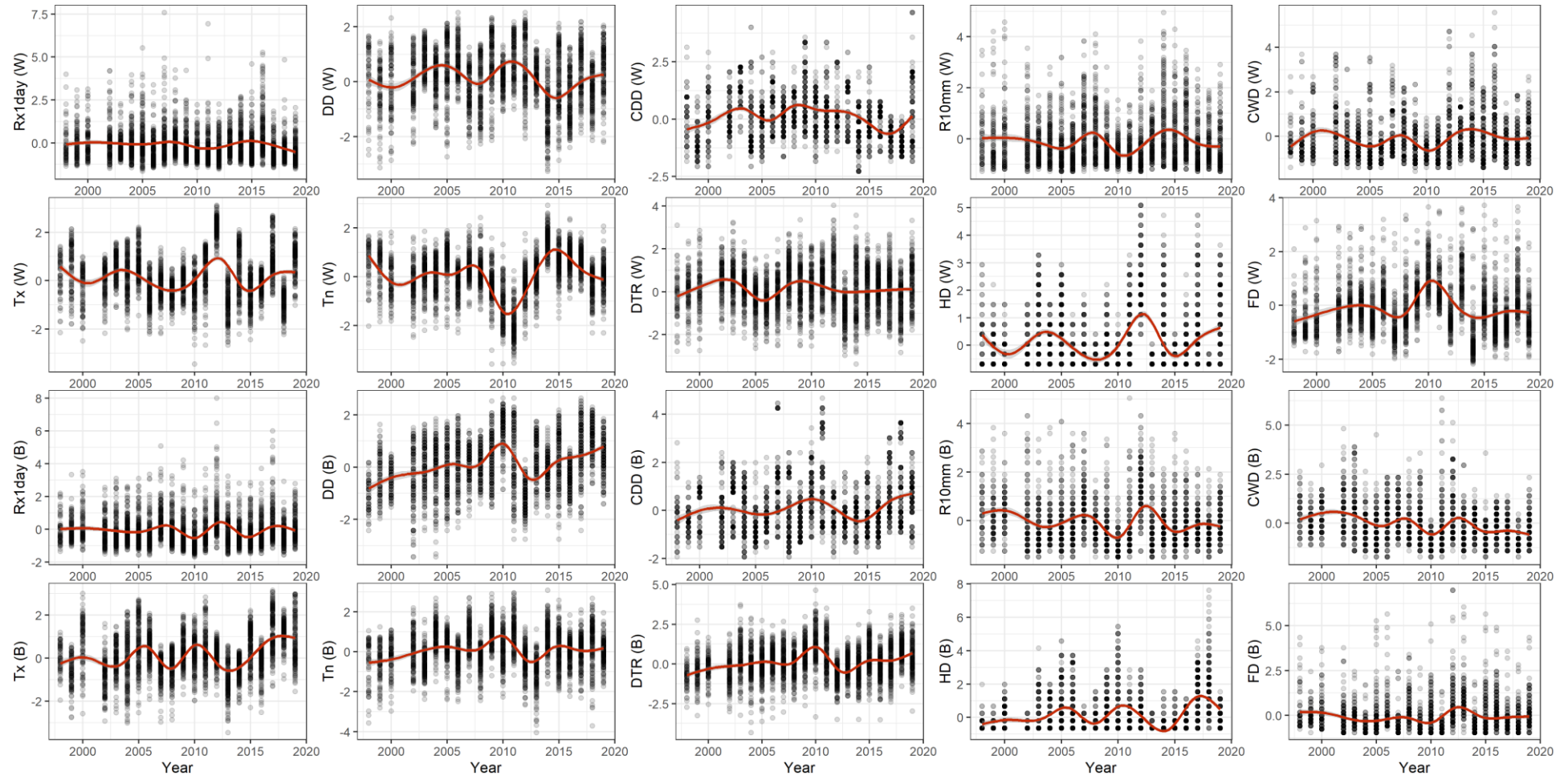


Figure A3.4-2: Scaled and centred annual variation in weather variables. Trend line is shown in red. Weather vars: Rx1day = max 1-day rainfall, DD = dry days, CDD = consecutive dry days, R10mm = days over 10mm rainfall, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, DTR = diurnal temperature range, HD = hot days, FD = frost days. Season is given in brackets after each variable: W = winter, B = breeding.

Appendix 3.5: Detrending species abundance and climate data

Detrending data is a common process in time series analysis, which reduces the risk of identifying spurious associations between variables that change simultaneously yet independently of each other (Lindström & Forchhammer, 2010) whilst retaining cyclical or stochastic fluctuations. As trends were detected in the species abundance (Figure 3.2) and weather data (Appendix 3.4) prior to analysis, both were detrended using linear regression, with the yearly residuals used in analysis.

For the abundance data, this used a generalised linear model (GLM) of abundance against year for each species, with a zero-inflated poisson distribution to account for the large number of zeros included in the data (*pscl* package; Zeileis, Kleiber & Jackman, 2008). The number of 500m transects were included as an offset to control for heterogeneity in survey effort (Appendix 3.3). This model detrends on year and survey effort simultaneously. For the weather data, this used a linear regression model (LM) of each variable against year. The results of detrending are demonstrated in Figures 3.5-1 and 3.5-2.

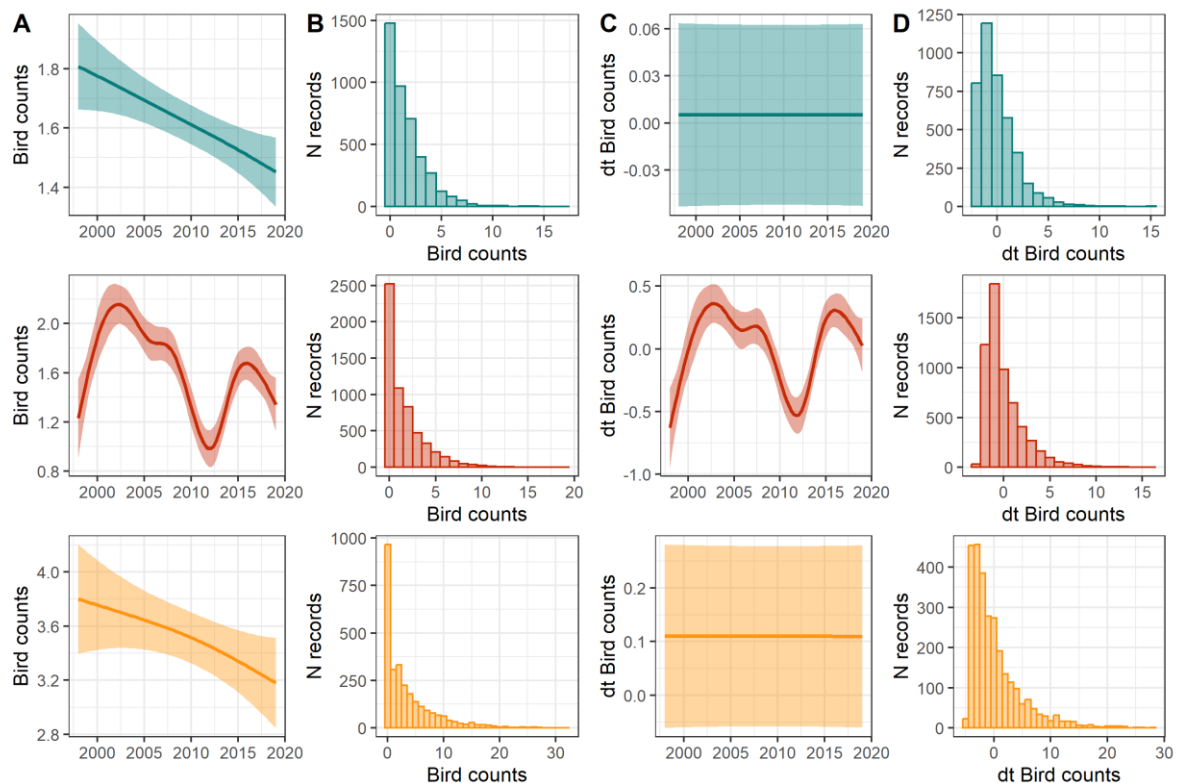


Figure A3.5-1: Raw and detrended pooled bird count (abundance) data by species. Blue = Dipper; red = Grey Wagtail; orange = Common Sandpiper. (A) Raw bird count trends across the study period. (B) Distribution of bird counts in raw data. (C) Trend of bird count residuals across the study period. (D) Distribution of bird count residuals.

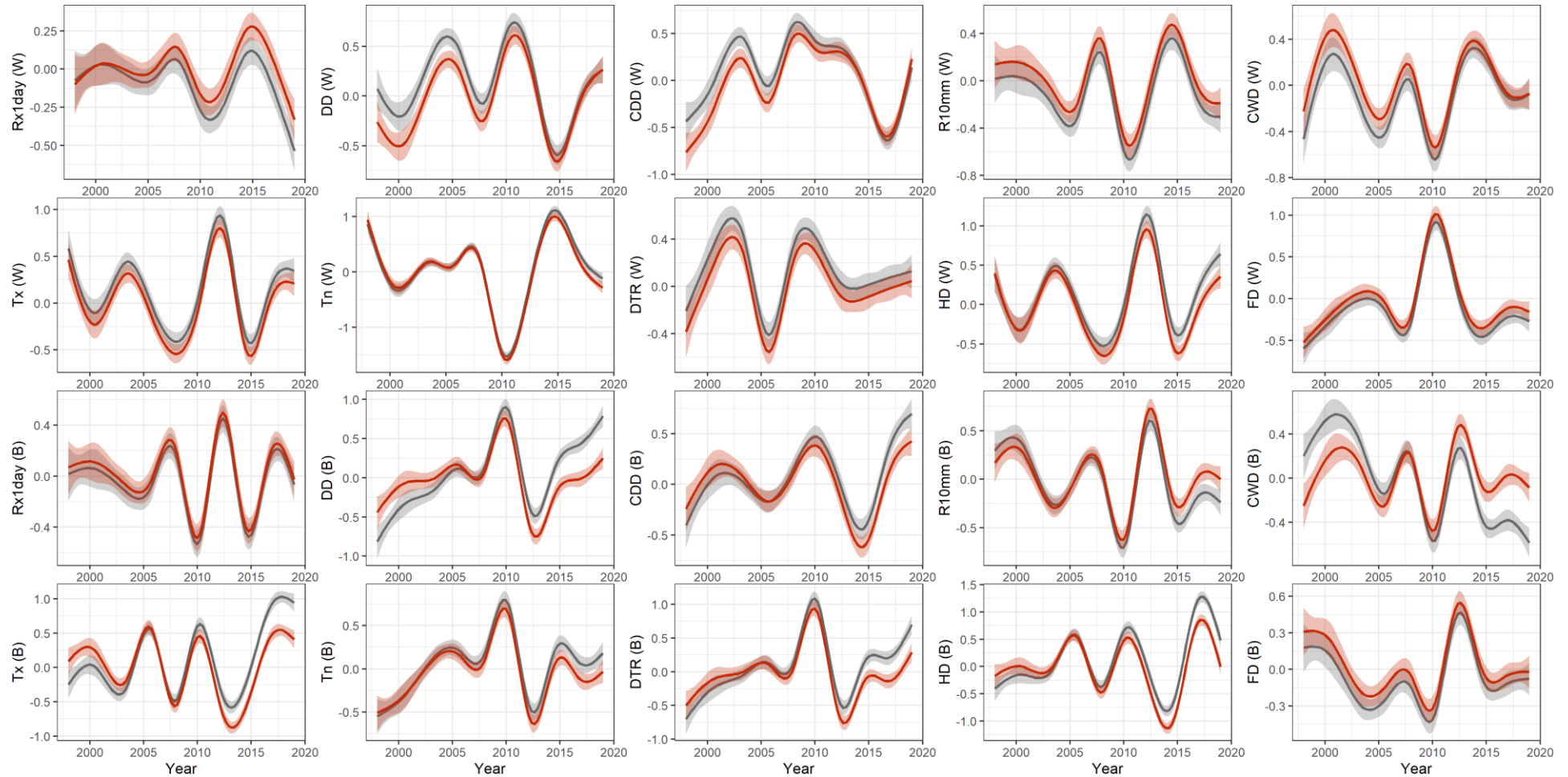


Figure A3.5-2: Comparison of trends present in the weather variables. Scaled and centred data is shown in grey; detrended data is shown in red.

Appendix 3.6: Univariate GAM results

Table A3.6-1: Results of univariate GAMMs between bird abundance and all weather variables. Edf = effective degrees of freedom, rounded to 4dp. AIC = Generalized Akaike Information Criterion. edf values of 0 indicate no effect on the fit of the model; non-significant terms with an edf > 0 indicate a small non-zero effect. Indices with the biggest reduction in AIC value relative to the null model in each group with an edf > 0 were selected for use in multivariate models (highlighted in bold). AIC values for null models: Dipper = 16976.95, Grey Wagtail = 25292.82, Common Sandpiper = 16308.39.

	Variable	Dipper				Grey Wagtail				Common Sandpiper			
		edf	P	R ₂ (adj)	AIC	edf	P	R ₂ (adj)	AIC	edf	P	R ₂ (adj)	AIC
Winter	Maximum 1-day rainfall	0.9073	< 0.05 *	0.00227	15074.42	0.5256	0.17	0.0075	22678.75	0.5256	0.672	-0.000351	13714.39
	Dry days	0	0.604	0.00153	15076.01	1.141	< 0.001 ***	0.0129	22670.38	0	0.976	-0.000351	13714.39
	Consecutive dry days	0	0.923	0.00153	15076.01	0.9336	< 0.05 *	0.00804	22676.49	0	0.843	-0.000351	13714.39
	Days over 10mm rainfall	0	0.949	0.00153	15076.01	1.643	< 0.01 **	0.0155	22672.51	0	0.824	-0.000351	13714.39
	Consecutive wet days	0	0.983	0.00153	15076.01	0.6855	0.102	0.00753	22678.31	3.83	< 0.001 ***	-0.000478	13705.6
	Absolute maximum temperature	0.5749	0.132	0.000991	15075.56	2.258	< 0.001 ***	0.0111	22672.55	0.542	0.151	0.003	13714.05
	Absolute minimum temperature	0.2619	0.246	0.00149	15075.96	2.166	< 0.001 ***	0.0146	22641.58	0.7874	< 0.05 *	0.00496	13712.89
	Mean diurnal temperature range	0.7462	0.0828 .	-0.00136	15075.11	0.9902	< 0.05 *	0.0137	22676.86	0	0.462	-0.000352	13714.39
	Hot days (>15°C)	0	0.39	0.00153	15076.01	0.8969	< 0.05 *	0.0095	22676.35	0	0.924	-0.000351	13714.39
	Frost days	0.9369	0.0566 .	0.00217	15074.68	2.074	< 0.001 ***	0.00959	22670.31	0.5512	0.155	0.00462	13714.07
Breeding	Maximum 1-day rainfall	0	0.889	0.00153	15076.01	0	0.900	0.00565	22679.00	0	0.976	-0.000351	13714.39
	Dry days	0	0.704	0.00153	15076.01	1.817	< 0.05 *	0.00578	22677.07	0	0.417	-0.000351	13714.39
	Consecutive dry days	0.8662	0.108	0.00257	15075.44	0	0.669	0.00565	22679.00	0.7616	0.0745 .	0.00225	13713.36
	Days over 10mm rainfall	0	0.591	0.00153	15076.01	3.304	0.001 ***	0.00217	22670.27	0.3697	0.219	-0.000179	13714.29
	Consecutive wet days	0	0.325	0.00153	15076.01	0	0.687	0.00565	22679.00	0.6973	0.113	0.00136	13713.80
	Absolute maximum temperature	0	0.714	0.00153	15076.01	0.254	0.249	0.00528	22678.95	0.1967	0.267	0.000649	13714.37
	Absolute minimum temperature	0.5034	0.168	0.00196	15075.75	0	0.686	0.00565	22679.00	0	0.863	-0.000351	13714.39
	Mean diurnal temperature range	0	0.511	0.00153	15076.01	0	0.770	0.00565	22679.00	0	0.917	-0.000351	13714.39
	Hot days (>25°C)	0.5293	0.182	0.00235	15075.8	0	0.602	0.00565	22679.00	0	0.403	-0.000351	13714.39
	Frost days	0	0.725	0.00153	15076.01	0	0.368	0.00565	22679.00	0.1019	0.293	-0.00106	13714.38

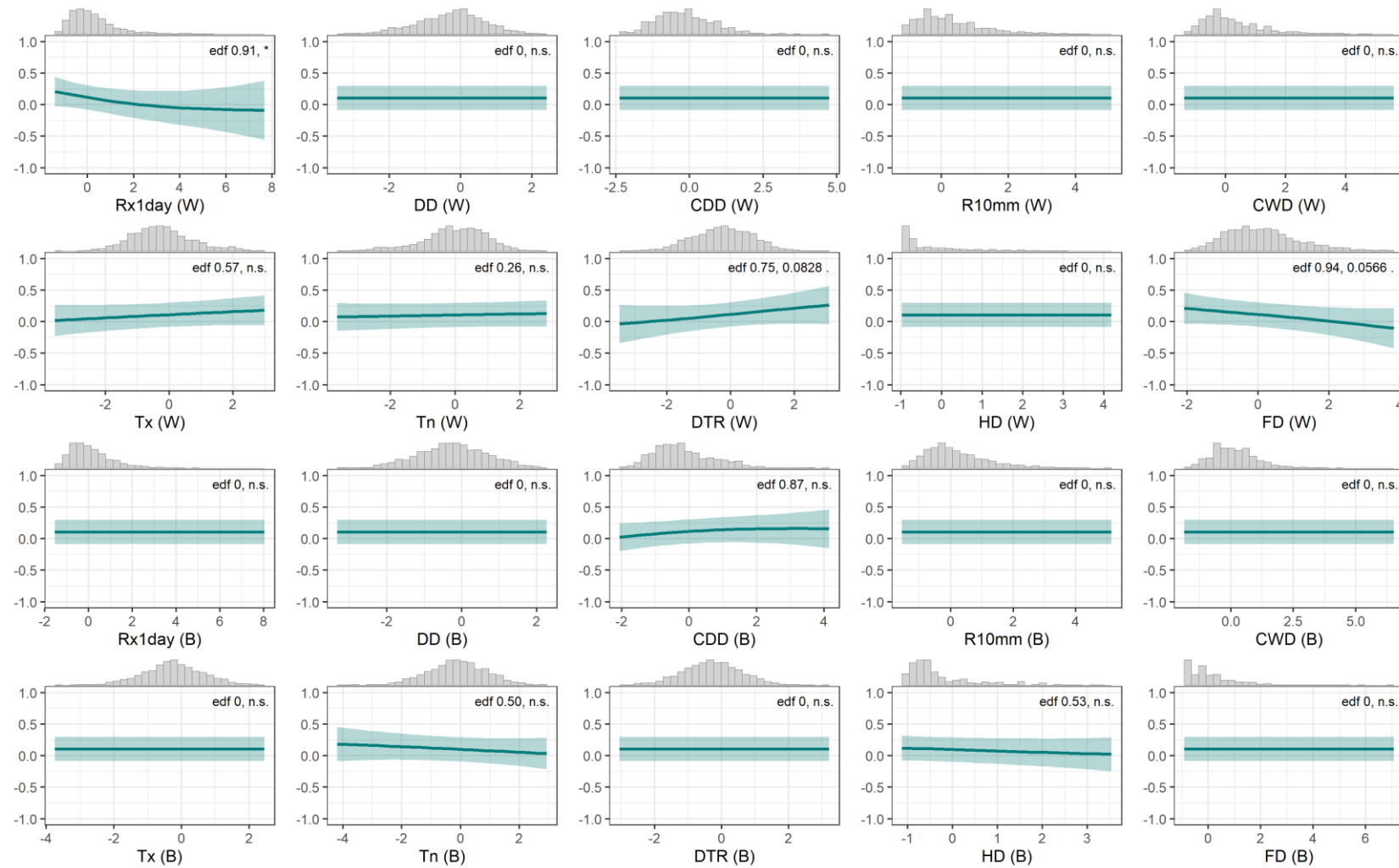


Figure A3.6-1: Partial effect plots for univariate GAMMs between Dipper abundance and each weather variable. Shaded area shows 95% CIs. Residuals of both abundance and weather variables are used. Weather variables: Rx1day = max 1-day rainfall, DD = dry days, CDD = consecutive dry days, R10mm = days over 10mm rainfall, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, DTR = diurnal temperature range, HD = hot days, FD = frost days. edf = effective degrees of freedom. Season is given in brackets after each x-variable: W = winter, B = breeding. P-values: n.s. non-significant, p-values given are near-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

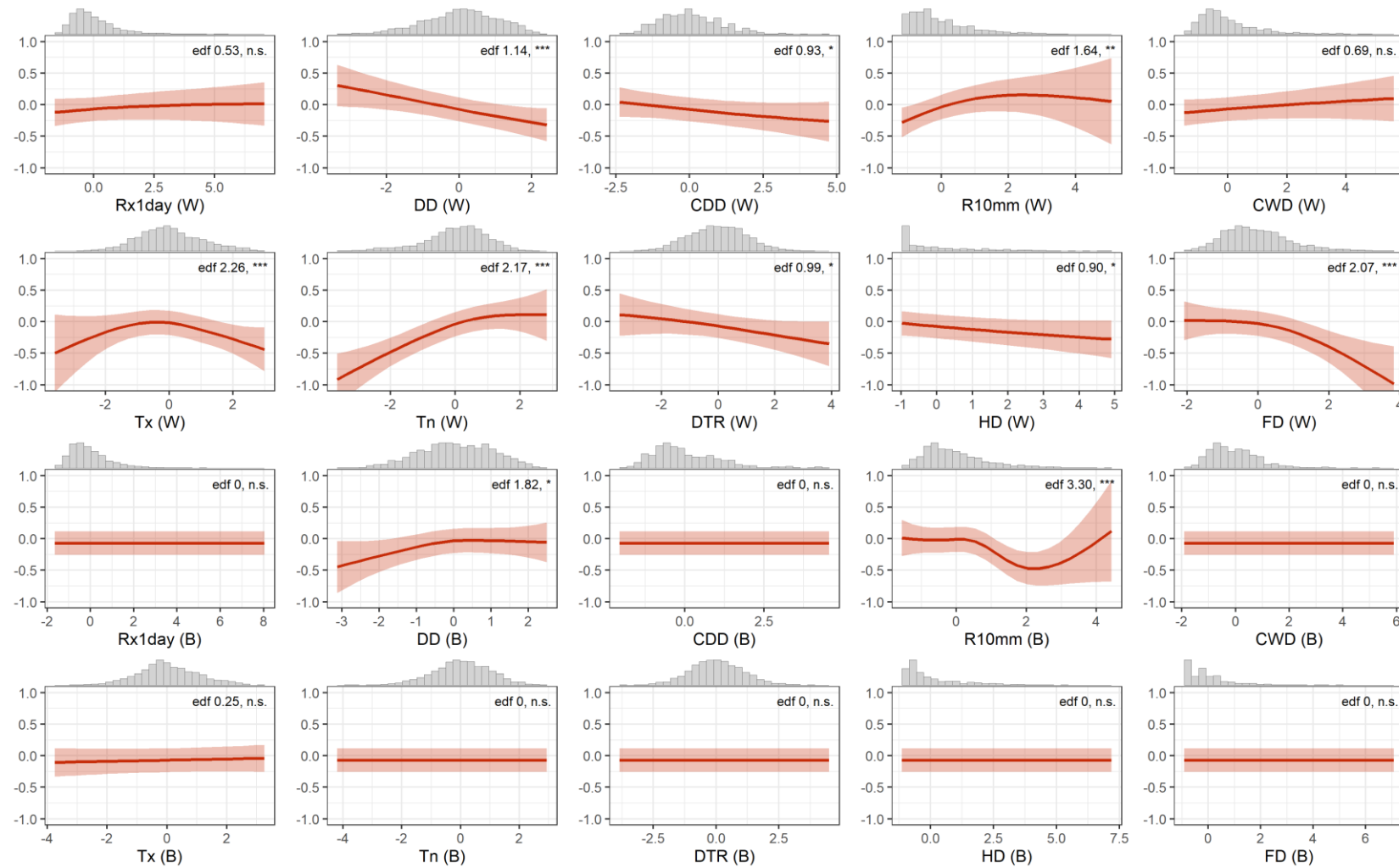


Figure A3.6-2: Partial effect plots for univariate GAMMs between Grey Wagtail abundance and each weather variable. Shaded area shows 95% CIs. Residuals of both abundance and weather variables are used. Weather variables: Rx1day = max 1-day rainfall, DD = dry days, CDD = consecutive dry days, R10mm = days over 10mm rainfall, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, DTR = diurnal temperature range, HD = hot days, FD = frost days. edf = effective degrees of freedom. Season is given in brackets after each x-variable: W = winter, B = breeding. P-values: n.s. non-significant, p-values given are near-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

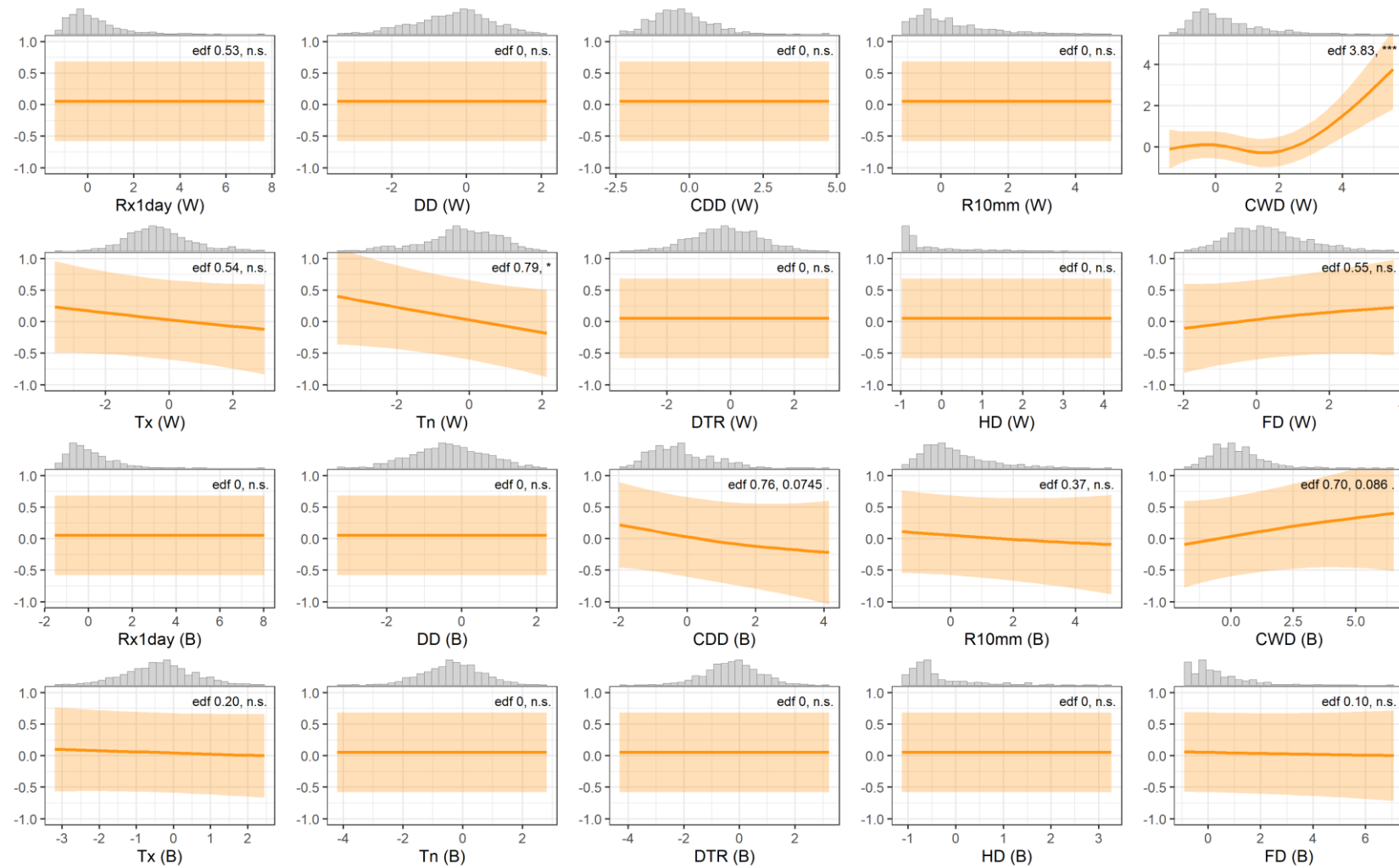


Figure A3.6-3: Partial effect plots for univariate GAMMs between Common Sandpiper abundance and each weather variable. Shaded area shows 95% CIs. Residuals of both abundance and weather variables are used. Weather variables: Rx1day = max 1-day rainfall, DD = dry days, CDD = consecutive dry days, R10mm = days over 10mm rainfall, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, DTR = diurnal temperature range, HD = hot days, FD = frost days. edf = effective degrees of freedom. Season is given in brackets after each x-variable: W = winter, B = breeding. P-values: n.s. non-significant, p-values given are near-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Appendix 3.7: Correlation test results

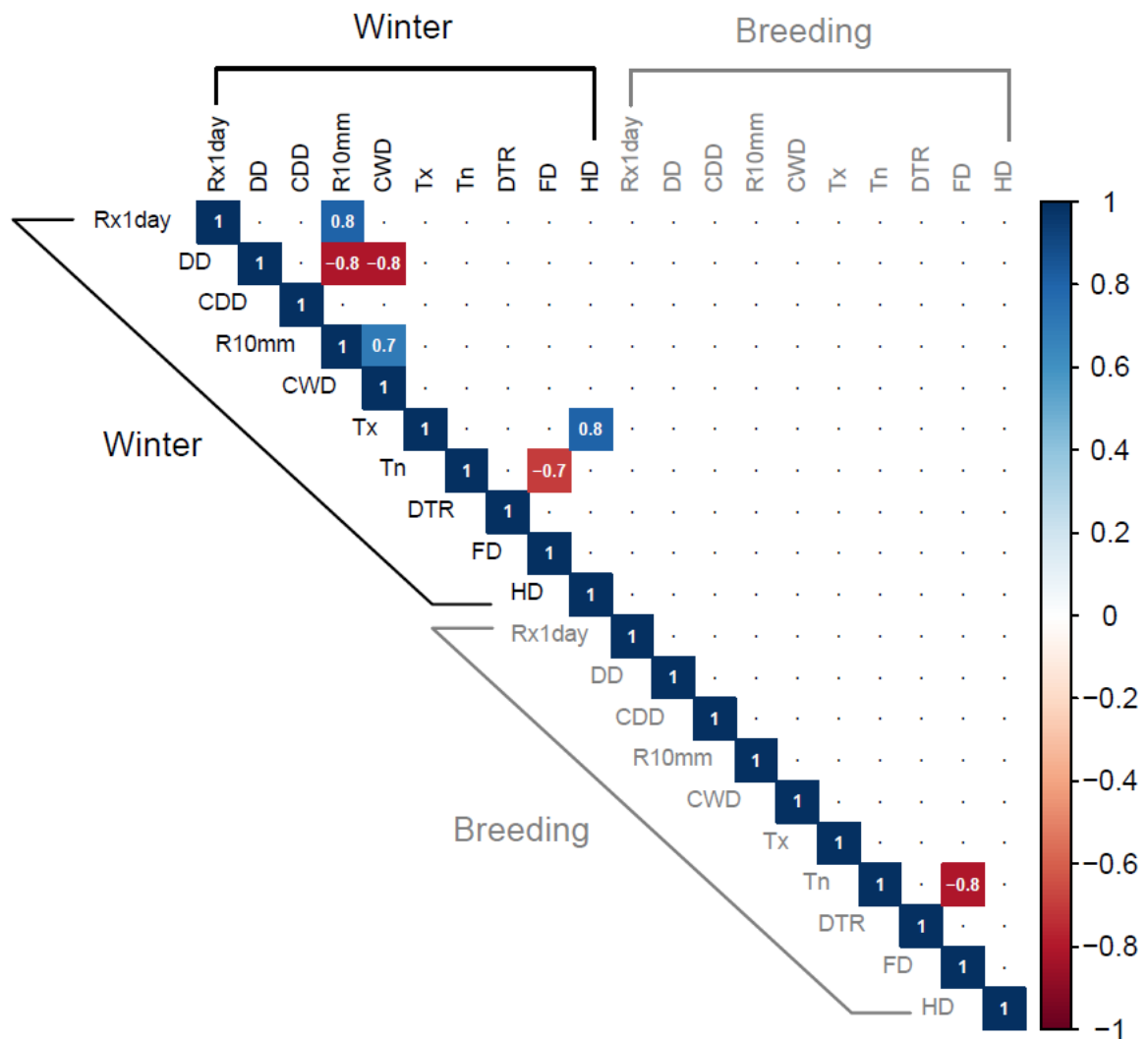


Figure A3.7-1: Correlation test results. *R* values between 0.7 and -0.7 are omitted (shown as dots) to highlight pairwise associations with high correlation (Dormann et al., 2013). Variables for winter are shown in black text, and for breeding in grey. Rx1day = Maximum 1-day rainfall. DD = Dry days. CDD = Consecutive dry days. R10mm = Days over 10mm rainfall. CWD = Consecutive wet days. Tx = Absolute maximum temperature. Tn = Absolute minimum temperature. DTR = Diurnal temperature range. FD = Frost days. HD = hot days.

Appendix 3.8: Multivariate model selection

Table A3.8-1: Multivariate GAMM structure for Dipper. Effective degrees of freedom (edf) and P-values are provided for smoothed terms to provide rationale for variable removal. Model 1 is the initial model, containing indices selected as described in section 3.3.3.3. Subsequent models involve stepwise removal of terms that displayed an edf of < 0.01, starting with the variable with the highest p-value (highlighted in orange if present). The final model is highlighted in yellow. Weather variables: Rx1day = max 1-day rainfall, CDD = consecutive dry days, Tn = min temperature, DTR = diurnal temperature range, HD = hot days, FD = frost days. Season: W = winter, B = breeding.

Model	Response	Smoothed terms	Fixed terms	Random terms	edf	P-values	AIC
1	Abundance	W Rx1day W DTR W FD B CDD B Tn B HD	Visit	Site Year	0.941 0.723 1.223 0.767 0.842 0.422	< 0.05 * 0.095 . < 0.05 * 0.124 0.055 . 0.205	15080.06

Table A3.8-2: Multivariate GAMM structure for Grey Wagtail. Effective degrees of freedom (edf) and P-values are provided for smoothed terms to provide rationale for variable removal. Model 1 is the initial model, containing indices selected as described in section 3.3.3.3. Subsequent models involve stepwise removal of terms that displayed an edf of < 0.01, starting with the variable with the highest p-value (highlighted in orange if present). The final model is highlighted in yellow. Weather variables: DD = dry days, CDD = consecutive dry days, R10mm = days over 10mm rainfall, Tx = max temperature, Tn = min temperature. Season: W = winter, B = breeding.

Model	Response	Smoothed terms	Fixed terms	Random terms	edf	P-values	AIC
1	Abundance	W CDD W R10mm W Tx W Tn B DD B R10mm B Tx	Visit	Site Year	0.046 1.610 0.806 2.120 0.000 1.193 0.882	0.183 < 0.05 * 0.091 . < 0.001 *** 0.368 < 0.01 ** < 0.05 *	22639.97
2	Abundance	W CDD W R10mm W Tx W Tn B R10mm B Tx	Visit	Site Year	0.046 1.610 0.807 2.120 1.193 0.882	0.183 < 0.05 * 0.091 . < 0.001 *** < 0.01 ** < 0.05 *	22637.97

Table A3.8-3: Multivariate GAMM structure for Common Sandpiper. Effective degrees of freedom (edf) and P-values are provided for smoothed terms to provide rationale for variable removal. Model 1 is the initial model, containing indices selected as described in section 3.3.3.3. Subsequent models involve stepwise removal of terms that displayed an edf of < 0.01, starting with the variable with the highest p-value (highlighted in orange if present). The final model is highlighted in yellow. Weather variables: Rx1day = max 1-day rainfall, CDD = consecutive dry days, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, FD = frost days. Season: W = winter, B = breeding.

Model	Response	Smoothed terms	Fixed terms	Random terms	edf	P-values	AIC
1	Abundance	Rx1day (W)	Visit	Site Year	0.000	0.614	13715.11
		CWD(W)			3.012	< 0.001 ***	
		Tx (W)			0.597	0.129	
		Tn (W)			0.874	< 0.05 *	
		CDD (B)			0.835	0.050 .	
		CWD (B)			0.783	0.077 .	
		Tx (B)			0.004	0.296	
		FD (B)			0.001	0.401	
2	Abundance	CWD(W)	Visit	Site Year	3.012	< 0.001 ***	13713.11
		Tx (W)			0.596	0.129	
		Tn (W)			0.874	< 0.05 *	
		CDD (B)			0.835	0.050 .	
		CWD (B)			0.782	0.077 .	
		Tx (B)			0.012	0.296	
		FD (B)			0.002	0.401	
3	Abundance	CWD(W)	Visit	Site Year	3.011	< 0.001 ***	13711.1
		Tx (W)			0.588	0.312	
		Tn (W)			0.875	< 0.05 *	
		CDD (B)			0.833	0.051 .	
		CWD (B)			0.778	0.078 .	
		Tx (B)			0.080	0.295	

Appendix 3.9: Multivariate model outputs

Table A3.9-1: Output from Generalised additive mixed model (GAMM) evaluating the effects of weather indices on Dipper breeding abundance. Reference level is set at early (visit). R^2 (adjusted) = 0.0034.

Smoothed terms				
	edf	Reference df	F	P-value
Rx1day (W)	0.9414	4	0.829	< 0.05 *
DTR (W)	0.7227	4	0.469	0.095 .
FD (W)	1.2232	4	1.360	< 0.05 *
CDD (B)	0.7669	4	0.420	0.124
Tn (B)	0.8419	4	0.676	0.055 .
HD (B)	0.4220	4	0.158	0.205
Fixed terms				
	Estimate	Std. Error	t-value	P-value
(Intercept)	0.107	0.098	1.097	0.273
Visit (L)	-0.158	0.039	-4.018	< 0.001 ***

Table A3.9-2: Output from Generalised additive mixed model (GAMM) evaluating the effects of weather indices on Grey Wagtail breeding abundance. Reference level is set at early (visit). R^2 (adjusted) = 0.0175.

Smoothed terms				
	edf	Reference df	F	P-value
W CDD	0.046	4	0.198	0.183
W R10mm	1.610	4	0.185	< 0.05 *
W Tx	0.807	4	0.510	0.091 .
W Tn	2.120	4	9.653	< 0.001 ***
B R10mm	1.193	4	2.301	< 0.01 **
B Tx	0.882	4	1.010	< 0.05 *
Fixed terms				
	Estimate	Std. Error	t-value	P-value
(Intercept)	-0.071	0.096	-0.741	0.459
Visit (L)	0.324	0.037	8.684	< 0.001 ***

Table A3.9-3: Output from Generalised additive mixed model (GAMM) evaluating the effects of weather indices on Common Sandpiper breeding abundance. Reference level is set at early (visit). R^2 (adjusted) = 0.0166.

Smoothed terms				
	edf	Reference df	F	P-value
CWD(W)	3.011	4	4.685	< 0.001 ***
Tx (W)	0.588	4	0.321	0.312
Tn (W)	0.875	4	1.000	< 0.05 *
CDD (B)	0.833	4	0.707	0.051 .
CWD (B)	0.778	4	0.536	0.078 .
Tx (B)	0.080	4	0.022	0.295
Fixed terms				
	Estimate	Std. Error	t-value	P-value
(Intercept)	-0.036	0.319	0.113	0.910
Visit (L)	-0.010	0.083	-0.119	0.906

Appendix 3.10: Concurvity test results

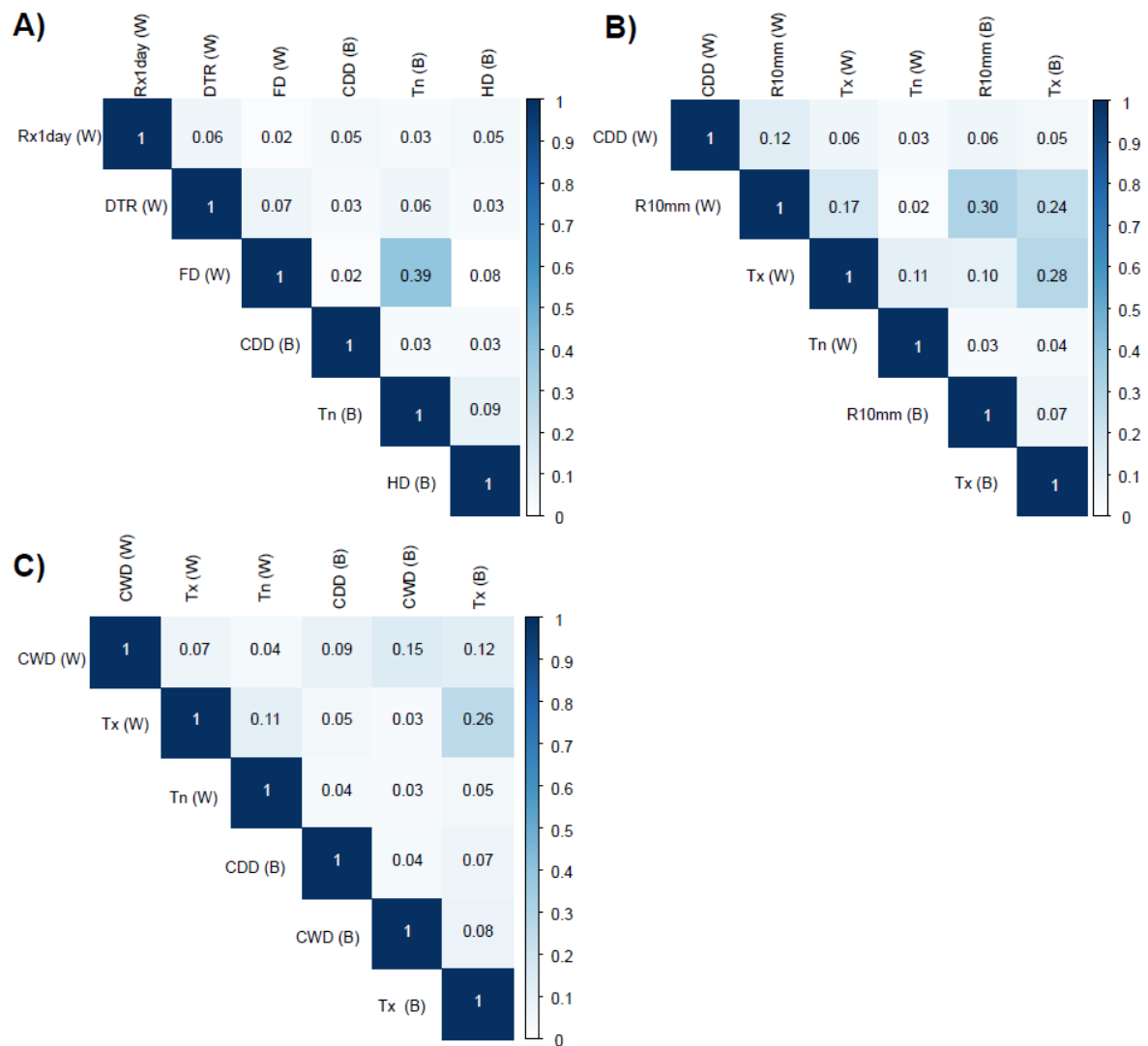


Figure A3.10-1: Concurvity test results for the (A) Dipper, (B) Grey Wagtail) and (C) Common Sandpiper multivariate GAMMs. Variable pairs with a score of >0.5 indicate a risk of poor parameter estimation, increased confidence intervals and increased risk of false significant effects if included in the same model (He, 2004). None of the multivariate models display concurvity. Weather variables: Rx1day = max 1-day rainfall, DD = dry days, CDD = consecutive dry days, R10mm = days over 10mm rainfall, CWD = consecutive wet days, Tx = max temperature, Tn = min temperature, DTR = diurnal temperature range, HD = hot days, FD = frost days. edf = effective degrees of freedom. Season is given in brackets after each x-variable: W = winter, B = breeding.

CHAPTER 4: LONG TERM BREEDING PERFORMANCE OF WHITE-THROATED DIPPER (*CINCLUS CINCLUS*) IN A SCOTTISH CATCHMENT

4.1. Abstract

Establishing causal relationships between population trends and environmental pressures is often challenging. In study systems where high-resolution environmental data is not available at an appropriate scale, it may be possible to infer causal links from ecological knowledge and recognised causes of decline in the focal species. This study investigated how breeding performance in a declining specialist passerine, the White-throated Dipper, is associated with breeding density and clutch initiation, and if these may be used as proxies for environmental change. We use a unique long-term dataset based on censusing, nest recording and bird ringing within the River South Esk (Midlothian) catchment conducted intermittently over a 43-year period. We identified a high spatial variability in Dipper breeding density despite the relatively small catchment, and a significant advancement in clutch initiation date of 14.9 days over the study period. Breeding performance was found to not vary over the study period, but some metrics displayed significant variation both within and among individual years. Furthermore, clutch initiation date had a higher impact on breeding performance than breeding density, suggestive of a seasonal decline in resource availability. These results suggest that for Dipper populations, clutch initiation, and to a lesser extent breeding density, may be suitable proxies for food resource availability and habitat quality respectively where supporting environmental data is unavailable.

4.2. Introduction

Bird populations have undergone significant decline in a variety of settings throughout Europe and Great Britain for the last few decades, with multiple studies recently highlighting the impacts of intensifying farmland practices and forest degradation on bird populations (Stanton, Morrissey & Clark, 2018; Betts et al., 2022; Rigal et al., 2023). Bird species with obligate associations with riverine and/or riparian ecosystems (e.g. White-throated Dipper (henceforth Dipper) all year, and in the breeding season, Grey Wagtail, Common Sandpiper) have similarly undergone broad-scale population decline and range contraction in recent decades (Balmer et al., 2013; BirdLife International, 2015; Massimino et al., 2023). Considering that rivers can integrate the impacts of land management and environmental change within their watershed through the contributing drainage network (Vannote et al., 1980; Durance & Ormerod, 2009), birds are likely capable of acting as an indicator for ecological degradation, both locally and within the wider catchment.

Environmental pressures on riverine ecosystems can affect birds both directly (e.g. freezing temperatures reduce body condition by limiting foraging access due to ice formation, uptake of toxic compounds through food-webs with varying lethal and sub-lethal impacts, high magnitude river flows reduce access to or wash out nests) or indirectly (e.g. pollution reduces prey richness and availability, temperature regulates prey reproduction and development). These direct and indirect pressures generate measurable responses in riverine bird occupancy and abundance (CHAPTERS 2 AND 3; Vickery, 1991; Ormerod, Boilstone & Tyler, 1985; Ormerod, Tyler & Lewis, 1985; Ormerod & Tyler, 1987; Sorace et al., 2002; Fernández et al., 2005; Nilsson et al., 2011; Royan et al., 2015; Sinha et al., 2019), body condition (Ormerod & Tyler, 1990; D'Souza et al., 2020; Pedersen, Nybø & Sandercock, 2020), breeding performance (Vickery, 1992; Morrissey et al., 2014; Nilsson et al., 2019, 2020b; Baláz et al., 2021; Elas, Rosendal & Meissner, 2023) and development (Ormerod et al., 1991; Morrissey et al., 2014).

Dippers have a close association with riverine ecosystems year-round, and are sensitive to a broad range of environmental stressors (e.g. acidification, pollution; Ormerod, Boilstone & Tyler, 1985; Ormerod & Tyler, 1987; Vickery, 1992; Morrissey et al., 2014; Pedersen, Nybø & Sandercock, 2020), making them a highly appropriate bioindicator for riverine health. However, where pressures exist, there is the potential for population decline through a variety of mechanisms, including reduced adult survival and poor recruitment to breeding populations, driven independently or by a combination of breeding performance and survival of first-year birds. As Dippers are partial migrants with a limited dispersal distance (<20km throughout their range, <10km in GB), population decline through any mechanism can result in localised, or more widespread decline. However, identifying likely causes of species decline is challenging, requiring evidence on the timing and magnitude of change, ecological knowledge of the species and the system in which they reside, and possible causes of deterioration to inform investigation.

Variation in Dipper populations has been linked to climate conditions, with reduced breeding abundance following hard or very wet winters (Chapter 3; Nilsson et al., 2011; Chiu et al., 2013) due to mortality in both adult and first-year birds. Furthermore, while acidification has declined significantly following strict regulations on air emissions (RoTAP, 2012), other pollutant sources (e.g. wastewater released from sewage and industry) are increasing in frequency (Environmental Audit Committee, 2022), alongside the persistent atmospheric deposition of toxic compounds (e.g. Polychlorinated biphenyls [PCBs], insecticides) in upland settings (Ormerod & Tyler, 1990; Totten et al., 2006). These can have equivocal ecotoxic effects on Dippers, ranging from no measurable response to altered behaviour, impaired development, eggshell-thinning, and reduced breeding performance (Maznikova, Ormerod & Gómez-Serrano, 2024). While breeding performance in British Dippers has improved on average since monitoring began in the late 1960s (Figure 4.1), metrics such as clutch size, brood size and the number of fledglings per breeding attempt display significant within and among year variation, and have begun to trend downwards. Thus, breeding

performance could be a contributing factor for decline at the population level, likely driven by environmental change.

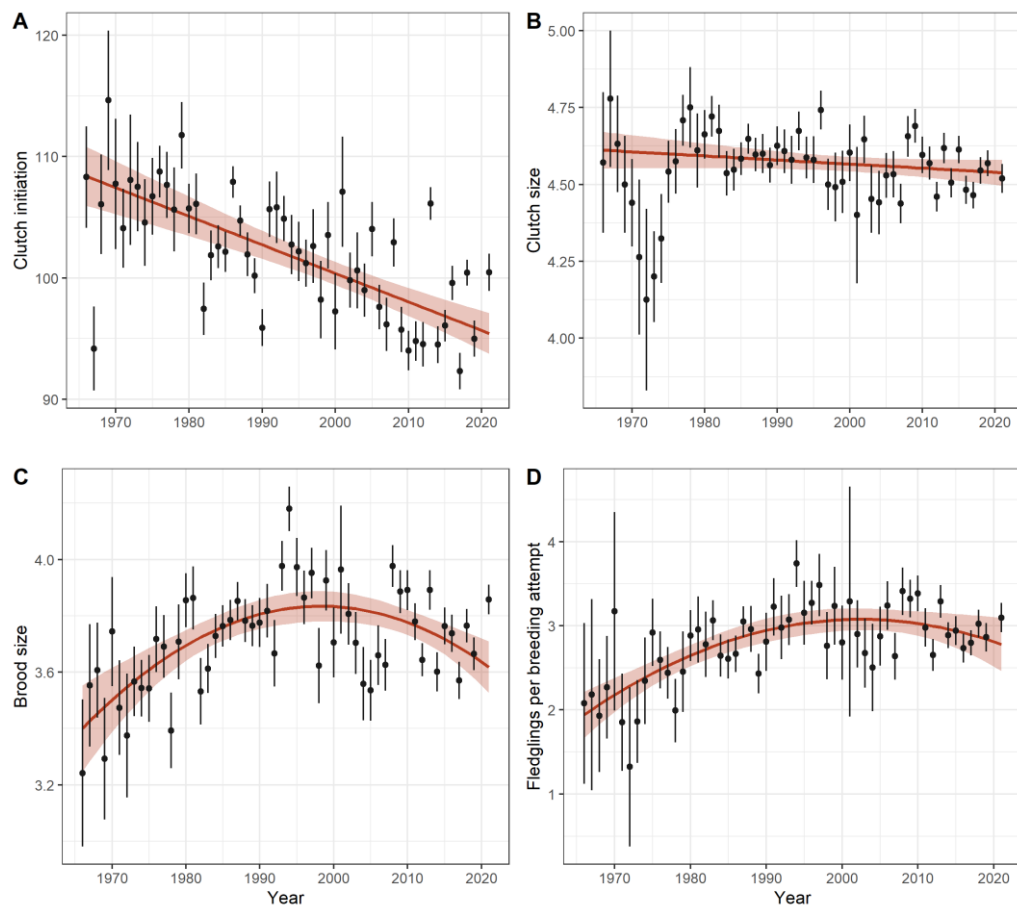


Figure 4.1: Metrics for Dipper breeding performance, estimated from data collected throughout the UK. (A) Clutch initiation date of first breeding attempts, given as day of the year. (B) Median number of eggs laid per nest. (C) Median number of chicks hatched per nest. (D) Estimated number of chicks fledged per breeding attempt. Dots show the mean value; error bars show standard error; smoothed trend is shown in red with 85% confidence limits. Reproduced from data given in Massimino et al., 2023.

This study aims to investigate whether breeding performance of Dippers in a Scottish catchment has changed significantly over the 43-year period over which it has been monitored. Identifying likely causes of any detected change is complicated by the absence of high-resolution land cover, biological or chemical monitoring data corresponding to the spatial and temporal scale of the study (1979-2022), but causal links may be possible to infer from other data, and thus inform subsequent investigation. For example, breeding density may be an appropriate proxy for habitat quality. Historically, Dippers have shown reduced density (e.g. territories per unit river length) along acidified or polluted watercourses due to the associated reduction in preferred prey items (e.g. Trichoptera, Ephemeroptera, Plecoptera; Ormerod & Tyler, 1987; Vickery, 1991), thus breeding density is likely indicative of habitat quality. However, this association may introduce

negative density dependence at both high- and low-quality habitats, whereby competition for available resources reduces breeding performance. Similarly, clutch initiation date of birds is often linked indirectly to temperature and climate change through thermal moderation of development and emergence of invertebrate prey (Crick & Sparks, 1999; Crick, 2004; Daufresne et al., 2004; Durance & Ormerod, 2007; Dunn & Winkler, 2010; Jonsson et al., 2015; Shave et al., 2019; Bründl et al., 2020). Thus, earlier lay dates are a common response to milder winters (Nilsson et al., 2019), which could be indicative of broader ecosystem responses or trends. This study uses long-term nest monitoring data to (1) explore how Dipper breeding density and clutch initiation vary within the River South Esk system (Midlothian), and (2) investigate the extent to which Dipper breeding performance is associated with year, breeding density and clutch initiation. This dataset is unique in offering a full river census; while this allows the calculation of breeding density across reaches within study system, whole river surveys are time-consuming and often avoided in favour of collecting nest recording data from multiple more easily accessible nests.

4.3. Methods

4.3.1. Study area and survey history

The Esk is a typical upland river system in central Scotland, lying south-east of Edinburgh (Midlothian, Scotland; Figure 4.2A). The 156km² catchment is dominated by highly permeable bedrock and has a median elevation of 250m. All reaches have a predominantly bedrock, boulder and gravel substrate with well distributed riffle habitat, and there is no history of acidification within the catchment (pH in 2020, range = 6.8-7.5). Mean gauged flows for the period 1998-2022 were 2.25m³s⁻¹ (NRFA, 2024). Land cover varies significantly across the study area (Figure 4.2, panels B & C), with grassland and heather dominating the upper parts of the catchment, shifting to arable, woodland, and urban at lower elevations. Land cover has remained fairly stable between 1990 and 2021 (Rowland et al., 2020; Marston et al., 2022) with slight increases in urban/suburban, broadleaved woodland, improved grassland and heather, and a reduction in arable farmland and upland acid grassland.

The breeding population of Dippers on the Esk river system has been surveyed intermittently over a 90-year period. An initial survey of both the North and South Esk rivers was completed in 1934 (Serle & Bryson, 1935), followed by annual censuses from 1962 to 1966 (Cowper, 1973). The focus of analysis in the present study applies to three subsequent survey periods, covering 1979-1986 (L.L.J. Vick, J. Ballantyne and colleagues), 1990-1991 (Wilson, 1996) and 2021-2022, which involved intensive population surveys and nest monitoring limited to the South Esk and its tributaries. Nestlings were also ringed under license during the 1990/91 and 2021/22 periods. While survey intensity varied over the three study periods due to differences in the number of

observers and onset of surveys, standardised protocols recommended by the British Trust for Ornithology (BTO) were closely followed by each observer (details on survey methods given in section 4.3.2), ensuring data consistency between survey periods. The surveys conducted between 1979 and 1991 cover 58.1km of river, ranging from 500m elevation in the Moorfoot Hills to the south, to 45m above sea level at Lothianbridge in the north. The most recent surveys in 2021 and 2022 focused on a subset of this area (29.8km of river) to maximise data collection under fieldwork limitations (i.e. river access, health and safety protocols, COVID-19). Furthermore, the southern-most area (Moorfoot) was only granted survey access prior to mid-April to reduce purported disturbance to hill-sheep lambing; this allowed censusing, but no further data collection (see section 4.3.2).

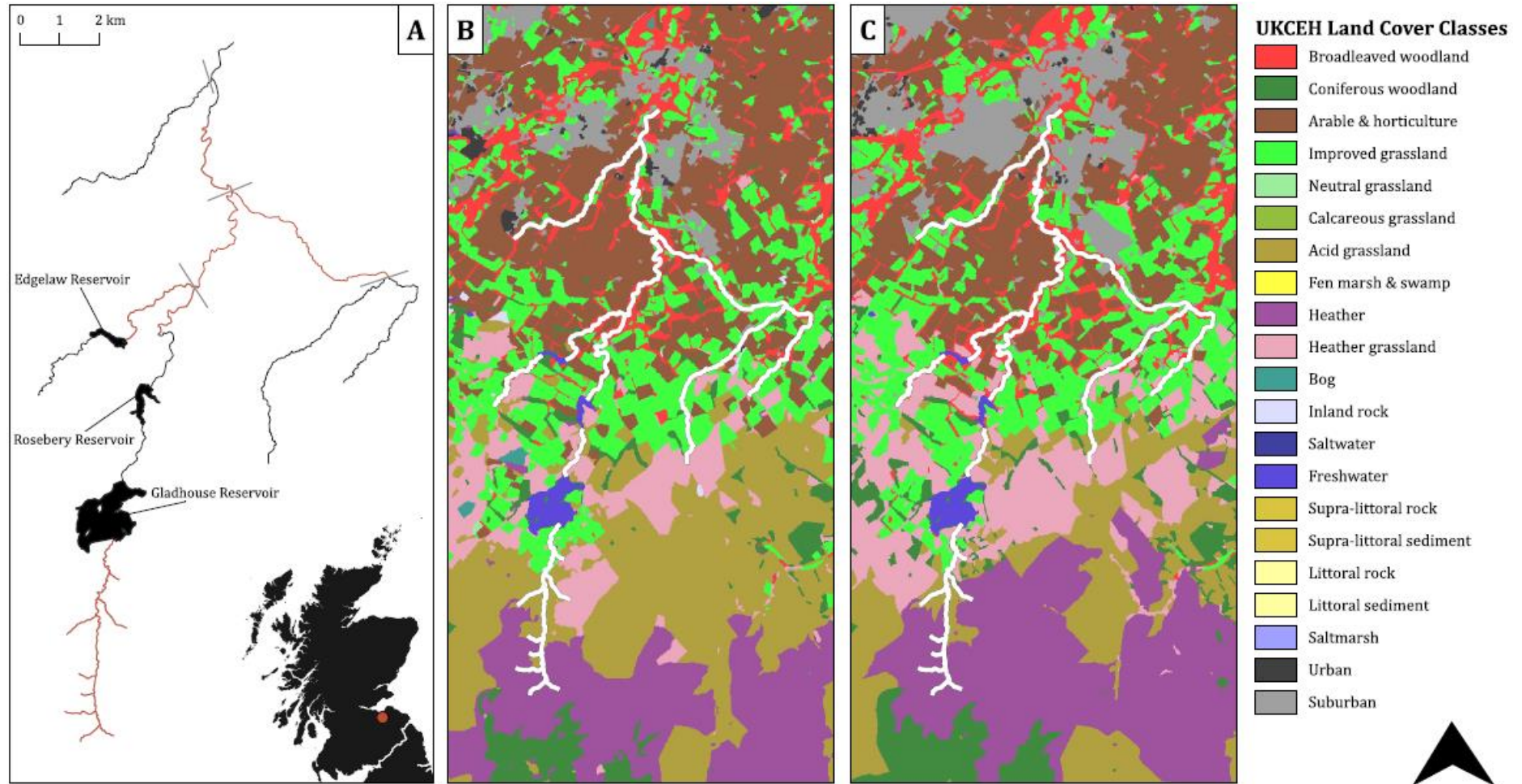


Figure 4.2: Study area location. (A) River South Esk in Midlothian, Scotland (inset); the 2021/22 study period is shown in red, 1979-1986 and 1990/91 study periods in black, reservoirs in black, and survey reaches demarked in grey. (B and C) 25m UKCEH Land cover classes for 1990 and 2021 respectively (Rowland et al., 2020; Marston et al., 2022), overlaid with the River South Esk study sections (white).

4.3.2. Data

4.3.2.1. *Territory surveys*

River sections were surveyed at least three times between January and April to record the presence of breeding pairs. Territory boundaries were estimated using the ‘doubling back’ technique (Balat, 1962), which involved driving one or both birds in a pair to the upper territory limit, at which point the bird(s) flies back downstream past the observer whilst alarm calling. Territory boundaries remained consistent to within roughly 50m until the conclusion of the breeding season in June/July. While survey intensity has varied over the years due to differences in the number of observers and onset of surveys, it is likely that a negligible number of occupied territories went undetected due to the linear nature of the habitat.

4.3.2.2. *Breeding performance*

For each territory, the active nest was located by either searching in suitable positions (Shaw, 1978; Appendix 4.1), or by following adults carrying nest material or food. Each nest was monitored, and information recorded following methods described in the BTO Nest Record Scheme (NRS; Ferguson-Lees et al., 2011). This monitoring scheme has existed in some form since 1939 (known then as the “Hatching and Fledging Inquiry”), with continual development resulting in a robust and straightforward protocol. Data collected during monitoring are detailed in Table 4.1. In 2021/22, inaccessible nests were carefully monitored using an endoscope where possible, allowing information on clutch size, brood size, nestling development, and outcome to be collected (Appendix 4.2). Where not known from field observations, lay date and hatch date were estimated based on average time periods calculated from nest record cards (Table 4.2; Shaw, 1978). Nests were not approached once nestlings were >14 days old due to the risk of premature fledging. All nest visits were timed to limit disturbance. Following the completion of a breeding attempt, the adult pair were observed to check if a subsequent breeding attempt occurred (second brood or replacement of failed attempt), which was also monitored to completion.

Table 4.1: Data collected during nest monitoring, with availability depending on study period. When unknown from field observations, variables shown in *italics* are estimated based on observations and time periods shown in Table 4.2 (Shaw, 1978). * In the absence of obvious signs of failure beyond 7–14-day old nestlings, success can be assumed.

Variable	Description	Data available		
		79-86	90-91	21-22
<i>Lay date</i>	<i>Date first egg in the clutch is laid</i>	X	X	X
Clutch size	Number of eggs in the completed clutch	X	X	X
<i>Hatch date</i>	<i>Date first egg in the clutch hatches</i>	X	X	X
Brood size	Number of live nestlings at 6-14 days old	X	X	X
Brood stage	Detail on development of nestlings:			X
	Eye development: blind, Eyes just open			
	Body feathering: naked, downy			
	Wing development: In-pin (IP), <1/3 emerged (FS), 1/3 - 2/3 emerged (FM), >2/3 emerged (FL)			
Outcome	Additional: young audible in nest			
	Failure, indicated by:			
	Observing an empty, damaged nest with/without egg-shell fragments (likely predation)		X	X
	Observing cold eggs on multiple visits, and/or deceased nestlings (likely desertion)			
	Absence of a nest which was previously identified as active (possible predation or other disturbance e.g. flood)			
	Success, indicated by:		X	X
	Observing live nestlings at 7-14 days old *			
	Observing chicks fledging the nest			
	Observing fledged young within the territory			

Table 4.2: Time periods used for estimation of key dates associated with breeding Dippers. Date ranges are calculated from nest record cards (Shaw, 1978).

Period	Description	Average time period
Incubation period	Number of days between the lay date of the last egg until the date the first egg hatches	16 days (range = 16-18)
Fledging period	Number of days from first egg hatching until first chick leaves the nest	22 days (range = 20-24)

4.3.2.3. Nestling biometrics

Data were collected from nestlings in accessible nests during the 1990-91 and 2021-22 survey periods following methods set in the British Trust for Ornithology's Ringing Scheme. Nestlings were ringed under license at 6-14 days old (Appendix 4.3), with individual colour rings also applied in 1990, 1991 and 2022 to aid identification outside of the nest without recapture. Additional information on biometrics were collected using methods described in Svensson (1992). In 1990/91, nestlings were weighed using a Pesola balance to the nearest 0.1g; the entire brood were weighed in a cotton bag, with individual weights calculated by subtraction on removal of each nestling for ringing and measuring, before being placed in a second bag. In 2021/22, nestlings were weighed individually on a digital scale to the nearest 0.1g by placing them in a plastic pot, insulated with a stretched black sock for warmth (Appendix 4.4, image A). Tarsus

length was measured to the nearest 0.1mm using an analogue calliper (methods described in Appendix 4.5). Wing codes were recorded in 2021/22 (Appendix 4.4, images B-E), with the length of exposed feather on the 4th primary also measured in 2022 using analogue callipers to the nearest 0.1mm (Appendix 4.4, image F) to assist with estimating age and assessing intra-specific development.

4.3.2.4. *Environmental data*

As some breeding performance metrics can be confounded by elevation (e.g. later clutch initiation at higher elevations) due to associations with temperature (Bründl et al., 2020), land height data were extracted from the 1:10,000 OS Terrain 5 digital terrain model gridded dataset (DTM; Ordnance Survey (GB), 2020) at each nest location (Appendix 4.6). As the nests are located along the river channel, extracted values for elevation may correspond to river level or top of a steep sided bank, thus data is used primarily as an approximation of elevation above sea-level.

4.3.2.5. *Additional metrics for breeding density and survival*

Survey reaches were established by previous surveyors as continuous sections of river, divided at confluences with main tributaries (Figure 4.2A). Over the study period, some breeding territories crossed reach boundaries, but nests remained fixed in location, only varying in occupancy. Breeding density was calculated by dividing the number of active territories in each survey reach by the distance surveyed. For some sections, this resulted in a shorter survey reach for 2021 – 22 than previous years due to focusing surveys in the core area (Appendix 4.6). Territories were determined by nest occupation (in 1979 – 91) and territory mapping data (in 2021 - 22) as nests in some territories of the latter study period were not located due to inexperience.

Nesting success was assessed using methods developed following Mayfield's original proposal for estimations (Mayfield, 1961, 1975). As many nests are located while active (e.g. during clutch incubation, or with a hatched brood) as opposed to during the build phase, the total nest success of a species or study population may be overestimated. This is particularly true for Dippers as nests often resemble natural moss growth at some stages of the build, and thus may go undetected. The Mayfield method recommends treating nests in terms of survival or mortality over the period in which it is observed (*e*, exposure days). This calculation can be subdivided into survival during incubation, hatching and to fledging, which would take into account varying conditions and therefore survival rates throughout the nesting cycle (Mayfield, 1975; Stanley, 2000). However, as nest visit intervals in this study were highly variable between observers, and visits were often postponed due to high river levels, survival is calculated for the total nesting cycle. Survival was only calculated from nests monitored between 1990 and 2022 as full nest records were not readily

available for prior surveys. Exposure (e) counts for each nest began on observation of a nest with at least 1 egg or nestling, and ended on either (1) the last day the nest was observed as active (often at ringing, but included up until the day of fledging), or (2) upon obvious signs of failure (examples in Table 4.1). As the exact date of failure is generally unknown, it is assumed as the midpoint between the last two visits (Mayfield, 1975).

This was calculated manually as a measure of overall probability of survival (P_{survival}) for the study period, but utilised statistical models to allow investigation of drivers (as described in section 4.3.3). Using Mayfield's method, the daily mortality rate (dmr) and P_{survival} is calculated as:

$$dmr = \frac{\Sigma m}{\Sigma e}$$

$$P_{\text{survival}} = (1 - dmr)^t$$

where Σm is the total number of nest failures, Σe is the total number of exposure days, and t is the average number of days from clutch initiation to fledging for Dippers ($t = 43$, totalled from laying [5 days], incubation [16 days], and fledge period [22 days]; Shaw, 1978).

4.3.3. Modelling approach

All data processing and analyses were completed in R (version 4.3.0; R Core Team, 2023). All response variables and model residuals were checked for normality prior to analysis. Normal terms were modelled using Linear Regression Models (LM), and non-normal (binomial) terms were modelled using Generalised Linear Models (GLMs), both available as functions in the standard *stats* package (R Core Team, 2023). As nests were not occupied consistently between years, nor guaranteed to be occupied by the same pair in subsequent years, a random effect for Nest ID was only included in models assessing nestling biometrics, which were required to control for non-independence of nestlings within a brood, thus were modelled using a Linear Mixed Model (LMM) in the *lme4* package (Bates et al., 2015).

A total of twelve models were run, and are detailed by response variable below. Year was set as a factor in some models to compare differences between years, and as a covariate in other models to explore change over the study period (exact period stated for each model below). Firstly, a bivariate LM was used to investigate how breeding density varied between the years of study (1979-2022) and between survey sites. Secondly, a multivariate LM tested how clutch initiation date of first breeding attempts varied over the study period (1979-2022), with breeding density and elevation. Thirdly, two identical multivariate LMs were run to assess how clutch and brood size varied over the study period (1979-2022), with breeding density, and with clutch initiation date for all breeding attempts. While clutch and brood size are counts, the concentration of values over a small range results in under-dispersion when modelled with a Poisson distribution (Zuur,

Hilbe & Ieno, 2013); hence, these response terms were modelled with a Gaussian distribution, supported by reduced AICc (Akaike Information Criterion corrected for small sample sizes) values compared with the Poisson-fitted models. Fourth, we assessed nestling growth in terms of weight and tarsus length as two separate models. For both, a univariate LMM modelled the size measure as a response to nestling age, with age treated as a second order polynomial due to the non-linear development indicated in prior research (Ormerod, Tyler & Lewis, 1986). Fifth, we assessed the effects of year, breeding density and clutch initiation date on nestling size as a two-stage process. Firstly, a bivariate LMM compared how nestling weight was associated with minimum tarsus length and study period (i.e. 1990/91 vs. 2021/22, to correct for bias between ringers), including both separate effects and an interaction term. Secondly, residual nestling weights from this model were extracted and used as the response variable in a LMM that investigated how nestling size varied over the study period (1990-2022), and in response to breeding density, clutch initiation date, and brood size. Sixth, we used two separate models to assess impacts on the probability of nest survival (P_{survival}). An initial univariate GLM explored how P_{survival} varied between survey years (1990-2022). A subsequent bivariate GLM assessed the effects of breeding density and clutch initiation date on P_{survival} . Both GLMs use a binomial distribution with a complementary log-log link function to include an offset of exposure days; the inverse form of this *cloglog* function (Gompertz function) allows nest success to be predicted rather than failure (Rodríguez, 2008). As there were only four years of data available, with a 30-year gap between survey periods and a small sample size in some years (e.g. $n=15$ in 2021), year was not included in the bivariate GLM. Finally, we used two separate models to investigate drivers of the probability of second brooding given a successful first breeding attempt (P_{second}). First breeding attempts were considered successful if at least one nestling survived to ringing age (6-14 days). An initial univariate GLM explored how P_{second} varied between survey years (1979-2022). A subsequent multivariate GLM assessed how P_{second} varied over the study period, with breeding density, and with clutch initiation date of first breeding attempts. Both GLMs utilised a binomial distribution.

All models were checked for overdispersion and heteroscedacity. Collinearity among explanatory terms in a given model were tested with Variance Inflation Factors (VIFs), using the *check_collinearity* function in the *performance* package (Lüdecke et al., 2021). All values were below 1.8, indicating an absence of multi-collinearity.

4.4. Results

4.4.1. Noteworthy nests

Many nests in the South Esk study were typical of Dipper nests i.e. they were positioned on a ledge or surface over moving water, constructed with a moss outer shell (Appendix 4.1). However, multiple nests were of unusual construction or positioned in a unique location. Furthermore,

many territories remained fixed in location between the early (1979-1991) and later (2021-22) study periods (Appendix 4.6), indicating that sites may be highly persistent through time, sometimes for many decades. Some of these nests and territories are detailed below.

4.4.1.1. Unusual nest locations/materials

Two nests monitored in 2021 were positioned in trees: one in the fork of a fallen tree directly over a small rapid (Figure 4.3, images A-B), and one in the hollow of a broken bough in a dead tree (Figure 4.3, images C-D). Very few records exist of Dippers nesting in trees (anecdotal; Shaw, 1978), which mostly utilise exposed roots (6.4%) or hollows (2.8%) overhanging the river channel. Tree nests are at considerable risk of predation from small mammals (e.g. squirrels, stoats) and birds (e.g. crows, magpies) due to their accessibility. The nest positioned in the tree fork failed at the brood stage, likely predated by a small mammal that created an access hole through the top of the nest. The nest in the hollow fledged at least one chick successfully, but the pair nonetheless moved upstream to a bridge for their second attempt.

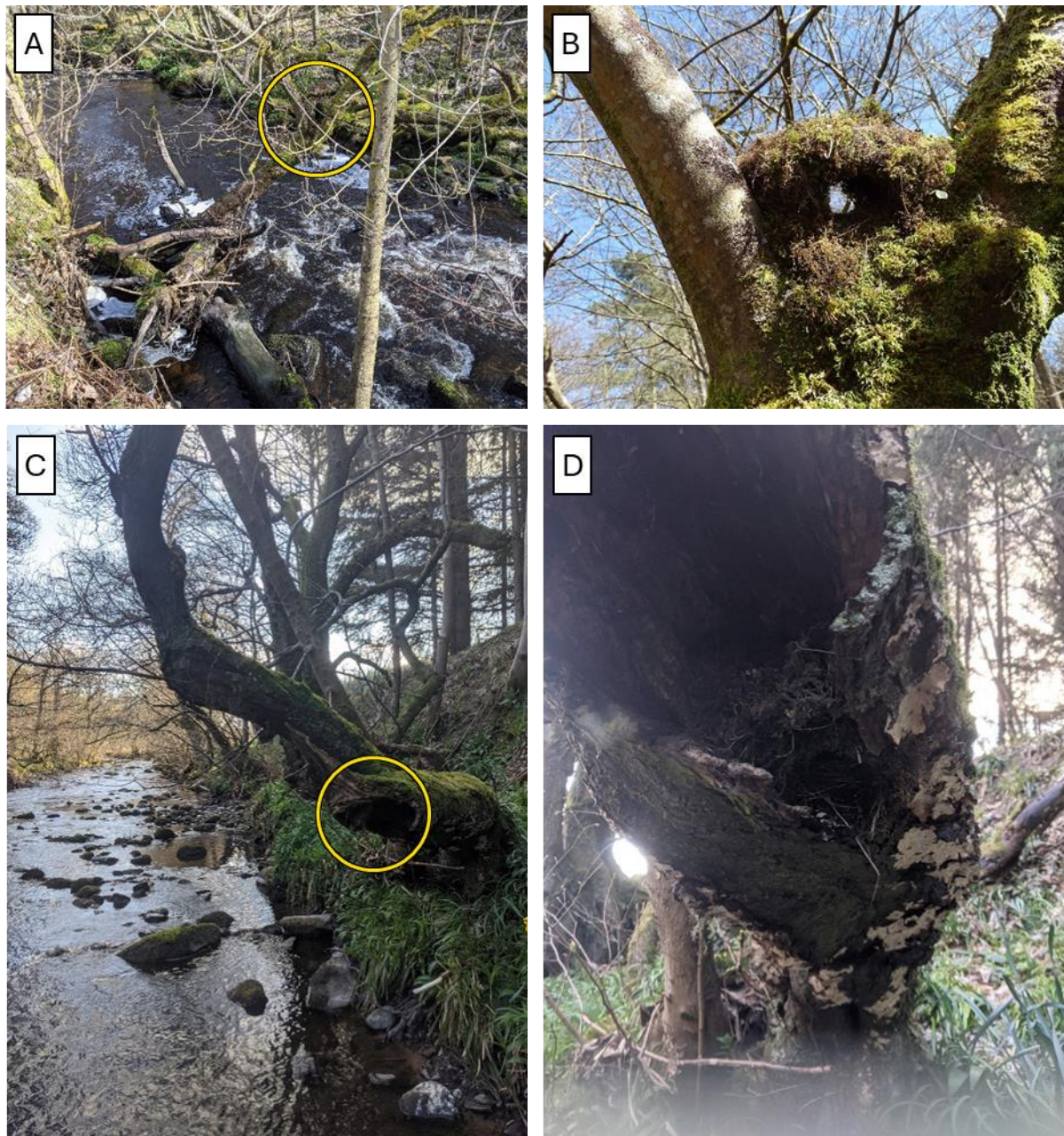


Figure 4.3: Two Dipper nests positioned in trees. (A-B) Nest positioned in the fork of a semi-fallen tree, Redside Burn. (B) Looking up through the original entrance showing the hole in the top of the nest, which was likely created during a predation attempt. (C-D) Nest positioned in the broken bough of a dead tree, River South Esk. (C) The entrance is still downwards facing, with the 'front' of the nest blocking the remainder of the hollow.

Another nest monitored in 2021-22 was positioned in a crack on the support wall of an old railway bridge (Figure 4.4). Manmade sites (e.g. bridges, walls, pipes) are regularly utilised by Dippers as they provide a stable support for the nest and can be reused year after year, in contrast to natural sites that are possibly more at risk of failure through bank erosion, vegetation management (e.g. tree felling) or cliff collapse. Generally, Dipper nests built on manmade structures still resemble the stereotypical Dipper nest, with the moss shell visible and positioned over moving water. This nest is notable for the entire nest being contained within the crack, with the entrance positioned

roughly 60cm from the wall opening. This required the breeding pair to transport nest detritus (e.g. eggshells, faecal sacs) further to the river for removal, but the nest was significantly less exposed to external conditions such as extreme temperatures or rainfall.



Figure 4.4: Dipper nest positioned in a crack within an old railway bridge support, Gorewater.

One nest monitored in 2022 was of a unique construction, rather than location. The nest was positioned under an overhanging bank within an area of improved grassland. While initially dismissed, a female Dipper was observed incubating a clutch in the nest, which was constructed primarily of grasses (Figure 4.5). There are limited supplies of moss in this territory, thus the breeding pair likely used what material was available. While highly unusual, the nest was able to support the weight of both the adult female and the completed clutch (~70g), and subsequently a brood of five nestlings to fledging.



Figure 4.5: Dipper nest positioned under an overhanging bank and constructed primarily of grass, Gorewater.

4.4.1.2. Nest site consistency

Many breeding territories have remained roughly fixed in location over the study period, as evidenced by the location of nest sites (Appendix 4.6) with only occupancy varying between years. This is indicative of a limited number of suitable nest sites, which territories are positioned around. Furthermore, while some nest sites contain multiple old nests (Figure 4.6) that pairs may be unwilling to re-use (e.g. due to high disturbance, prior predation, mite infestation), other sites contain a single nest that is rebuilt every year the territory is occupied. For example, a nest located in a disused pipe in the roof of a culvert underlying housing (Figure 4.7) was recorded as active in all three study periods (1979-86, 1990/91 and 2021/22). This highlights the importance of stability in riverine systems for nesting Dippers, with manmade sites more likely to be consistent between and within years than natural sites.



Figure 4.6: Example of three old Dipper nests at a single site that were not re-used. All nests, including those not immediately visible in the photo, are circled.

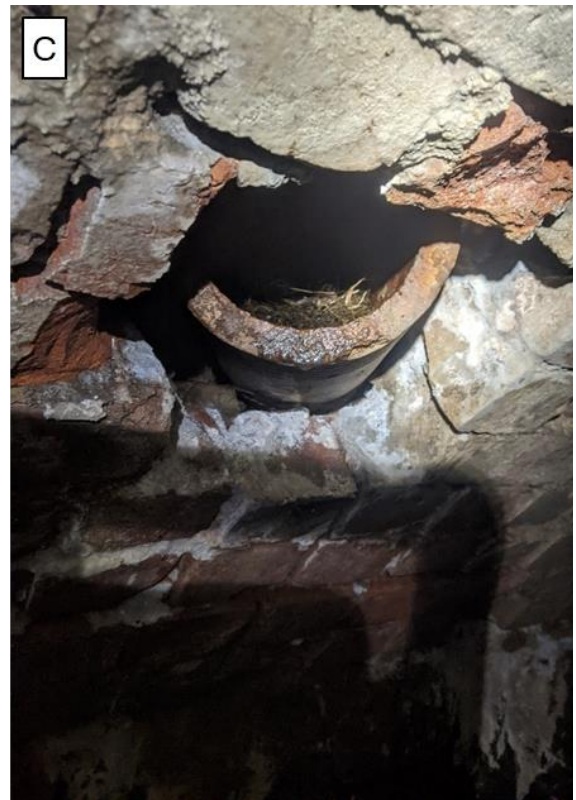


Figure 4.7: Culvert nest, which was active in all three study periods. Images show (A) the culvert opening; (B) the view looking out of the culvert from near the nest; (C) the disused pipe which supported the nest; due to the small pipe opening, this nest does not have the traditional moss front.

4.4.2. Breeding performance

4.4.2.1. Breeding density

A total of 488 active territories were identified between 1979 and 2022, giving an average breeding density of 0.82 pairs/km (± 0.58 SD) over the study system (range = 0–2.13 pairs/km). Breeding density varied significantly between reaches (LM, sum of squares [SS] = 28.782, $P < 0.001$; Figure 4.8; Tables 4.3 and 4.4), and to a lesser extent between years (LM, SS = 2.602, $P < 0.001$). Across the study area, above average densities (> 0.82 birds/km) were more common along reaches that were wider and at lower elevations (e.g. sites 2, 3 and 4), while lower densities (< 0.82 birds/km) were generally found along narrow or high elevation reaches (e.g. sites 1, 6, 10 and 11). Controlling for site, breeding densities in 1985 and 1986 were significantly lower ($P < 0.05$ and $P < 0.01$ respectively) than the reference level of 1979.

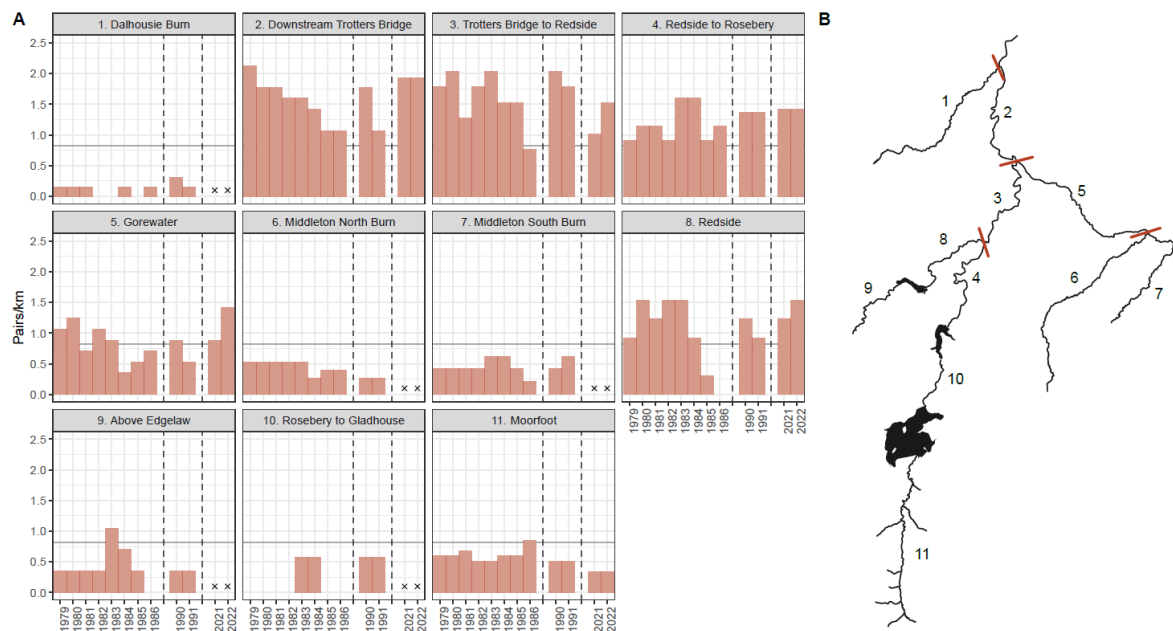


Figure 4.8: Breeding density (pairs/km) in the study area. (A) Breeding density by year and site; horizontal grey line denotes mean breeding density across study period (0.82 birds/km); dashed lines denote gaps between study periods; 'x' denotes a year in which site was not surveyed. Site numbers in (A) correspond to river stretches shown in (B); red lines demark study sections.

Table 4.3: Output from Linear model (LM) evaluating the effects of year (factor) and site on breeding density. Reference levels are set at 1979 and Dalhousie Burn (site 1) for year and site respectively. Sites are numbered to match Figure 4.8. Adjusted $R^2 = 0.785$.

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.15700	0.11506	1.364	0.1755
1980	0.08455	0.11506	0.735	0.464
1981	-0.05364	0.11506	-0.466	0.642
1982	-0.01364	0.11506	-0.119	0.906
1983	0.19000	0.11506	1.651	0.102
1984	-0.01091	0.11506	-0.095	0.925
1985	-0.24909	0.11506	-2.165	< 0.05 *
1986	-0.32364	0.11506	-2.813	< 0.01 **
1991	0.08000	0.11506	0.695	0.489
1991	-0.06364	0.11506	-0.553	0.581
2021	-0.03367	0.13895	-0.242	0.809
2022	0.19133	0.13895	1.377	0.172
2. DS TB	1.45653	0.11642	12.511	< 0.001 ***
3. TB to Redside	1.45569	0.11642	12.504	< 0.001 ***
4. Redside to Rosebery	1.10403	0.11642	9.484	< 0.001 ***
5. Gorewater	0.71319	0.11642	6.126	< 0.001 ***
6. Middleton North Burn	0.29500	0.12068	2.444	< 0.05 *
7. Middleton South Burn	0.33800	0.12068	2.801	< 0.01 **
8. Redside	0.93653	0.11642	8.045	< 0.001 ***
9. Above Edgelaw	0.29900	0.12068	2.478	< 0.05 *
10. Rosebery to Gladhouse	0.11100	0.12068	0.920	0.360
11. Moorfoot	0.41403	0.11642	3.556	< 0.001 ***

Table 4.4: Output from type-II analysis of deviance, evaluating the effects of year and site on breeding density.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Year	11	2.602	0.4517	3.248	< 0.001 ***
Site	10	28.782	2.8782	39.525	< 0.001 ***
Residuals	100	7.282	0.0728		

4.4.2.2. Date of clutch initiation

Clutch initiation date was available for 340 first breeding attempts. Clutch initiation advanced significantly by 14.9 days between 1979 and 2022 (LM, SS = 3484, $P < 0.001$; Figure 4.9A; Tables 4.5 and 4.6). Lay dates in 1986 were inconsistent with the overall trend, with a delayed median lay date of 23rd April. While clutch initiation of first breeding attempts over the whole study period spanned an average of 41 days, this ranged from 16 (in 2021) to 67 (in 1983). Clutch initiation was later at higher elevations (LM, SS = 4621, $P < 0.001$; Figure 4.9B), with an average delay of 4.2 days per 100m gain in elevation. Clutch initiation was only marginally affected by breeding density (LM, SS = 468, $P = 0.059$; Figure 4.9C), advancing by 2.6 days per additional 1 pair/km (i.e. transitioning from 0.5 to 1.5 pairs/km).

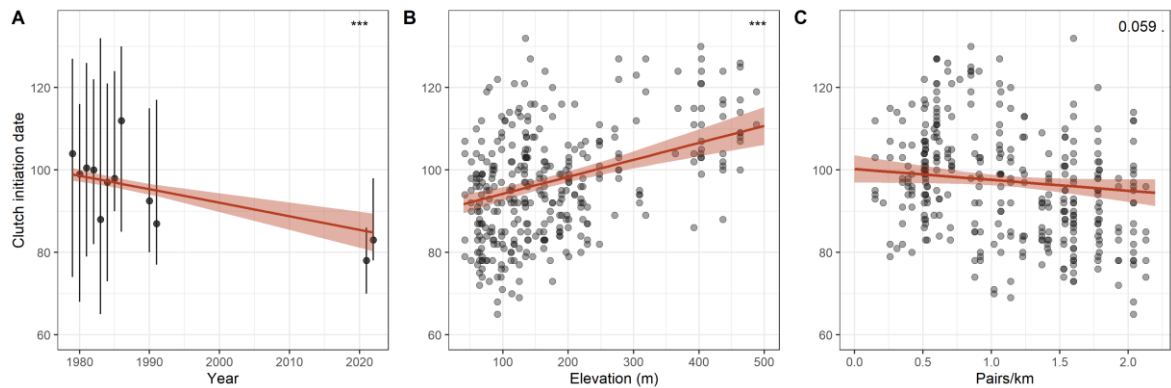


Figure 4.9: Marginal effects of (A) year, (B) elevation and (C) breeding density on Clutch initiation date for first breeding attempts. (A) and (B) show annual median lay dates and all first breeding attempts respectively. Non-focal variables are held constant at 1984 (year), 174.91 (elevation) and 1.12 (breeding density). Shaded area shows 95% confidence intervals. P-values are indicated in the top right: n.s. = non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 4.5: Output from Linear model (LM) evaluating the effects of year, elevation, and breeding density on clutch initiation date for first breeding attempts. Adjusted $R^2 = 0.266$.

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	744.263	126.234	5.896	< 0.001 ***
Year	-0.328	0.064	-5.168	< 0.001 ***
Elevation (m)	0.041	0.007	5.952	< 0.001 ***
Breeding density	-2.637	1.393	-1.893	0.059 .

Table 4.6: Output from type-II analysis of variance, evaluating the effects of year, elevation, and breeding density on clutch initiation date for first breeding attempts.

	Df	Sum Sq	F value	Pr(>F)
Year	1	3484	26.709	< 0.001 ***
Elevation (m)	1	4621	35.426	< 0.001 ***
Breeding density	1	468	3.584	0.059 .
Residuals	336	43832		

4.4.2.3. Clutch and brood sizes

Completed clutch sizes were available for 422 breeding attempts. More than 90% of clutches contained 4 or 5 eggs (Figure 4.10A), remaining consistent with previous estimates at 4.6 ± 0.66 eggs per clutch (Wilson, 1996). Clutches of six eggs were rare (3.1% of total), and more common at wider, lowland reaches (2.4%) than narrow or upland (0.7%). Only two occurrences of 2-egg-clutches were observed (1991 and 2022); these are possibly true completed clutches, but may be the result of partial clutch failure (e.g. embryo mortality, predation) where the true clutch size was missed. Clutch size did not vary significantly between 1979 and 2022 (LM, SS = 0.006, $P =$

0.905; Figure 4.10B; Tables 4.7 and 4.8), nor with breeding density (LM, SS = 0.569, $P = 0.240$; Figure 4.10C). However, clutch size decreased as the season progressed (LM, SS = 3.531, $P < 0.01$; Figure 4.10D), with average clutch dropping by 0.2 eggs for every 30-day delay in clutch initiation.

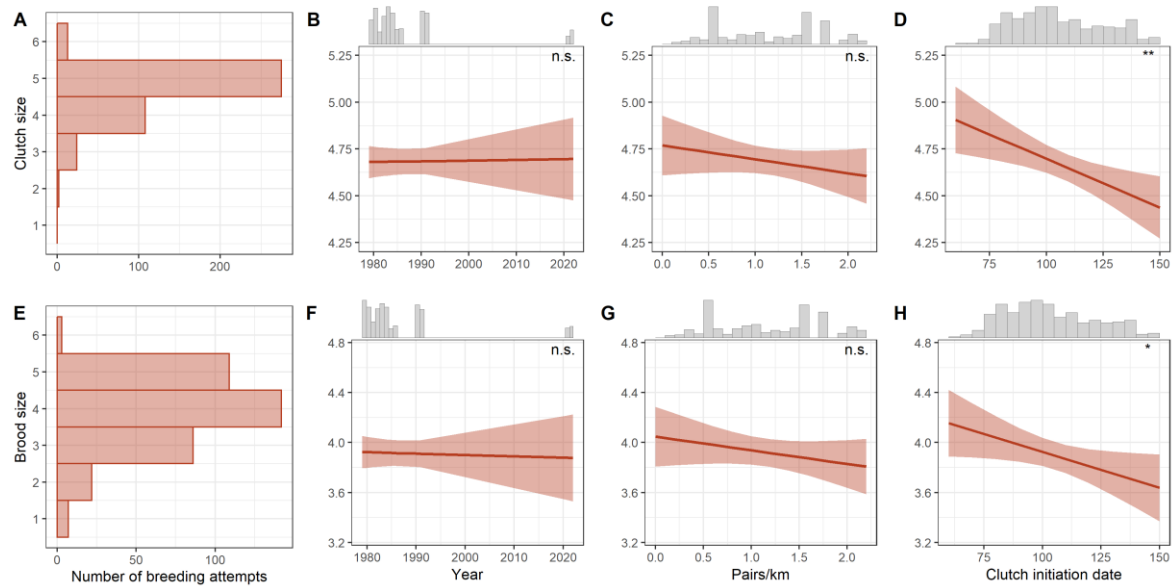


Figure 4.10: Histograms (A, E) and marginal effects of year (B, F), breeding density (C, G), and clutch initiation date (D, H) on clutch size and brood size respectively. Non-focal variables are held constant at 1984 (year), 1.17 (breeding density), 103 [A-D] and 101 [E-H] (clutch initiation). Shaded area shows 95% confidence intervals. Histograms above marginal effect plots show value ranges underlying predictions. P-values are indicated in the top right: n.s. = non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 4.7: Output from Linear model (LM) evaluating the effects of year, clutch initiation date and breeding density on clutch size. Adjusted $R^2 = 0.019$.

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	4.561	6.235	0.731	0.465
Year	0.0003	0.003	0.120	0.905
Breeding density	-0.074	0.063	-1.176	0.240
Clutch initiation date	-0.005	0.002	-2.93	<0.01 **

Table 4.8: Output from type-II analysis of variance, evaluating the effects of year, clutch initiation date and breeding density on clutch size.

	Df	Sum Sq	F value	Pr(>F)
Year	1	0.006	0.014	0.905
Breeding density	1	0.569	1.382	0.240
Clutch initiation date	1	3.531	8.585	<0.01 **
Residuals	352	144.758		

Brood size at ringing age (6-14 days old) was available for 369 breeding attempts, excluding attempts with total brood losses. Brood sizes were, on average, smaller than clutch sizes, with a mean of 3.9 ± 0.98 nestlings per brood, remaining consistent with previous estimates at (Wilson, 1996). Only 68% of broods contained 4 or 5 nestlings, and only three breeding attempts involved broods of 6 nestlings (0.8%; Figure 4.10E). Brood size did not vary significantly over the study period (LM, SS = 0.05, $P = 0.824$; Figure 4.10F; Tables 4.9 and 4.10), nor with breeding density (LM, SS = 1.30, $P = 0.246$; Figure 4.10G), but did decrease by an average of 0.2 nestlings per 30-day delay in clutch initiation (LM, SS = 4.18, $P < 0.05$; Figure 4.10H).

Table 4.9: Output from Linear model (LM) evaluating the effects of year, clutch initiation date and breeding density on brood size. Adjusted $R^2 = 0.007$.

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	6.783	9.751	0.696	0.487
Year	-0.001	0.005	-0.222	0.824
Breeding density	-0.109	0.094	-1.163	0.246
Clutch initiation date	-0.006	0.003	-2.086	< 0.05 *

Table 4.10: Output from type-II analysis of variance, evaluating the effects of year, clutch initiation date and breeding density on brood size.

	Df	Sum Sq	F value	Pr(>F)
Year	1	0.05	0.608	0.824
Breeding density	1	1.30	0.208	0.246
Clutch initiation date	1	4.18	7.598	< 0.05 *
Residuals	355	341.13		

4.4.2.4. Nestling biometrics

Between 1990 and 2022, measurements were collected from a total of 389 nestlings, of which 108 had high confidence in age estimates. Weight increased by an average of 4.7g per day (Figure 4.11A; Table 4.11A), with almost linear growth between 8 and 12 days of age. Tarsus length increased by an average of 1.6mm per day (Figure 4.11B; Table 4.11B), with a rapid rate of growth until 9 days old (+1.8mm/day), before beginning to level off at 11+ days (+0.5mm/day). Independent of age, development was found to be equivalent between the two study periods (LM, $P = 0.097$; Figure 4.11C; Table 4.12), with minimal differences in measurements between observers following transformation to correct for differences in tarsus measurement methods (LM, $P = 0.480$; Appendix 4.5). Residuals of nestling weight did not vary significantly over the four-year period (LMM, $P = 0.566$; Figure 4.11D; Table 4.13), nor with breeding density (LMM, $P = 0.665$; Figure 4.11E). However, residual nestling weight marginally declined as the season

progressed (LMM, $P = 0.085$; Figure 4.11F), and was significantly lower in larger broods (LMM, $P < 0.001$; Figure 4.11G).

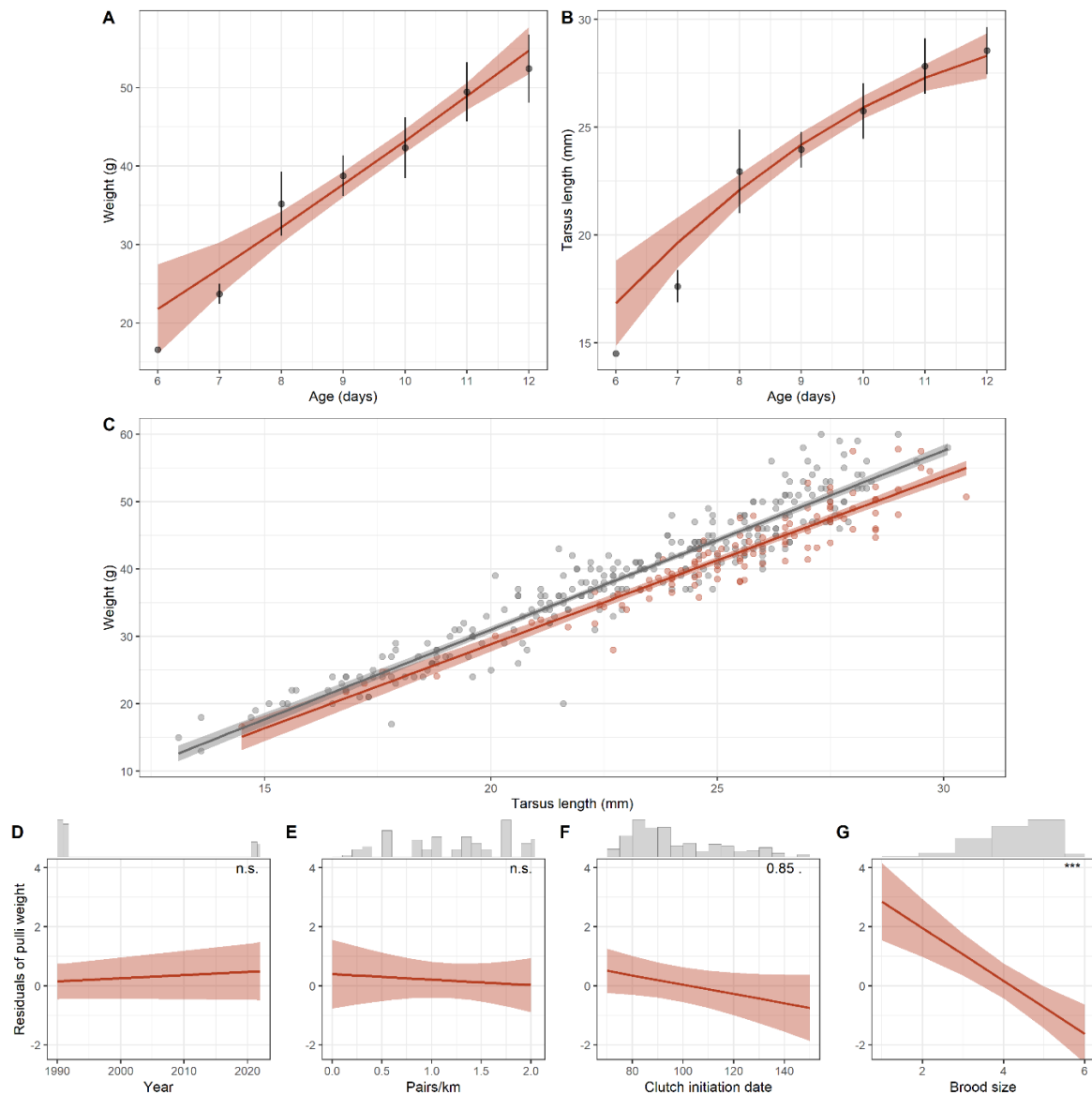


Figure 4.11: Nestling biometrics. Mean $\pm$ sd ($n = 1$ to 44) of actual values are shown for (A) Weight (g), and (B) Minimum tarsus length (mm), with a predicted quadratic curve. These are non-repeat measurements on individual nestlings. (C) Minimum tarsus length (mm) against weight (g) for the 1990/91 (black) and 2021/22 (red) study periods. Method for measuring minimum tarsus length is shown in Appendix 4.5. Marginal effects of year (D), breeding density (E), clutch initiation date (F) and brood size (G) on residuals of nestling weight. Non-focal variables are held constant at 1991 (year), 92 (clutch initiation), 4 (brood size) and 1.25 (breeding density). Shaded area shows 95% confidence intervals. Histograms above marginal effect plots show value ranges underlying predictions. P-values are indicated in the top right: n.s. = non-significant, marginal p-values (<0.1) are written, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 4.11: Output from Linear Mixed-effect Model (LMM) evaluating the effects of age on nestling weight (A) and tarsus length (B). Age is modelled as a second order polynomial term. Intraclass correlation coefficient (ICC) and pseudo R^2 values for the random effect of Nest ID are calculated with the performance package (Lüdtke et al., 2021).

	A. Nestling weight				B. Nestling tarsus length			
	Estimate	Std. Error	t value	Pr(> t)	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	42.031	0.694	60.571	< 0.001 ***	25.275	0.248	101.81	< 0.001 ***
Age ¹	71.765	5.433	13.210	< 0.001 ***	22.864	1.895	12.07	< 0.001 ***
Age ²	1.446	4.585	0.315	0.753	-3.896	1.584	-2.46	< 0.05 *
Random effects (Nest ID)								
σ^2		5.80				0.67		
τ_{00}		11.06				1.43		
ICC		0.66				0.68		
N		26				26		
Observations		108				108		
R^2 (marginal/conditional)		0.741 / 0.911				0.705 / 0.906		

Table 4.12: Output from Linear Mixed-effect Model (LMM) evaluating the effects of tarsus length and study period (i.e. 1990/91 vs. 2021/22) on nestling weight, including an interaction term. Reference level for 'observer' is set at 1990/1991. Intraclass correlation coefficient (ICC) and pseudo R^2 values for the random effect of Nest ID are calculated with the performance package (Lüdtke et al., 2021).

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-21.532	3.070	-7.014	< 0.001 ***
Tarsus	2.5160	0.120	20.922	< 0.001 ***
Observer	-2.416	3.418	-0.707	0.480
Tarsus * Observer	0.226	0.136	1.664	0.097 .
Random effects (NestID)				
σ^2		5.99		
τ_{00}		3.57		
ICC		0.37		
N		65		
Observations		377		
R^2 (marginal/conditional)		0.899 / 0.937		

Table 4.13: Output from Linear mixed-effect model (LMM) evaluating the effects of year, clutch initiation date, brood size and breeding density on residuals of nestling weight. Intraclass correlation coefficient (ICC) and pseudo R^2 values for the random effect of Nest ID are calculated with the performance package (Lüdtke et al., 2021)

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-16.033	37.133	-0.432	0.667
Year	0.011	0.019	0.577	0.566
Breeding density	-0.188	0.432	-0.435	0.665
Clutch initiation date	-0.016	0.009	-1.729	0.085 .
Brood size	-0.894	0.200	-4.478	< 0.001 ***
Random effects (NestID)				
σ^2		5.78		
τ_{00}		3.09		
ICC		0.35		
N		65		
Observations		377		
R^2 (marginal/conditional)		0.080 / 0.401		

4.4.2.5. Survival

Of 135 breeding attempts where exposure days could be calculated, the overall probability of nest survival (P_{survival}) from clutch initiation to fledging was estimated at 62.0% for the South Esk system, with a daily failure rate of 1.1%. P_{survival} remained fairly consistent between 1990, 1991 and 2021 at an average of $85.3\% \pm 3.6$ sd, but experienced a significant fall to 57.9% in 2022 (GLM, $P < 0.05$; Figure 4.12A; Table 4.14). Independent of year, P_{survival} was unaffected by both breeding density (GLM, $P = 0.126$; Figure 4.12B; Table 4.15), but was unaffected by clutch initiation date (GLM, $P = 0.179$; Figure 4.12C).

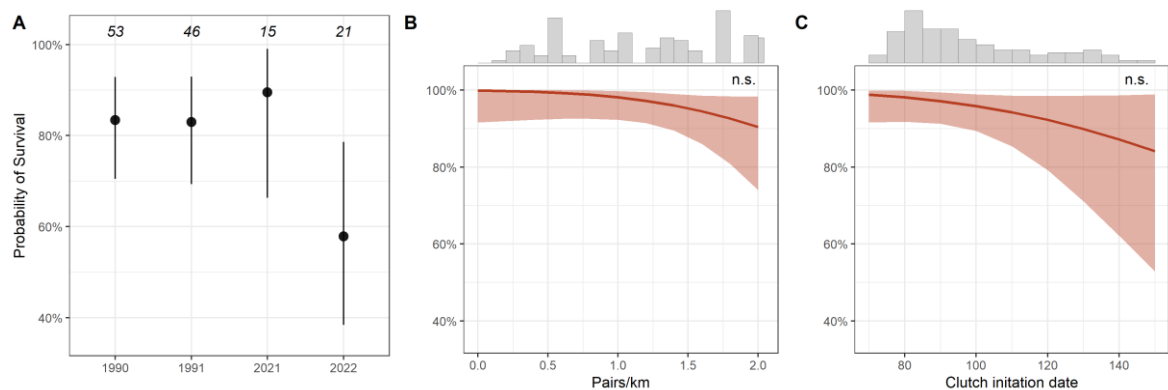


Figure 4.12: Probability of survival (P_{survival}) for year (A), breeding density (B), and clutch initiation date (C). P_{survival} for (A) is predicted from a univariate GLM, with year as a factor, with the offset of exposure held constant at 15.18 days; sample sizes are given at the top of each category. P_{survival} for (B) and (C) are predicted from a bivariate GLM; the offset of exposure held constant at 17.46 days, and non-focal variables are held constant at 92 days (clutch initiation) and 1.26 pairs/km (breeding density). Lines (A) and area (B, C) show 95% confidence intervals. Histograms above marginal effect plots show value ranges underlying predictions. P-values are indicated in the top right: n.s. = non-significant, marginal p-values (< 0.1) are written, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 4.14: Output from Generalised linear model (GLM) evaluating the effects of year (factor) on the probability of survival. Reference level is set at 1990 (year). Nagelkerke's $R^2 = 0.075$.

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-2.132	0.197	-10.814	< 0.001 ***
1991	-0.015	0.285	-0.053	0.958
2021	0.227	0.420	0.541	0.589
2022	-0.730	0.355	-2.058	< 0.05 *

Table 4.15: Generalised linear model (GLM) evaluating the effects of clutch initiation date and breeding density on the probability of survival. Nagelkerke's $R^2 = 0.128$.

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.072	0.880	0.081	0.935
Breeding density	-0.533	0.348	-1.531	0.126
Clutch initiation date	-0.011	0.008	-1.343	0.179

4.4.2.6. Second breeding attempts

Of 323 first breeding attempts where nestlings survived to ringing age (6-14 days), 71 (22.0%) were followed by a second breeding attempt. When broken down by year, there is high variation in the probability of second broods (P_{second} , Figure 4.13A). Three years saw no second broods following a successful first attempt (1981, 1985 and 1986), which may be due to false absences in second breeding attempts where observers did not visit the nest. In contrast, 2021 had significantly higher P_{second} at 69% (GLM, $P < 0.05$). There was no overall change in P_{second} with breeding density (GLM, $P = 0.112$; Figure 4.13C), but second breeding attempts were significantly more common with earlier clutch initiation (GLM, $P < 0.001$; Figure 4.13D). However, despite the overall advance in clutch initiation date by 14.9 days over the study period, the probability of second brooding did not become more common (GLM, $P = 0.700$; Figure 4.13B). This seems contradictory, but is likely due to the high variability in clutch initiation dates within some years (Figure 4.9), whereby a small proportion of pairs laid clutches early relative to the median and subsequently produced a second brood; this minority of cases is sufficient to identify the significant association between clutch initiation date and second brooding (Figure 4.13D), but is obscured in the trend for the overall study period (Figure 4.13B).

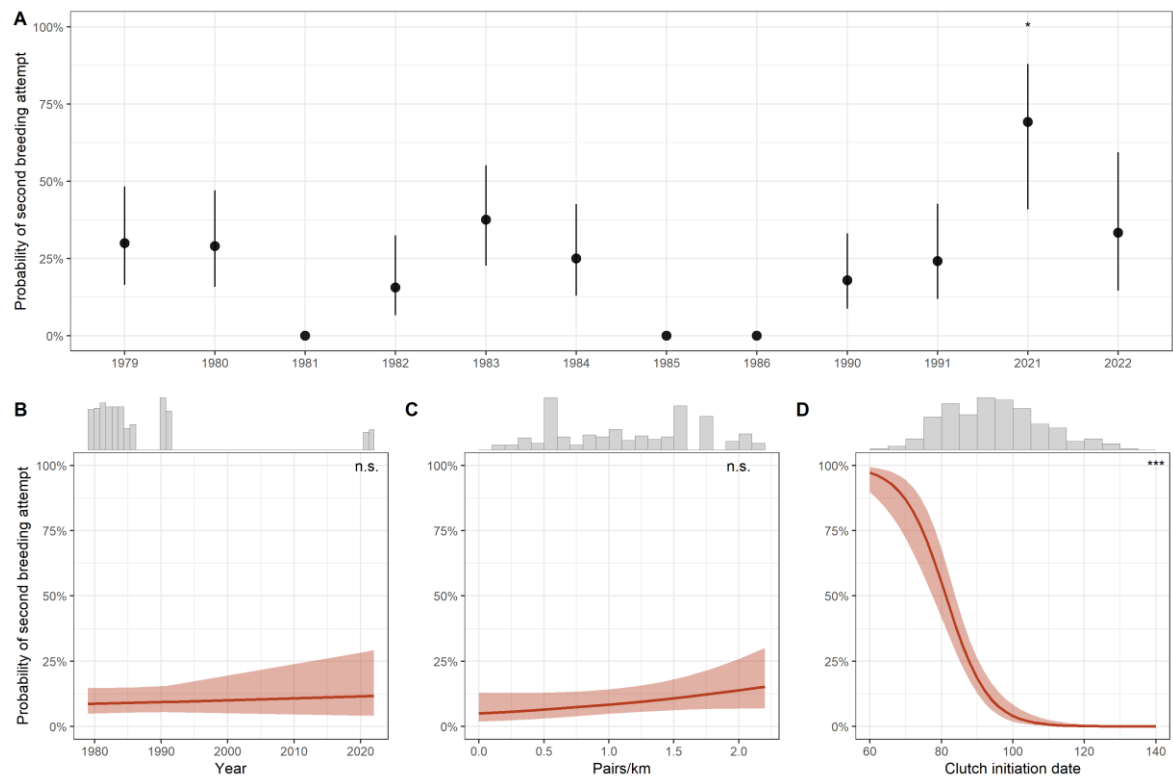


Figure 4.13: Probability of second breeding attempts following a successful first (P_{second}) for individual years (A), year trend (B), breeding density (C), and clutch initiation date (D). P_{second} for (A) is predicted from a univariate GLM with year as a factor. P_{second} for (B), (C) and (D) are predicted from a multivariate GLM; non-focal variables are held constant at 1984 (year), 1.12 pairs/km (breeding density) and 95 days (clutch initiation). Lines (A) and area (B, C, D) show 95% confidence intervals. Histograms above marginal effect plots show value ranges underlying predictions. P-values are indicated in the top right: n.s. = non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 4.16: Output from Generalised linear model (GLM) evaluating the effects of year (factor) on the probability of a second breeding attempt. Reference level is set at 1979 (year). Tjur's $R^2 = 0.141$.

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-0.847	0.398	-2.127	< 0.05 *
1980	-0.047	0.562	-0.083	0.9340
1981	-17.719	1102.527	-0.016	0.987
1982	-0.839	0.629	-1.334	0.182
1983	0.336	0.540	0.623	0.534
1984	-0.251	0.570	-0.441	0.660
1985	-17.719	1630.660	-0.011	0.991
1986	-17.719	1496.396	-0.012	0.991
1990	-0.673	0.577	-1.166	0.244
1991	-0.298	0.589	-0.506	0.6132
2021	1.658	0.721	2.300	< 0.05 *
2022	0.154	0.677	0.228	0.820

Table 4.17 Generalised linear model (GLM) evaluating the effects of clutch initiation date and breeding density on the probability of a second breeding attempt. *Tjur's $R^2 = 0.396$.*

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-2.707	29.207	-0.093	0.926
Year	0.008	0.014	0.550	0.582
Breeding density	0.563	0.354	1.590	0.112
Clutch initiation date	-0.168	0.025	-6.675	< 0.001 ***

4.5. Discussion

By using a long-term dataset from monitoring within a single river catchment, this study demonstrates the variability of breeding density and clutch initiation dates, and the subsequent effects on breeding performance of Dippers. Breeding performance (as assessed through clutch size, brood size, nestling weight, P_{survival} [probability of survival] and P_{second} [probability of second attempt following a successful first]), was found to not vary over the study period, but some metrics (e.g. P_{survival} and P_{second}) displayed significant variation between individual years that more continuous survey effort may reveal to constitute a long-term trend. Furthermore, clutch initiation date had a higher impact on breeding performance than breeding density, suggestive of a seasonal decline in resource availability.

The dataset used in this study largely follows protocols set by the British Trust for Ornithology in their Nest Record Scheme (Ferguson-Lees et al., 2011), but provides a unique insight into breeding density through census of the full river system (central core in 2021/22), a time-consuming process that is often avoided in favour of collecting data on a larger number (but perhaps biased sample) of easily accessible nests. However, while the surveys were conducted over a >40-year period, there is a significant gap in data collection between 1991 and 2021, which makes it difficult to evaluate the significant trends (e.g. clutch initiation date) across the whole study period (1979-2022) with confidence. This is alleviated slightly by comparing between years for some response variables (e.g. for P_{survival} and P_{second}) to identify the presence of anomalous years, but it is undeniable that any trends may have been supported further by surveys conducted in the interim period or an additional field season in 2020, which was unfortunately cancelled due to the Covid-19 pandemic.

4.5.1. Variation in breeding density and clutch initiation within the South Esk catchment

Breeding density averaged 0.82 pairs/km across the entire study period (range = 0 – 2.2 pairs/km), which is at the midpoint of average densities observed in neutral watercourses with similar physiography (0.5-1.0 pairs/km in Vickery, 1991). This varied significantly throughout the

study system, with higher densities generally observed along wider ($> 3\text{m}$ width) and/or lower elevation reaches ($< 300\text{m}$). One exception to this is the Gorewater (site 5 in Figure 4.8), which frequently contained reduced breeding density relative to other wide, lowland reaches in the river system; this is possibly due to the proximity of urban and improved grassland land cover (an area of low river banks often used for cattle grazing; Figure 4.2, panels B and C), in addition to a wastewater treatment plant and frequent incidents of ochre pollution caused by leachate from nearby former mines. As breeding density is negatively associated with territory length (i.e. lower densities contain longer territories on average), observations of low density are indicative of either reduced habitat quality in reaches that are subject to diffuse or point source pollution, or longer territories necessary to secure sufficient foraging habitat in narrow, but not necessarily poor quality, upland reaches. Furthermore, breeding density may reflect availability of nest sites, whereby the carrying capacity of a reach is controlled not by the availability of foraging habitat, but of suitable locations for building nests.

Clutch initiation of first breeding attempts varied both within and among years, but on average advanced by 14.9 days over the 43-year period. Lay dates were generally delayed at higher elevations, in line with observations seen in bird populations globally and likely due to lower/more variable temperatures at elevation, which may constrain invertebrate phenology (Ormerod et al., 1991; Crick & Sparks, 1999; Crick, 2004; Dunn & Winkler, 2010; Nilsson et al., 2019; Bründl et al., 2020; Baláž et al., 2021). Breeding density had no association with clutch initiation date, though this may be partially masked due to some correlation between breeding density and elevation (< 0.6 threshold value). This suggests that Dippers may utilise cues from temperature and habitat quality to gauge potential prey quality and availability, displaying flexibility in clutch initiation depending on conditions at their selected breeding site. Thus, clutch initiation date may be a better proxy for food resource availability than temperature alone.

4.5.2. Association between year, breeding density, clutch initiation, and breeding performance

While breeding density was marginally associated with earlier clutch initiation, there were no effects on other breeding performance metrics. In contrast, clutch initiation date were associated with multiple breeding performance metrics. None of the metrics considered varied over the study period, but some displayed significant variation between individual years.

Breeding density was not associated with median clutch size, likely due to strong selection on an optimum clutch of 4-5 eggs that compromises between resource availability and energy expenditure, providing flexibility in clutch size and number of breeding attempts depending on conditions at the breeding site. This contrasts sharply with other passerines such as Blue Tit (*Cyanistes caeruleus*), that have highly variable clutch sizes (2 - 16 eggs) in a single breeding

attempt, often resulting in a higher failure rate than observed in Dippers (Massimino et al., 2023). Although brood size is dependent on both the clutch size and external environmental factors that may reduce survival post-hatching (e.g. food availability, parental provisioning rates, uptake of toxic compounds through food webs, predation), breeding density was not associated with partial brood losses, nestling weight nor nest survival. Breeding density was originally proposed as a proxy for habitat quality, but this may be confounded by factors discussed above, such as watercourse width and availability of nest sites. In narrow reaches, a longer territory may be necessary to secure sufficient foraging habitat to raise young, but this is unlikely to correspond to a decline in prey quality in upland reaches due to limited potential influx of pollutants. Thus, broods located on narrow reaches are likely provisioned with high quality prey items (e.g. larvae and nymphs of the orders Trichoptera, Ephemeroptera and Plecoptera; Ormerod & Tyler, 1987; Vickery, 1991), but longer flights may result in slightly reduced provisioning rates relative to shorter territories in lowland reaches. Availability of nest sites is a limiting factor for Dippers due to their reliance on ledges or similar structures positioned over running water (Shaw, 1978; Tyler & Ormerod, 1994). Thus, reaches with limited potential nest locations may appear to have a low breeding density, despite territories being equivalent in length to reaches of a similar physiography and quality, but areas between breeding pairs remain unoccupied. Thus, breeding density alone may not accurately predict habitat quality.

Clutch initiation had a significant effect on a greater number of breeding performance metrics than breeding density. Pairs that bred earlier in the year laid larger clutches and had larger broods relative to late breeders, with no consequent impacts on nest survival, and a higher likelihood of producing a second clutch. However, smaller broods unsurprisingly yielded heavier nestlings, likely because pairs were able to focus food provisioning on a smaller number of offspring. Seasonal decline in clutch and brood sizes has been observed for sub-populations of multiple single- and multi-brooded bird species, likely as a function of declining food availability, but very few exhibit no reduction in nest survival or number of fledglings (Shaw, 1978; Winkler & Allen, 1996; Winkel & Hudde, 1997; Tyler & Ormerod, 1994; Dunn & Winkler, 2010; Bründl et al., 2020). Dippers breed unusually early in the year for passerines, with prior research indicating a synchronisation between nestling provisioning and the period of peak aquatic invertebrate biomass prior to peak emergence (early summer within temperate zones; Shaw, 1978; Baxter et al., 2017); this pattern is commonly observed in insectivorous birds, relative to their own preferred prey. As multiple taxonomic groups advance in their phenology, birds must advance their clutch initiation dates to reduce the risk of phenological mismatch between nestling demand and peak prey availability (Crick & Sparks, 1999; Crick, 2004; Thackeray et al., 2016), but there is often a lag in synchronisation between the ectothermic prey and their endothermic predators (Bründl et al., 2020). However, physical and behavioural adaptations in Dippers may allow them to benefit from earlier breeding, whilst avoiding mortality and nest failure. Firstly, through

adaptations to diving and foraging in cold-water environments (e.g. significant waterproofing, preventing water infiltration and reductions in body temperature; Tyler & Ormerod, 1994), Dippers can continue foraging even with partial ice formation (Nilsson et al., 2011). Secondly, their average clutch of 4-5 eggs is optimised to be covered fully by the brood patch of the incubating female, thus eggs are rarely exposed to lethal temperatures unlike the much larger clutches of other species (e.g. Blue Tit; Bründl et al., 2020); this may also explain why clutches of six are rare in Dippers. Thirdly, females will continue to brood young nestlings flexibly around feeding, ensuring warmth is retained in nests through cooler periods. Finally, in general, the temperature buffering effects of water, and surface runoff times also mean that freshwaters are more temporally stable than their terrestrial equivalents. Thus, while flow peaks and drought may restrict resource availability at times, Dippers may be largely insulated from the temperature and wind extremes that regularly constrain avian foraging of aerial prey (Bures, 1995).

4.5.3. Comparison with national metrics and trends

As the BTO report and provide annual predicted median estimates for multiple breeding performance metrics (Figure 4.1; Massimino et al., 2023), observations from this study population can be compared with national averages (UK). Clutch initiation in the South Esk catchment in 1979 was roughly equivalent to the UK average, with median dates of 9th and 15th April respectively; lay dates were more dissimilar in 2021 however, with the South Esk population advancing by 14.9 days over the 43-year period to the 26th March compared with a national 10-day advancement to the 4th April. This is a relatively small difference, but the faster rate of advancement observed in the South Esk catchment is consistent with steeper phenological adjustment reported in other ecosystems at more northerly latitudes, possibly due to higher variability in temperatures and overall greater impact of recent mild winters (Shave et al., 2019; Slingo, 2021).

Median clutch and brood sizes remained relatively stable from 1979 to 2021 in both groups, but were marginally larger in the South Esk population compared to the UK average, with 0.09 to 0.16 more eggs/clutch and 0.24 to 0.26 more nestlings/brood. As discussed earlier, the modal clutch of 5 eggs is relatively constant through time, but there may be high interannual variation in response to local, catchment or national conditions and pressures (Figure 4.1B) that is not reflected in an overall trend. As brood size is dependent on both the clutch size of a given attempt and environmental conditions during incubation and rearing, reductions in habitat quality potentially exacerbated by climate change may drive a larger degree of variation both within and between years compared with clutch size alone (Gaufin & Tarzwell, 1952; Maltby et al., 1995; Nedeau, Merritt & Kaufman, 2003; Ormerod et al., 2010; Morrissey et al., 2014; Windsor et al., 2019; Albin et al., 2023). Consequently, the declining national trend in brood size may be

indicative of a mechanism behind Dipper population decline (Massimino et al., 2023), though precisely what is driving this remains unclear.

Nest survival cannot be directly compared between the South Esk population and the UK averages due to differences in the methods of calculation (probability of nest survival from clutch initiation to ringing age vs. the number of fledglings per breeding attempt [Figure 4.1D] or the division of nest survival into egg and chick stages [not shown here]) and the small sample size available in this study ($n = 4$ years). Given a larger within year sample size to allow similar division of survival into egg and chick stages, alongside access to historic field notes with which to estimate exposure days, a comparison with the UK average could be made.

4.5.4. Conclusions

Dipper breeding performance within the South Esk catchment has remained relatively consistent over the 43 years since censusing was first combined with nest recording in 1979, with some metrics such as clutch size and brood size sitting slightly above the national average. Breeding performance was found to not vary over the study period, but some metrics displayed significant variation both within and among individual years that may constitute a long-term trend provided a more consistent survey effort. Furthermore, clutch initiation date had a higher impact on breeding performance than breeding density, suggestive of a seasonal decline in resource availability.

While it would be more stringent to use high-resolution data (e.g. land cover, average air/water temperature, precipitation) to model variation in breeding performance, environmental data is not always available at the spatial or temporal scale appropriate to the study, particularly when using historic data for which the direct collection of supporting environmental data is not possible. In the absence of these data, using proxies such as breeding density and clutch initiation may be appropriate, but care should be taken with interpretation. Furthermore, it should be supported by good knowledge of the study system (e.g. presence of potential pollution inputs, estimates of river widths). Breeding density may be a suitable proxy for habitat quality in Dippers, but should consider the presence of confounding factors such as watercourse width and nest site availability. However, clutch initiation may be associated with both temperature and habitat quality indirectly through prey quality and availability, and thus may be better used as a proxy for food resources than temperature alone.

4.6. Appendix

Appendix 4.1: Dipper nests construction and positioning



Figure A4.1-1: Dipper nest construction. Dipper nests are generally constructed of a moss outer shell, interior grass cup and leaf lining. The entrance is often downward facing and positioned over moving water, allowing any detritus (e.g. eggshells, faecal sacs) to be dropped from the nest and carried away by the river, concealing the nest position from potential predators. Image and illustration by R. Steenson.



Figure A4.1-2: Example Dipper nest positioning. Dipper nests are almost always positioned over moving water, on natural rock surfaces/embankments, or on human structures (e.g. bridge supports, pipes). Nest heights on the South Esk ranged from 0.5 - 3.5m over the river at 'normal' flows. Images by R. Steenson.

Appendix 4.2: Use of endoscope for nest monitoring



Figure A4.2-1: Endoscope used to view inside of otherwise inaccessible nests. The unit consists of a double-view (front and bottom) camera, connected to a Wi-Fi and battery pack. This connects to a phone, allowing a live video feed of nest contents. Image by R. Steenson.

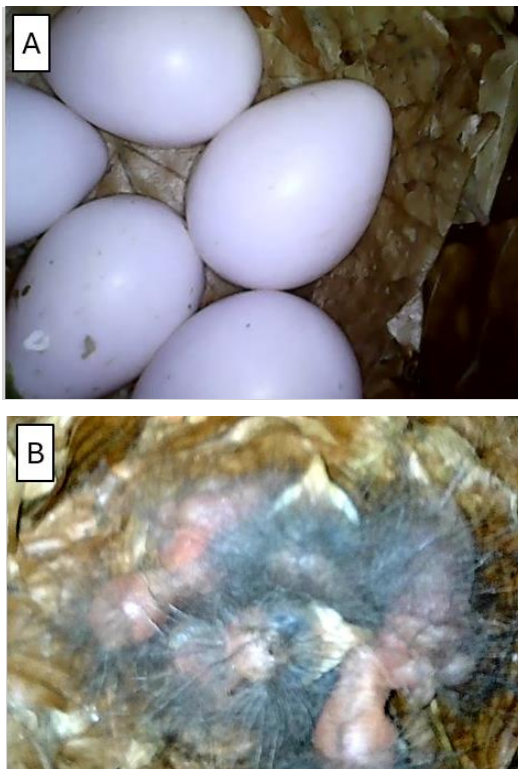


Figure A4.2-2: Example views using an endoscope to monitor Dipper nests. (A) A clutch of 5 eggs. (B) A brood of 5 young nestlings. (C) A brood of 3 chicks, estimated at 9-11 days old. Images by R. Steenson.

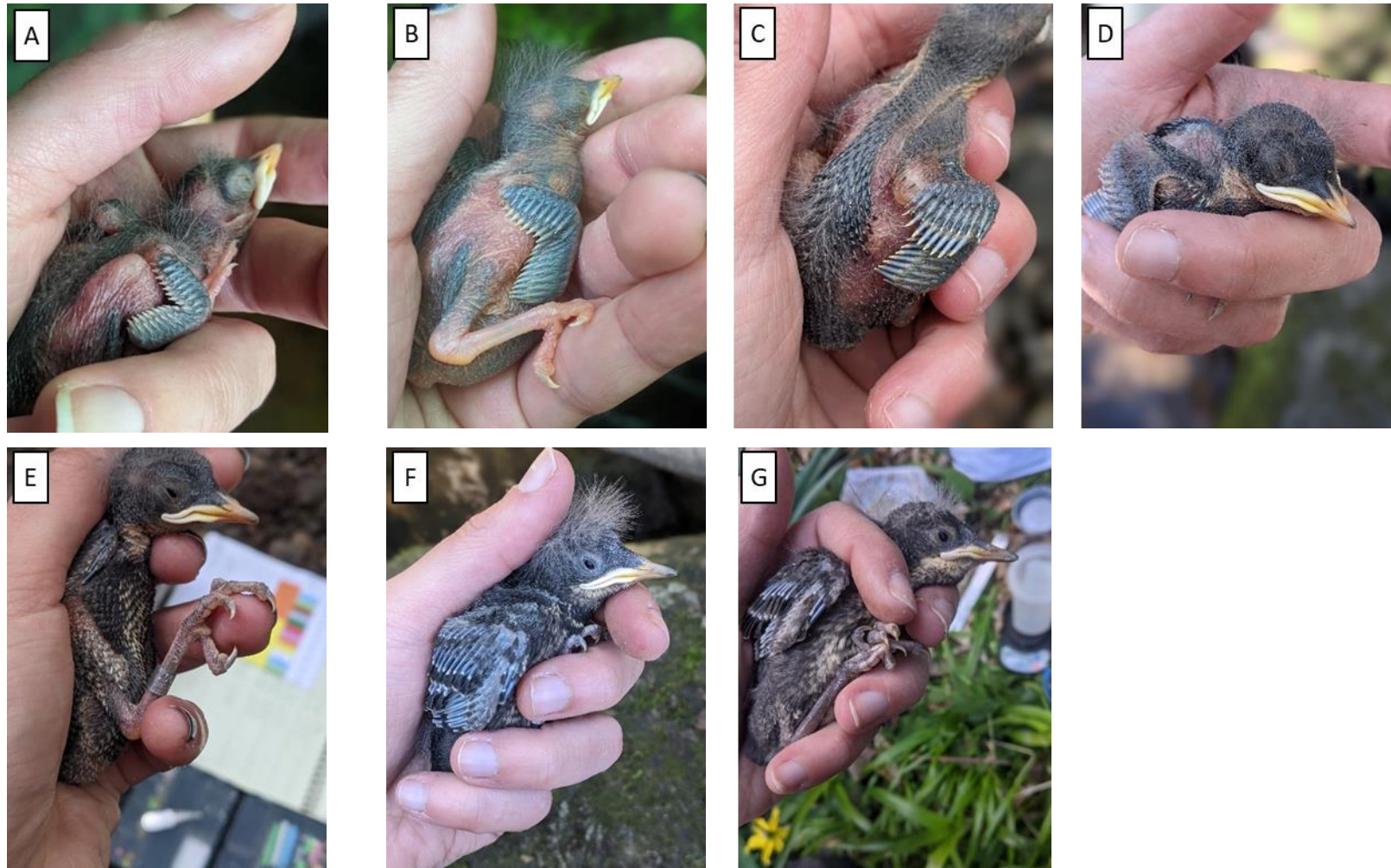
Appendix 4.3: Examples of Dipper nestling development at 6 to 12 days old

Figure A4.3-1: Images demonstrating development of Dipper nestlings at (A) six, (B) seven, (C) eight, (D) nine, (E) ten, (F) eleven and (G) twelve days old (day zero = day of hatching). Images were taken by R. Steenson during ringing to limit disturbance.

Appendix 4.4: Data collection techniques used during nestling ringing.

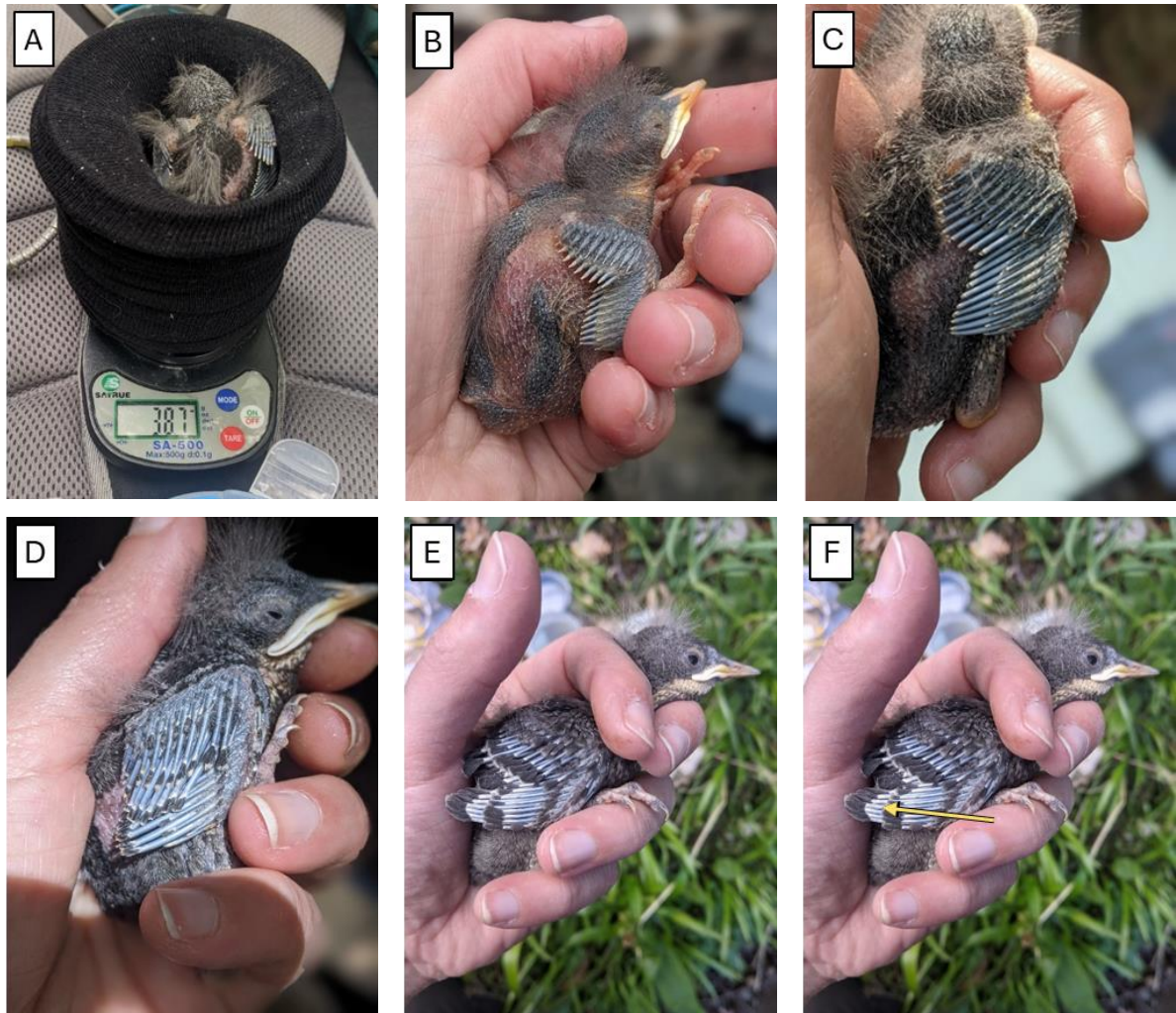


Figure A4.4-1: Images showing data collection methods during nestling ringing. (A) Nestling being weighed on a digital scale to 0.1g; the black sock is stretched over a plastic pot to create a warm and dark environment that nestlings can cling to, which was observed to reduce stress. The sock was washed in gentle detergent after use to avoid transferring mites between nests. (B) Nestling approaching IP (feathers in-pin) wing code. (C) Nestling with wing code of IP. (D-E) Two nestlings with wing codes of 'FS', indicating emergence of primary feathers between 0-1/3 of full length. (F) For nestlings with a wing code of FS, the length of the exposed feather on the 4th primary (indicated by the yellow arrow) was measured using analogue callipers to the nearest 0.1mm. Images by R. Steenson.

Appendix 4.5: Comparison of tarsi measurement methods

The tarsus length on birds is a commonly used metric for bird ringing and research, including to identify sex, for comparison of intra-specific growth rates, and as a proxy for body condition skeletal body size. There are several methods of measuring the tarsus, with the two most common shown in Figure 4.5-1. The exact method of tarsus measurement in 1990/91 is unknown, but as all birds processed in 2022 had both the minimum and maximum tarsi measurements collected to act as a reference dataset, the two methods can be compared against the 1990/91 data (Figure 4.5-2). From this, it is likely that the maximum tarsus length was measured in 1990/91.

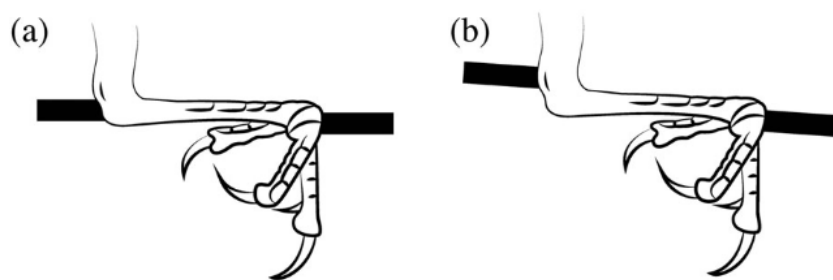


Figure A4.5-1: Methods for measuring (a) minimum and (b) maximum tarsi on birds. Image from Caravaggi et al. (2021).

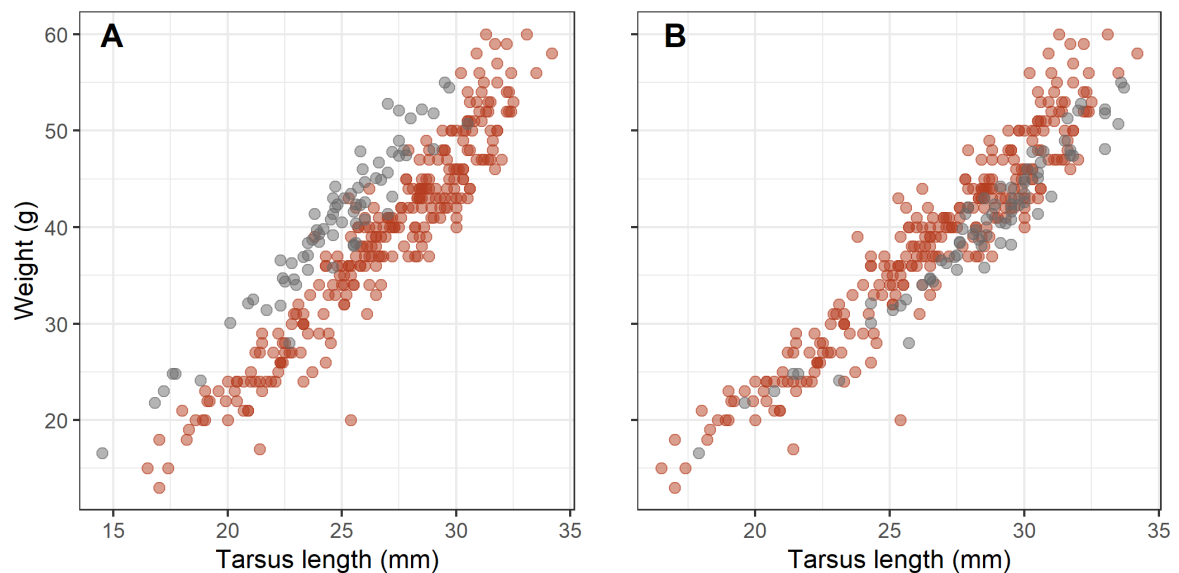


Figure A4.5-2: Comparison of tarsus length (mm) methods against weight (g). Measurements for minimum (A) and maximum (B) tarsus by R. Steenson are shown in grey, and measurements with unknown method by J. Wilson in red.

To allow for comparison of data between the two time periods (1990/91 and 2021/22), measurements of maximum tarsi (method b) recorded by J. Wilson were transformed to minimum

tarsi (method a) using a correlation slope intercept equation (described by Caravaggi et al., 2021).

This uses the formula:

$$y = mx + a$$

where y is the minimum tarsus length, m is the slope of the correlation, and x is the maximum tarsus length. The slope of the correlation was calculated as:

$$m = r \frac{SDy}{SDx}$$

where SD is the standard deviation of each of the two variables, and r is the correlation coefficient ($r = 0.9898$). The unknown variable a was calculated as:

$$\underline{y} = m\underline{x} + a$$

where $\underline{y}$ and $\underline{x}$ are the means of their respective variables. This method was tested for White-throated Dipper using the reference data collected in 2022 where both tarsi measurements were collected, before transforming the 1990/91 data (Table A4.5-1).

Table A4.5-1: Summary statistics for minimum tarsus measurements. Actual and estimated values are calculated from raw data and the correlation slope intercept equation respectively. All birds processed in 2022 had both the minimum and maximum tarsi measurements collected, allowing for a reference dataset for comparison below.

Dataset	Actual n = 72			Estimated N 2022 = 108, N 1990/91 = 214		
	min	max	Mean ± sd	min	max	Mean ± sd
2022	14.5	30.5	24.57 ± 3.14	14.4	29.6	24.57 ± 3.11
1990/91				13.1	31.7	22.95 ± 3.67

Appendix 4.6: Nest and territory position maps

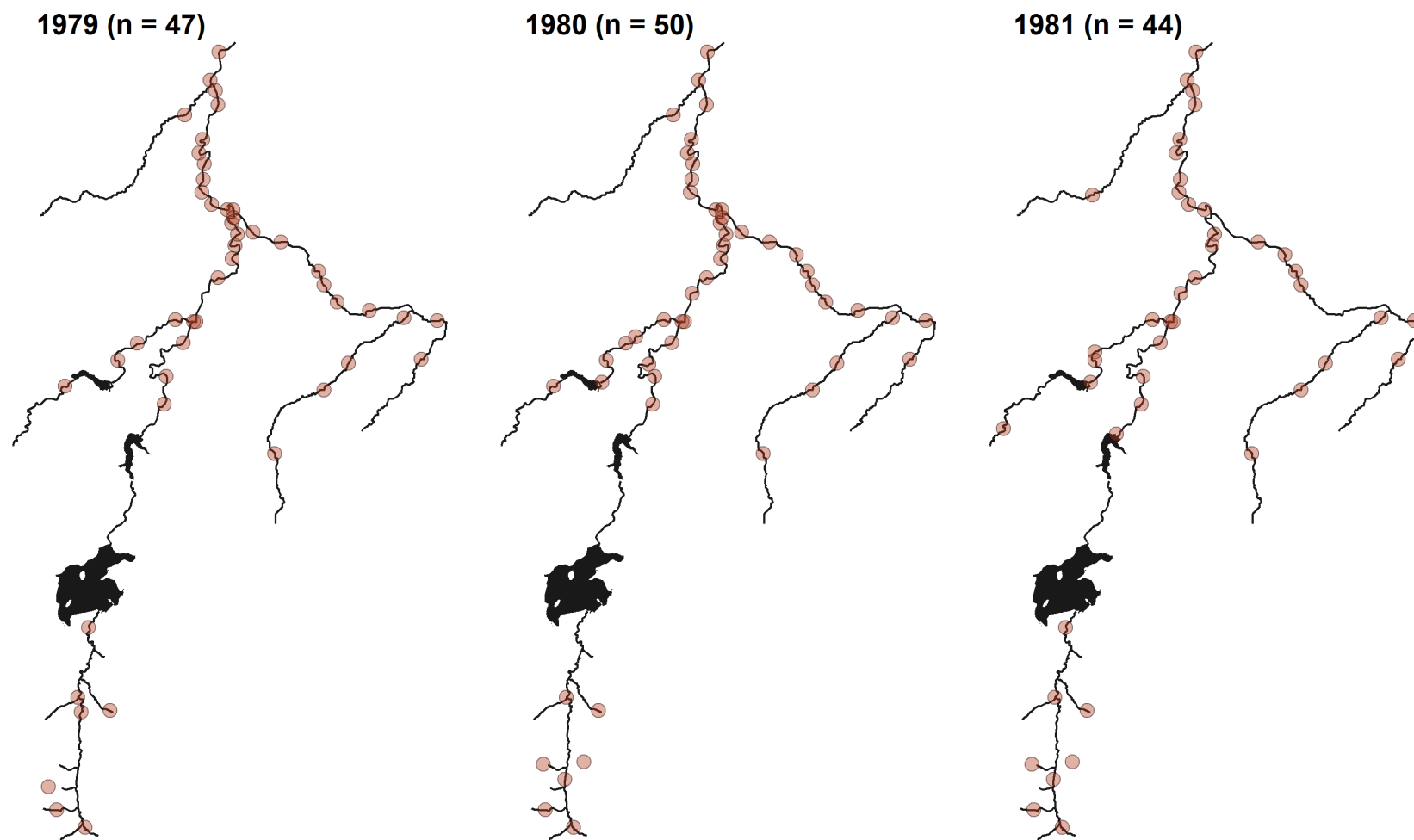


Figure A4.6-1: Location of active nests surveyed on the River South Esk in 1979, 1980 and 1981. Number of nests monitored is given in brackets. Reservoirs are shown in black.

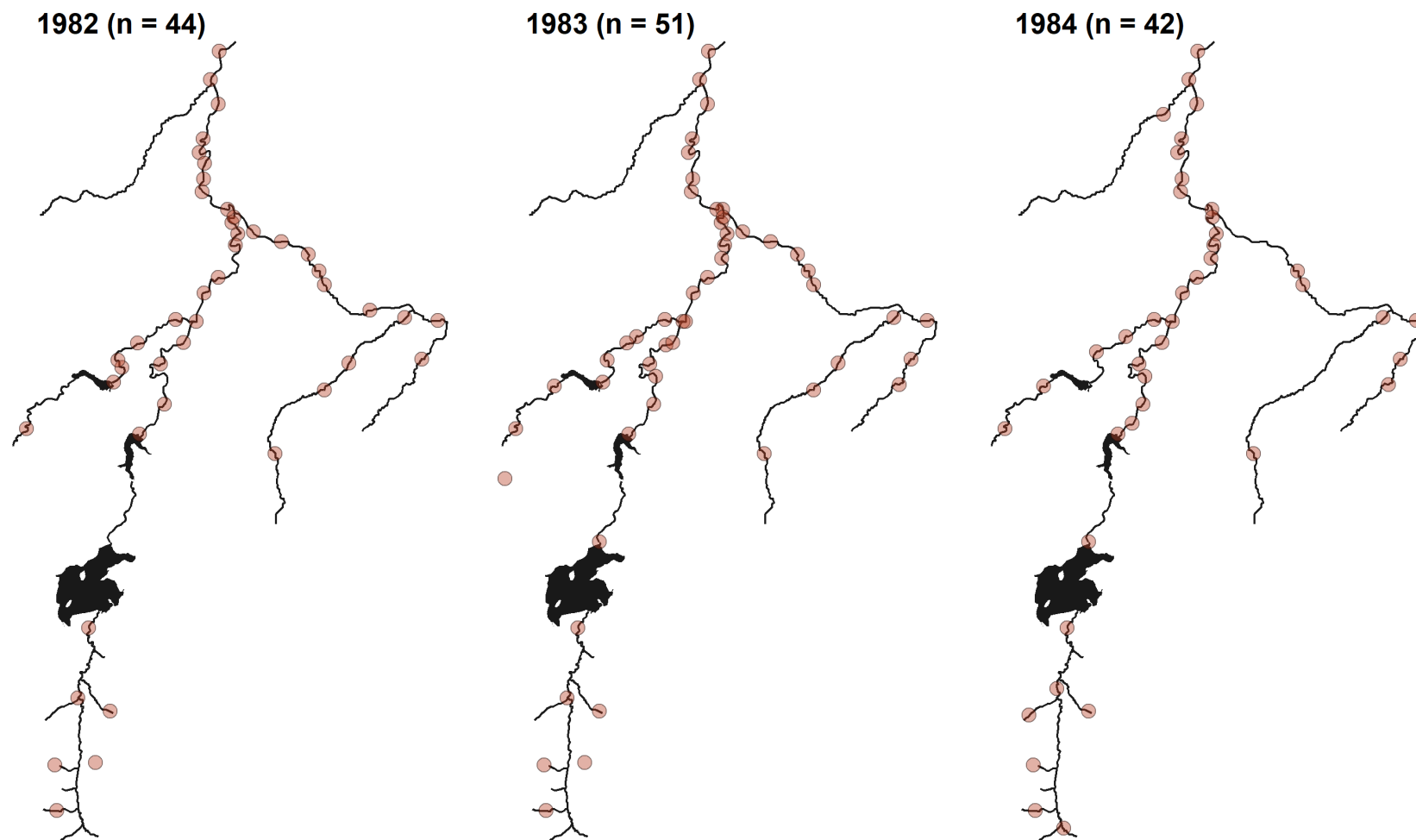


Figure A4.6-2: Location of active nests surveyed on the River South Esk in 1982, 1983 and 1984. Number of nests monitored is given in brackets. Reservoirs are shown in black.

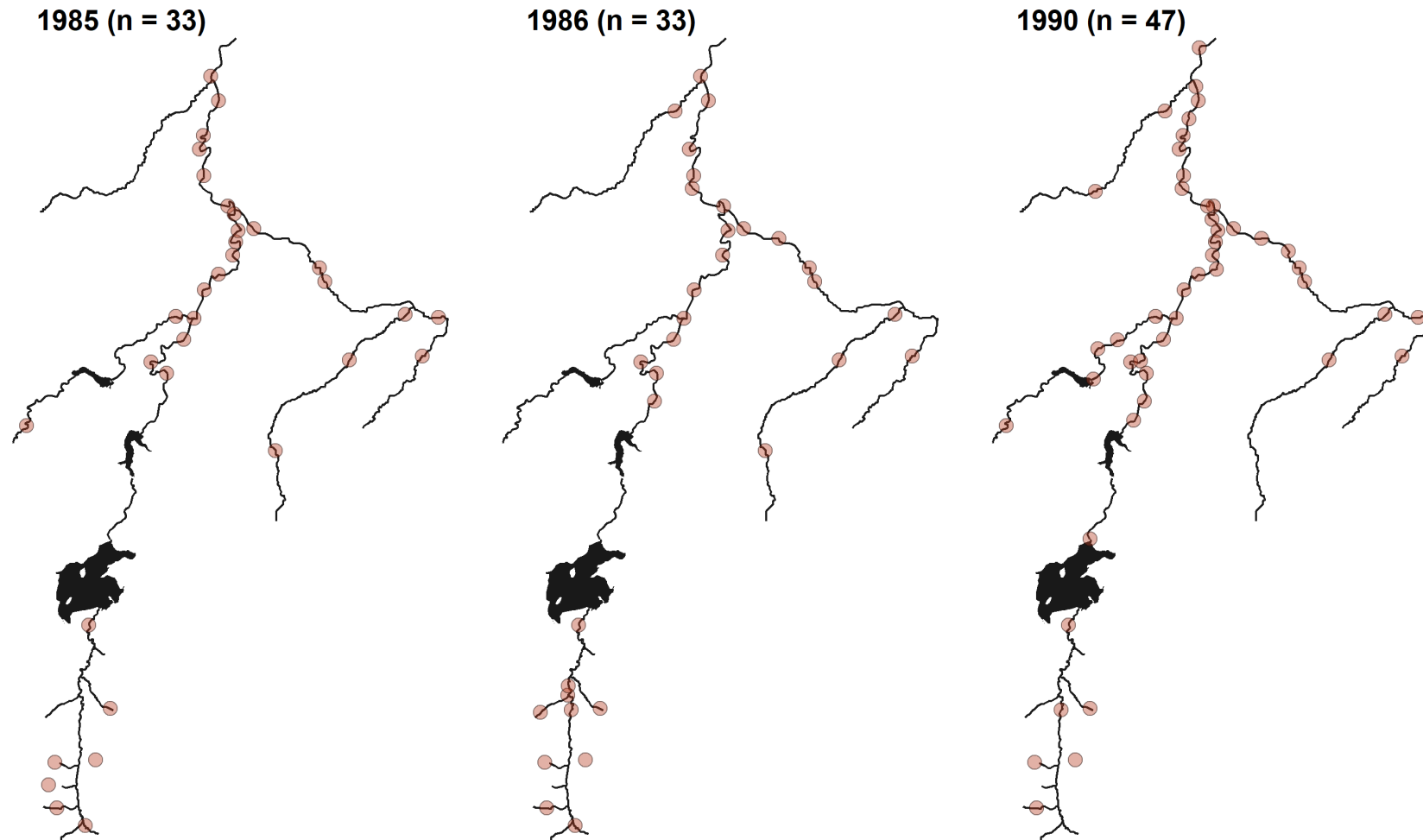


Figure A4.6-3: Location of active nests surveyed on the River South Esk in 1985, 1986 and 1990. Number of nests monitored is given in brackets. Reservoirs are shown in black. It should be noted that in 1985/86, repairs to Edgelaw reservoir (northern-most in map above) discharged a volume of silt into Redside Burn; this resulted in complete desertion by breeding Dippers in 1986, but no evidence of silting remained by the time surveys were conducted in 1990, and breeding Dippers were once again present on Redside Burn.

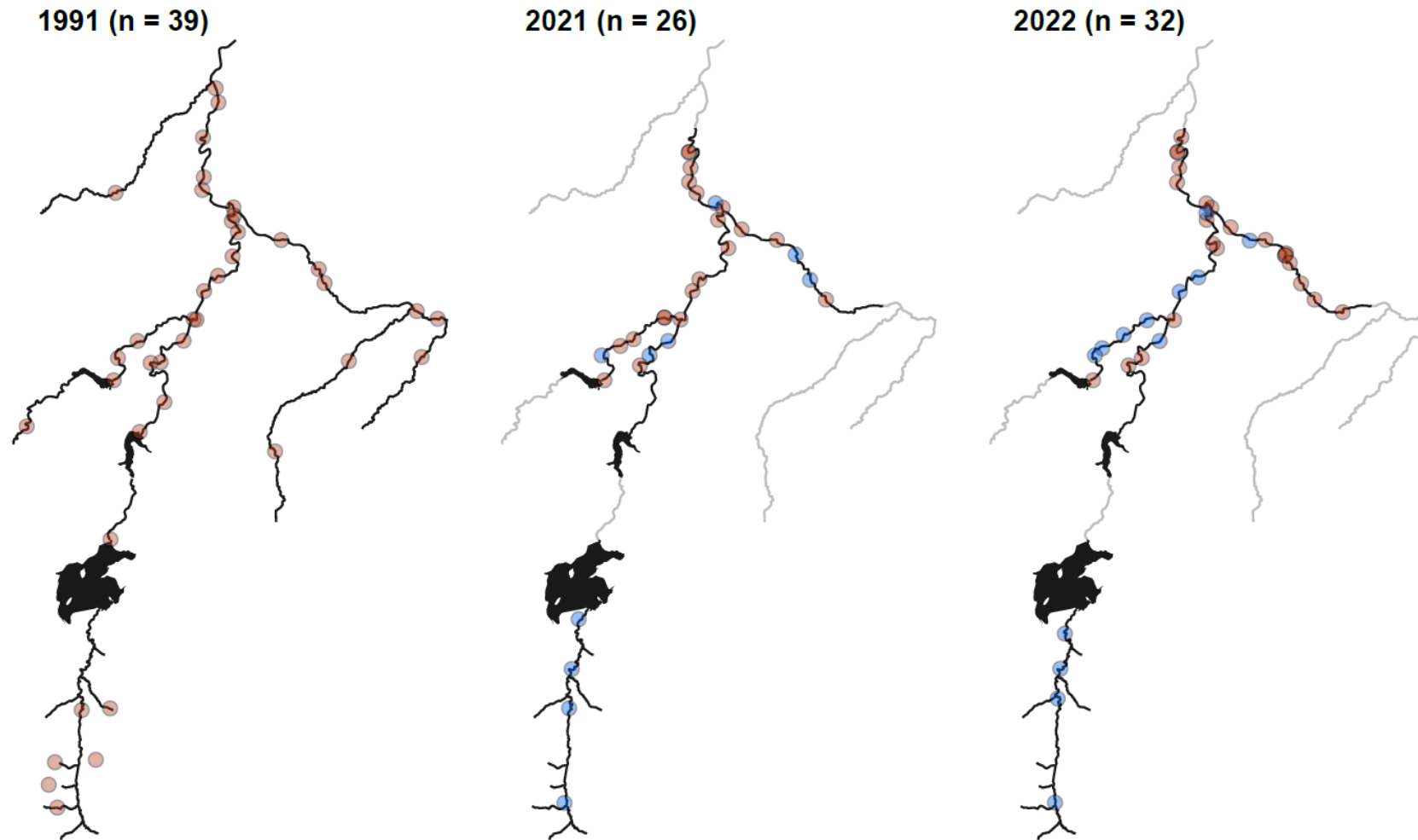


Figure A4.6-4: Location of active nests surveyed on the River South Esk in 1991, 2021 and 2022. Number of nests (red) monitored is given in brackets; where nests were not located in 2021/22, the centre point of the territory is shown in blue (included in the total count). Reservoirs are shown in black. For 2021/22, river sections not surveyed are shown in light grey.

CHAPTER 5: GENERAL DISCUSSION

Rivers are one of the most sensitive ecosystems in the world, subject to environmental pressures integrated across local, landscape and catchment scales (Vannote et al., 1980; Durance & Ormerod, 2009; Feld et al., 2018). There is a growing imperative to effectively and efficiently assess the ecological health and resilience of freshwater ecosystems (Ormerod et al., 2010), particularly to inform management strategies for restoration and conservation, but detecting the impacts of multiple - often integrated - stressors is also challenging. Traditional bioindicators such as macroinvertebrates or diatoms provide multiple advantages over direct measures, but require time and skill to quantify ecological status (Li, Zheng & Liu, 2010; Parmar, Rawtani & Agrawal, 2016; Fierro et al., 2017). Predatory birds may offer an alternative or complementary approach, applicable across a range of settings and pressures. Extensive research has reinforced the use of White-throated Dippers (henceforth Dipper) as bioindicators due to their high sensitivity to multiple riverine stressors such as acidification, organic pollution, and heavy metals (Ormerod, 1985; Ormerod, Boilstone & Tyler, 1985; Ormerod, Tyler & Lewis, 1985; Ormerod et al., 1986; Vickery, 1991, 1992; Sorace et al., 2002; Sinha et al., 2019; D'Souza et al., 2020; Pedersen, Nybø & Sandercock, 2020). However, the limited geographical or temporal scope of multiple supporting studies may neglect the complex interactions present in riverine ecosystems, which become evident over larger scales or broader gradients and combinations of stressors. More recent studies that attempt to assess multiple integrated stressors may overlook impacts on riverine birds (Birk et al., 2020) or use highly specialised datasets that may be spatially or temporally limited (e.g. pollution events, river flow; Royan et al., 2013, 2015), which may prevent their extension to national or continental scales.

5.1. Summary of research

This thesis comprises research that examines the responses of riverine birds (White throated Dipper, Grey Wagtail and Common Sandpiper) to integrated stressors of riverine and riparian ecosystems in the UK, largely utilising large-scale and open-source datasets. Chapter 1 detailed the broad range of historic and modern pressures imposed on riverine and riparian environments, and the direct and indirect responses to these of taxa across multiple trophic levels. A pertinent knowledge gap was identified in the understanding of current drivers of decline in the three focal species, highlighting their possible utility as bioindicators for both riverine and riparian ecological health.

Chapter 2 utilised Waterways Breeding Bird Survey (WBBS) data alongside a broad range of remotely derived spatially matched data on environmental variables describing site and catchment characteristics to explore the environmental drivers of spatial variation in occupancy

and abundance of the three focal species. Analyses identified that occupancy, and to a lesser extent, abundance of Dipper, Grey Wagtail and Common Sandpiper is governed by underlying physiography (slope, catchment geology, climate), but are also heavily reshaped by land cover at channel, local landscape, and catchment scales. For example, Dipper and Grey Wagtail were positively associated with riparian broadleaved/mixed woodland, but Common Sandpiper were significantly less likely to be present at a site with either riparian broadleaved/mixed or coniferous woodland. However, all three species were negatively associated with arable and horticultural land in the upstream catchment. Furthermore, while occupancy in Dipper and Grey Wagtail shared similar environmental controls, divergent responses for abundance in these two species imply different controls on bird densities, such as the territory length necessary to raise young. However, Common Sandpiper showed rather distinct occupancy and abundance responses, suggestive of a weaker association with the riverine environment. These findings are consistent with smaller scale studies (both spatially; Buckton & Ormerod, 1997, and temporally, Vaughan, Noble & Ormerod, 2007) at the site-level, but upscale knowledge in terms of responses to catchment level environmental pressures.

Chapter 3 similarly used WBBS data but in this case temporally resolved and paired with annual temperature and rainfall indices for the period 1998-2019. This study was designed to compare the sensitivity of the three focal species to variation in local weather conditions at breeding sites and to identify the species-specific weather-based drivers of abundance. Our findings indicated that all three species displayed sensitivity to at least one of the selected indices, particularly those constrained to the winter preceding the breeding season, despite some birds being yet to arrive at their breeding site. Grey Wagtail displayed significant sensitivity to hard winters, consistent with theorised drivers of decline in this species following responses to the severe winters of 1962/63 and 1981/82 (Dobinson & Richards, 1964), while Common Sandpiper were more positively responsive to implied elevated flow conditions, benefitting from consistently wet conditions both over winters preceding the breeding season and during breeding. Dipper proved the least weather-sensitive species of the three considered, but their breeding abundance was negatively impacted by hard and/or very wet winters. The differing responses observed are likely reflective of contrasting foraging, nesting, and developmental strategies of the focal species, but overall, these findings suggest that local weather conditions impose multiple direct and indirect pressures on breeding riverine bird populations.

Chapters 2 and 3 both demonstrate the unique or collective responses of riverine birds towards potential environmental pressures imposed on riverine ecosystems (Table 5.1), whether linked to hydromorphology, local land cover, catchment scale influencers of water quality, or weather conditions, and highlight the multiple direct and indirect pressures likely imposed on other taxa within riverine ecosystems. These findings support the value of riverine birds as broad indicators of riverine ecosystem health, but as the observed responses are likely reflective of the focal

species' contrasting foraging, nesting, and developmental strategies, and consequently the strength of their association with the riverine environment, their utility as indicators varies between species. Dipper and Grey Wagtail shared similar positive responses towards physical characteristics and weather conditions that would benefit multiple aspects within the broader riverine ecosystem (e.g. invertebrate richness, habitat complexity), suggesting that their presence and abundance are likely representative of riverine and riparian condition. Common Sandpiper however displayed mostly negative responses to physical characteristics (e.g. land cover) and limited response to weather conditions while at breeding sites, which complicates inference of their relationship with riverine ecosystems. Thus, Dipper and Grey Wagtail are likely suitable indicators of riverine ecosystem health, whereas the stronger association between Common Sandpiper and nearby terrestrial environments limits their utility. Furthermore, the weak-to-marginal responses exhibited by all three species towards local land cover (50/500m buffer) that may influence water quality (e.g. arable & horticulture, urban) suggests that these species may not be suitable as an indication of water quality, at least at national scales or within an integrated framework as demonstrated here.

Chapter 4 uses a long-term (43-year) dataset based on intermittent censusing, nest recording and nestling ringing to investigate how Dipper breeding performance is associated with breeding density and clutch initiation date, and whether these are appropriate to use as proxies for environmental change. We identified high spatial variability in the breeding density, indicative of varying habitat quality throughout the relatively small catchment size, but clutch initiation date was a stronger driver of breeding performance metrics (e.g. seasonal declines in clutch and brood size), likely due to declining food availability. Unusually, despite an advancement in lay date of 14.9 days over the 43-year period, none of the breeding performance metrics changed significantly over time. This pattern is most stark in the probability of second brooding, whereby earlier clutches are significantly more likely to be followed by a second breeding attempt, yet, overall, second broods have not become more common over the study period. This suggests that there is significant variation in response variables between years (consistent with national trends; Figure 4.1; Massimino et al., 2023), which may be obscured in the overall trend (e.g. 2021 had a remarkably high proportion of second brooding compared with all other survey years). Despite this, our findings suggests that for Dipper populations, clutch initiation, and to a lesser extent breeding density, may be suitable proxies for food resource availability and habitat quality respectively. Thus, Dipper breeding performance may supplement evidence of ecosystem health deterioration identified through transect surveys of breeding adults (e.g. BTO WBBS), but this information should be obtained through existing annual surveys (e.g. BTO NRS) rather than as an additional specialised survey due to the intensive effort required.

Table 5.1: Summary of results from chapters 2 and 3. Results are grouped by analysis and species, with the strength of the association identified through modelling given as strong ($p<0.001$), moderate ($p<0.01$), weak ($p<0.05$) or marginal ($p<0.1$). Relationships indicate an increase in the variable results in a positive (blue) or negative (red) response in bird occupancy or abundance.

Strength of the association found in analysis				
	Strong	Moderate	Weak	Marginal
Chapter 2: Physical characteristics				
Occupancy				
<i>Dipper</i>	Gradient Upstream arable & horticulture	Upstream peat	Broadleaved/mixed woodland (50m) Mountain, heath & bog (500m)	Arable & horticulture (500m)
<i>Grey Wagtail</i>	Gradient Bedrock permeability	Broadleaved/mixed woodland (50m) Coniferous woodland (500m)	Mountain, heath & bog (50m) Upstream arable & horticulture	Average temperature Upstream peat Arable & horticulture (500m)
<i>Common Sandpiper</i>	Gradient Upstream improved grassland	Annual rainfall Average temperature Upstream peat Upstream arable & horticulture	Broadleaved/mixed woodland (50m) Coniferous woodland (50m)	Mountain, heath & bog (500m)
Abundance				
<i>Dipper</i>			Broadleaved/mixed woodland (50m)	Gradient Mountain, heath & bog (500m) Upstream peat
<i>Grey Wagtail</i>		Broadleaved/mixed woodland (500m) Upstream arable & horticulture	Coniferous woodland (500m)	
<i>Common Sandpiper</i>			Gradient Annual rainfall Upstream arable & horticulture	Urban (500m) Upstream improved grassland
Chapter 3: Weather conditions				
Winter				
<i>Dipper</i>			High maximum daily rainfall	Below freezing/low variability in temp.
<i>Grey Wagtail</i>	Dry conditions Very cold temps.	Multiple heavy rainfall days Cooler maximum temps.	Warm or high variability in temp.	
<i>Common Sandpiper</i>	Consistent rainfall		High minimum temperatures	
Breeding				
<i>Dipper</i>			Cooler temperatures	Multiple days above 20°C
<i>Grey Wagtail</i>	Multiple heavy rainfall days		Dry conditions	
<i>Common Sandpiper</i>				Consistent rainfall



Figure 5.1: Dipper nestlings waiting at the nest entrance for food. Image taken by R. Steenson (2021).

This final discussion chapter uses the main findings of this research to examine the suitability of the focal species (Dipper, Grey Wagtail and Common Sandpiper) as indicator species for riverine and riparian quality and propose guidance for management in the context of broader ecosystem health, before reviewing approaches used in this thesis in the context of future research needs, with suggestions for additional techniques to further research in this field.

5.2. Implications for conservation and biodiversity of riverine ecosystems

5.2.1. Birds as bioindicators

In ecology, an indicator species (or group of species) should be able to effectively reflect the state of an environment, often in terms of its quality or health, and can provide multiple advantages over traditional direct measures (Parmar, Rawtani & Agrawal, 2016; Fierro et al., 2017). While periphyton, benthic macroinvertebrates and fish are the most commonly used bioindicators in lotic ecosystems, each have weaknesses related to the small proportion of the ecosystem they represent, adaptations to specific substrate or temperature ranges, or difficulty of capture (Li, Zheng & Liu, 2010; Fierro et al., 2017). The use of birds as bioindicators has been building in popularity across a broad range of settings, largely because they are conspicuous, relatively long-lived, widespread, diverse and mobile, hold mid to high positions in food webs, yet are easily and cheaply surveyed (Baillie, 1991; Becker, 2003; Egwumah, Egwumah & Edet, 2017). Furthermore, birds are highly sensitive to environmental change (Ormerod & Tyler, 1993; Amat & Green, 2010; Gregory & Strien, 2010), particularly habitat modification (D'Amico et al., 2000; Sinha et al., 2019),

climate change (Crick & Sparks, 1999; Crick, 2004; Usui, Butchart & Phillimore, 2017; Samplonius et al., 2018) or the presence of various pollutants (Hardy, Stanley & Greig-Smith, 1987; Becker, 1989; Furness, 1993; Newton, Wyllie & Asher, 1993; Becker, 2003; Dahlmann et al., 1994; Egwumah, Egwumah & Edet, 2017; O'Hanlon et al., 2019).

The proposed use of Dippers as bioindicators is not new; their high sensitivity to a broad range of water quality stressors has been highlighted over previous decades of research, initially with acidification (Ormerod, Boilstone & Tyler, 1985; Ormerod, Tyler & Lewis, 1985; Ormerod et al., 1986; Ormerod & Tyler, 1987b; Vickery, 1992), and more recently as a general reflection of prey availability (Sorace et al., 2002; Sinha et al., 2019), and contaminant presence (Morrissey et al., 2014; D'Souza et al., 2020; Pedersen, Nybø & Sandercock, 2020). In contrast, Grey Wagtail and Common Sandpiper are rarely considered as bioindicators in riverine environments as their weaker reliance on aquatic prey results in limited responses towards degraded water quality (e.g. acidification; Ormerod & Tyler, 1987b, 1991; Vickery, 1991). By shifting the historical associations with aquatic bioindicators from water quality to general ecosystem health, riverine birds may act as a highly visible initial indication of temporary or persistent issues prior to subsequent investigation, such as testing the physical and biochemical properties of the water.

For this latter purpose, the findings from this thesis suggest that occupancy and abundance of Dipper and Grey Wagtail, as assessed through simple transect surveys, are likely representative of riverine and riparian conditions, thus they are highly suitable as broad-spectrum indicators for riverine ecosystem health, particularly in terms of habitat structure and prey availability. Their use should take account of the underlying physiography (e.g. slope) however, as some habitats may be inherently unsuitable for one or more of the focal species, thus not appropriate as indicators for that setting. Furthermore, while Dipper breeding performance is likely indicative of ecosystem health, the intensity of the surveys alongside confounding factors such as river width and nest site availability complicate inference of results, thus is likely unsuitable unless information is obtained through existing annual surveys (e.g. BTO NRS). Conversely, Common Sandpiper are likely unsuitable bioindicators for riverine ecosystem health. Their mixed use of riverine and terrestrial environments during breeding and unspecialised invertebrate diets mean they are more flexible in their use of the landscape, thus breeding territories along rivers may remain populated (i.e. adults observed during count surveys) even if the river ecosystem becomes degraded as adjacent habitats may retain resources necessary to reproduce (e.g. prey, nest sites).

5.2.2. Lessons for managing rivers for riverine biodiversity

While it would be inappropriate to manage rivers solely for the benefit of riverine birds, associations identified throughout this thesis suggest that there are multiple existing policies and practical initiatives that are likely to benefit them while supporting aquatic and riparian

biodiversity more generally. Examples include the installation of buffer strips and retention ponds to reduce diffuse pollution (Muscutt et al., 1993; Forestry Commission, 2014, 2019), restoration of peatland and broad-leaved woodland expansion to support natural flood management (Allott et al., 2019; Cooper et al., 2021), alongside broader restoration of rivers, their floodplains and riparian woodland to improve habitat structure or complexity, and mitigate against weather or climate extremes (Dohet et al., 2015; Johnson & Wilby, 2015; Thomas, Griffiths & Ormerod, 2016; Turunen et al., 2021). As highlighted in chapters 2 and 3, riparian woodland may not be appropriate for all settings, particularly upland grassland or moorland habitat (Buckton & Ormerod, 1997); these landscapes may benefit more from buffer strips consisting of tall grasses, rushes and low scrub that provide temperature regulation and runoff control benefits, but would require additional management (e.g. occasional cutting or low-level grazing) to prevent natural succession to woodland.

Furthermore, responsible best practice management of existing land uses may limit further degradation or provide additional benefits. For example, responsible felling of mature plantation may reduce soil erosion and nutrient leaching (e.g. 'legacy' acidic compounds; Murgatroyd & Ternan, 1983; Alewell et al., 2000; Nisbet, 2001; Evans et al., 2014; Forest Research, 2023). Another example is the shift from 'minimum' to 'environmental' flows (e-Flows) in abstraction or impoundment schemes, which seek to simulate site-specific natural flow regimes to sustain key ecosystem processes (e.g. substrate redistribution and regeneration) and meet the varying flow requirements of the life histories of lotic organisms (Bragg et al., 2005; Arthington et al., 2006; Dudgeon et al., 2006; European Commission & Directorate-General for Environment, 2016; Webster et al., 2017; Schmutz & Moog, 2018).

Collectively, these actions are likely to improve aquatic and riparian invertebrate taxonomic and functional richness (e.g. via improved water quality, water velocity moderation, temperature regulation, habitat complexity and litter inputs; Gurnell, Gregory & Petts, 1995; Nedeau, Merritt & Kaufman, 2003; Schneider & Winemiller, 2008; Dohet et al., 2015; Johnson & Wilby, 2015; Thomas, Griffiths & Ormerod, 2016; Theodoropoulos et al., 2017; Windsor et al., 2019; Turunen et al., 2021), benefit water clarity and hence foraging efficiency of visual predators (Da Prato, 1981; Hedström et al., 2017), and increase quality and availability of habitat for reproduction or development, whether for invertebrates (Theodoropoulos et al., 2017), fish (Lobón-Cerviá, 1996; Taylor et al., 2019), or birds (Alder, 1963; Tyler & Ormerod, 1994; Wilson, 1996; Elas, Rosendal & Meissner, 2023).

5.2.3. Reflection on changes in river and catchment management

Rivers have historically been managed for the benefit of human development, being utilised for food and drinking water, as an environment for tourism and recreation, and in support of industry,

agriculture, navigation, waste disposal and electricity generation (Critchlow-Watton et al., 2014; WWF, 2022). However, many of these services paradoxically impose chemical, biological or physical pressures on lotic ecosystems, degrading ecological health and subsequently impacting the ongoing quality and delivery of these services (Dudgeon et al., 2006; Miranda, Hermoso & Hassall, 2019; Reid et al., 2019). As freshwaters are integral to life for a disproportionate number of species, from both aquatic and terrestrial backgrounds, it is imperative that watercourses are improved, restored, and protected as resources for nature and humans alike (Dudgeon et al., 2006; Miranda, Hermoso & Hassall, 2019).

Conservation of terrestrial resources traditionally focuses on areas containing high quality habitat or rare species/communities that can be bounded and protected, but this approach of 'Fortress Conservation' is not applicable for freshwaters due to their high network connectivity (Dudgeon et al., 2006). Firstly, there is no easy location to draw the boundary line for conservation priority or protection of a specific area. Secondly, as all parts of catchments are ultimately interconnected, management should focus on ecological improvement and restoration at multiple scales including channel, riparian, floodplain, and catchment.

Legislation to promote sustainable use of water resources, such as the EU Water Framework Directive (WFD), daughter directives such as the Floods and Groundwater Directives and the River Basin Management Plans (RBMPs) via which WFD actions are implemented, is key to ensuring the ecological improvement of rivers, lakes and groundwater. However, poor implementation of integrated approaches to water management or maintenance of existing infrastructure, often in the face of economic pressures, legacy issues and competing priorities introduces severe challenges to achieving long-term statutory targets, particularly when penalties are insufficient to dissuade further degradation (Environmental Audit Committee, 2022). The transitioning of agri-environment schemes post-Brexit under Environmental Land Management schemes (ELMS) in England, and equivalents yet to be announced in detail for other countries in the UK, may bring benefits through rewarding farmers for the delivery of environmental goods and services needed most in the midst of a nature and climate emergency (Department for Environment Food & Rural Affairs, 2023). Within ELMS, the Countryside Stewardship (CS) and Landscape Recovery schemes are likely to offer the greatest potential for bespoke enhancement of the natural environment, but concern remains that these schemes will be underfunded.

5.3. Research complications from Covid-19

The Covid-19 pandemic significantly impacted the research planned for this PhD, necessitating a change in aims and introducing challenges to data collection. Intensive time-sensitive fieldwork was originally planned for late-February to June in 2020, 2021 and 2022, whereby data would be collected on breeding Dippers from two regions in Scotland (Midlothian, and Dumfries and

Galloway [henceforth D&G]). These sites would enable both a temporal comparison in breeding performance from historic data (Vickery, 1991, 1992; Wilson, 1996), and an investigation into recovery from acidification at, historically, some of the most acidified catchments in the UK. However, initial site familiarisation and subsequent data collection had to be terminated due to the first national lockdown in March 2020.



Figure 5.2: The iconic viaduct over the Big Water of Fleet, above Gatehouse of Fleet in Galloway. Both the Big and Little Waters of Fleet were planned for surveys, alongside the Minnoch Water and the Scour Water. Image taken by R. Steenson (2020).

Significant safeguards to protect against Covid-19 impacted fieldwork in 2021, with travel to D&G not permitted due to the necessary overnight stays, and a delay of six-weeks before the Midlothian surveys could commence in mid-March. While travel was permitted to D&G in 2022, access to the rivers was not permitted due to local riparian felling and clearance works following Storm Arwen in November 2021. This reduced the spatial spread of breeding season data to a single river catchment, and removed the possibility of exploring recovering from acidification as the Midlothian catchment has remained pH neutral over all periods of data collection.

An alternative data source became available during training with Kenny Slater and Mike Nicholl of the Tay Ringing Group, which comprised 50-years of nest record data (1970-2019) throughout Perthshire and Angus (henceforth P&A); use of the data was permitted for this PhD in return for digitizing the dataset. This significantly broadened both the temporal and spatial scale of breeding performance that could be considered, and allowed the division into two chapters: (1) the full census of the South Esk in Midlothian granted a unique examination of the effects of breeding

density on breeding performance; (2) the huge temporal range and spatial spread of the P&A data would enable an investigation into climate effects on breeding performance. However, due to ill-health, there were delays in receiving paper records for digitization (Figure 5.3), which meant that this chapter could not be produced in time for submission of this thesis. A brief overview of aims and proposed analysis is included in section 5.4.1.

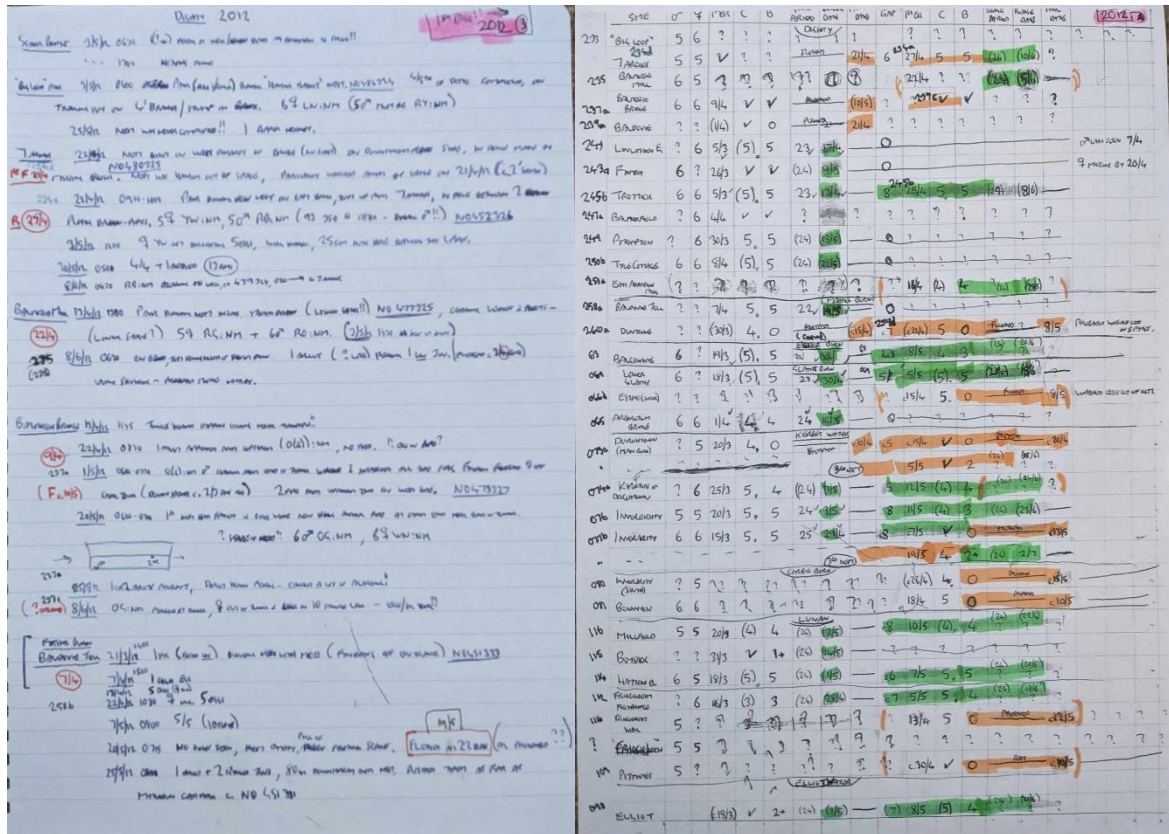


Figure 5.3: Example paper nest records from Mike Nicholl. Notes from field observations (left) are summarised in a table (right), allowing relatively straightforward data input with the ability to check on discrepancies.

5.4. Future research

Environmental change is, and will continue to be, a significant threat to riverine ecosystems. The chapters in this thesis complement and enhance understanding of how riverine birds are likely to be impacted, both directly and indirectly, by a broad range of environmental pressures, and provides a foundation for development of more integrated approaches. The following sections offer opportunities for further development of analyses used in this thesis, or future work.

5.4.1. Development of analyses in this thesis

5.4.1.1. *Further integration of integrated pressures*

Chapters 2 and 3 modelled environmental drivers of spatial variation in riverine birds, and responses to climate indices respectively. These chapters fill a vital knowledge gap by modelling response of riverine birds to some of the integrated pressures of riverine and riparian ecosystems in Britain, but unfortunately omit some of the more complex and dynamic interactions in riverine environments. A natural progression would be to combine site characteristics and pressures (e.g. physiography, land use, climate indices) into a single analysis to identify responses under highly dynamic conditions, the findings of which could be more effectively used in predictive or scenario modelling (see section 5.4.2.1), advancing our capacity to anticipate and adapt to future environmental change. Specifically, this would identify if there are combinations of local conditions that magnify or reduce sensitivity of climate variation. However, achieving this is complicated by availability of land cover data at equivalent spatial and temporal scales to the survey data, whether abundance (e.g. Waterways Breeding Bird Survey [WBBS]), or breeding performance (e.g. Nest Record Scheme [NRS]).

High-resolution (i.e. vectorised, or 25m raster) UKCEH Land Cover Map (LCM) products are available at an annual scale between 2017 and 2021, but are periodic prior to this (i.e. 1990, 2000, 2007, 2015), which complicates pairing to annual survey data. Moreover, UKCEH advise against using their LCM products to compare land cover data between years at a site level (Rowland et al., 2017). An alternative would be the habitat data collected directly by citizen scientists conducting surveys on behalf of the BTO, which utilise broad habitat groups (e.g. woodland, farmland, human sites), with options to provide additional detail on sub-habitat (e.g. for woodland: mixed-aged or semi-natural, dense scrub layer, dead wood present). These data will be vulnerable to variability between surveyors due to the subjective nature of habitat classifications, but could still provide a good indication of broad habitat covering all survey years. The trade-off however is that the habitat data is limited to the immediate riparian zone, which would not allow analysis of pressures imposed at the landscape or catchment scale. Moving forwards, a possible approach would be to use surveyor-collected habitat data to provide highly detailed information at the site level, in combination with UKCEH Land Cover Maps (or equivalents, e.g. CORINE Land Cover) extracted at the landscape and/or catchment scale and matched to the closest years in the survey records (i.e. WBBS, NRS). This may allow for a more fully integrated model to assess riverine bird responses to common pressures of riverine and riparian environments and could be extended to explore effects on breeding performance. The addition of routine chemical and biological surveillance and operational data collected by environment agencies may provide further information on responses to persistent and emergent pressures, but similarly risks data reduction due to spatial mismatching between bird survey and monitoring sites, further constrained by devolved environmental management in the UK.

5.4.1.2. *Addition of a lagged phase*

As mentioned in chapter 3, bird counts during the breeding season are subject to detection bias, particularly when avian behaviour changes to reflect nest development stage (e.g. incubation), weather or river flow conditions, thus the findings may partially reflect behavioural responses or detection bias during the breeding season. This analysis may be improved by an allowance for lagged effects i.e. where abundance in year t is modelled against climate indices in year t , year $t-1$ and year $t-2$. As climate-based pressures may be imposed on different trophic levels or demographic stages at different time points through direct and indirect pathways, responses may be asynchronous to conditions or event (Pearce-Higgins et al., 2010; Lindström et al., 2013; Pearce-Higgins et al., 2015; Bårdsen, Hanssen & Bustnes, 2018; Gaüzère & Devictor, 2021). For example, abundance of European golden plover (*Pluvialis apricaria*) negatively correlated with August temperatures 2 years prior, likely due to reductions in their adult Crane fly (Tipulidae) prey in the intermediary year (Pearce-Higgins et al., 2010). Thus, the inclusion of lagged effects may indicate among-season responses and revise the picture of climate sensitivity over the breeding season.

5.4.1.3. *Addition of a combined breeding productivity measure*

Chapter 4 models multiple breeding season metrics; while both brood size (effectively the number of fledglings per breeding attempt) and the probability of survival are included in this study, a more concise combined metric to indicate breeding productivity may be the total number of fledglings per territory (breeding female) per year. This metric could be calculated from nest recording data collected in the South Esk catchment as the censusing ensured full recognition of breeding pairs, even if a pair moved nests mid-season, but would necessitate extraction of data from the raw field notes (1979-2022) to ensure territories were correctly identified and any cases of polygyny were accounted for (Wilson, 1996). This metric may give a better indication of within and among year variation in breeding performance as it takes into account pairs that produce two successful broods.



Figure 5.4: Colour-ringed Dipper fledgling in the River South Esk study system. Image taken by R. Steenson (2022).

5.4.1.4. Environmental drivers of breeding performance

Chapter 4 highlighted multiple associations between breeding performance metrics (e.g. clutch size, brood size, likelihood of second brooding) and clutch initiation date, which is often linked indirectly to temperature and climate change through thermal moderation of development and emergence of invertebrate prey (Crick & Sparks, 1999; Crick, 2004; Daufresne et al., 2004; Durance & Ormerod, 2007; Dunn & Winkler, 2010; Jonsson et al., 2015; Shave et al., 2019; Bründl et al., 2020). The effects of climate on Dipper breeding performance have been explored relative to hydrology in Norway (Nilsson et al., 2019, 2020a, 2020b) and temperature in Slovakia (Baláz et al., 2021), but rarely within an integrated framework designed to capture the conditions experienced during breeding, and the impacts they may have on specific performance metrics. This could be investigated by pairing nest recording data with temperature and rainfall indices such as those extracted in chapter 3 (e.g. maximum 1-day rainfall, number of days below 0°C), and controlling for site physiography (e.g. elevation, slope). This was planned for chapter 5, but unfortunately could not be produced in time for submission of this thesis as ill-health delayed the receipt of paper records for digitization.

The dataset planned for this analysis comprises 50-years of nest record data (1970-2019) collected throughout Perthshire and Angus in Scotland, where 342 individual nest sites were monitored over a total of 1,978 breeding attempts (Figure 5.5). This dataset covers a significantly larger spatial and temporal scale than data collected in Midlothian, enabling a more detailed investigation into variation in breeding performance and the possible associations with local weather conditions or long-term change in average climate. Furthermore, as pairs were followed

for the full breeding season (February – June), data were collected on overall breeding success (e.g. total number of fledglings per pair per year), occurrence of failures with possible causes (e.g. inundation, predation), and the presence of second brooding, which is often not available from nest record data such as those collected by citizen scientists on behalf of the BTO.

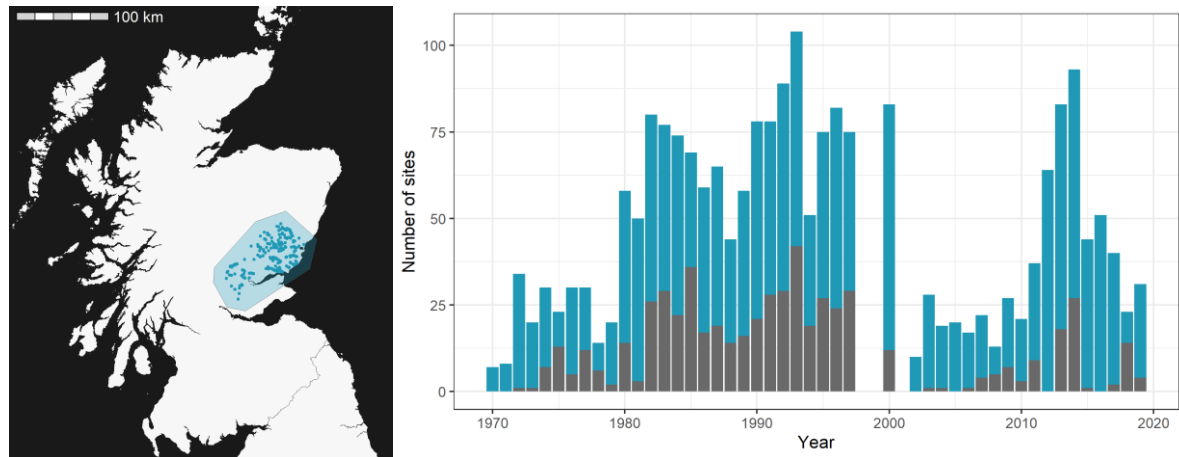


Figure 5.5: Details of long-term nest record data collected in Perthshire and Angus, Scotland. (left) Location of nest recording sites, with individual nest sites shown as points. (right) Distribution of active (blue) vs. inactive (grey) nests monitored from 1970 to 2019.

Following the exploration and use of weather indices in chapter 3, analysis here would likely utilise Generalised Additive Mixed Models (GAMMs) to allow for the combination of linear and smoothed terms in the same model. Response variables such as clutch initiation date, clutch size, brood size, survival, and probability of second brooding could be modelled against the full set of temperature and rainfall indices, elevation and slope extracted at a site-level. The overall responses to local conditions could be investigated by controlling for year as a random effect or modelled as trends by including year as an explanatory term. This would provide insight into the impacts of varying weather conditions on Dipper breeding performance and indicate how breeding performance may change in the future in response to climate change and extreme events.

5.4.2. The next steps

5.4.2.1. Predictive modelling

Scenario modelling is a widely utilised tool to predict the scale and direction of impacts imposed by future land use and climate change (Jessel & Jacobs, 2005; Nel et al., 2009; Arriana Brand et al., 2011; Royan et al., 2015; O’Keeffe et al., 2023). This approach is particularly applicable for riverine birds and the ecosystems in which they live due their sensitivity to a broad range of both natural

and anthropogenic stressors, and flexibility allows for a range of possible responses to be modelled, from occupancy and abundance, to breeding performance metrics. As Dipper, Grey Wagtail and Common Sandpiper have all experienced population declines over recent decades, it is imperative that appropriate conservation and restoration strategies are developed to optimise the often-contrasting habitat requirements of riverine species or communities, both for current conditions and a range of potential future scenarios.

Ecological Niche Models (ENMs) are another possible approach, whether used solely to identify areas of high habitat suitability for riverine birds (hence high riverine and/or riparian taxonomic and functional richness), or in combination with scenario modelling to predict how riverine bird distributions may respond to future environmental change. In both cases, these predictions could indicate areas of high priority for targeted conservation and restoration management at channel, landscape, and catchment scales.

5.4.2.2. *Responses to invasive species*

Given how sensitive riverine and riparian ecosystems are to the presence of invasive species, the extent to which riverine bird communities (particularly the focal species in this thesis) are impacted is poorly understood. Chapter 1 highlights some of the potential threats to riverine birds, whether directly through predation (e.g. American Mink), or indirectly through impacts to channel morphology, shading, substrate diversity, water turbidity, or invertebrate diversity and abundance (Moore, Roy & Helyar, 2003; Faller et al., 2016; Greenwood et al., 2018; Seeney et al., 2019a, 2019b; Mathers et al., 2020a; Matte, Boivin & Lavoie, 2022; Mathers et al., 2022). However, these are largely inferred relationships, and given that the presence of invasive species is predicted to increase globally by 36% by 2050 due to anthropogenically-mediated introduction, transport, and habitat modification (Mathers, Guareschi & Pattison, 2022), the association between riverine bird indicators and invasive species is important to quantify. This could be achieved through field observations of riverine bird occupancy, abundance, and habitat usage at sites within known invasive species, both within and outside of the breeding season. Other approaches would be to link WBBS data to mapped distributions of invasive species such as Himalayan Balsam or Giant Hogweed, available either through the UK National Biodiversity Network (NBN), or derived remotely via high resolution satellite imagery.

5.4.2.3. *eDNA*

Environmental DNA (e-DNA) is a rapidly emerging biodiversity monitoring technique that can provide information on occurrence, abundance, diversity, and distribution of species within the sampled environment (Fernández et al., 2019; Mächler et al., 2019; Beng & Corlett, 2020). In rivers

and streams, e-DNA offers distinct benefits over conventional surveying methods, such as improved field sampling efficiency (e.g. compared with kick-net or Serber sampling for invertebrates, electro-fishing; Pont et al., 2018; Fernández et al., 2019; Pont et al., 2021), detection of organisms upstream of the sampling location (Pont et al., 2018; Wood et al., 2021) from both aquatic and terrestrial sources (Deiner et al., 2016; Broadhurst et al., 2021; Macher et al., 2021), whilst remaining non-invasive (Maruyama et al., 2018). Much existing research demonstrates the effectiveness of e-DNA as an alternative assessment method, especially for fish, but rarely reports on the presence of birds. Given a knowledge of flow rates and network connectivity, e-DNA metabarcoding data may provide a ‘complete picture’ of the taxa present at a given site, enabling an investigation of overlaps between taxa (e.g. potential predators and prey) and the focal species of this thesis, which may help better resolve causes of their decline. Furthermore, e-DNA may simplify detection of invasive species for the potential research described in section 5.4.2.2.

5.4.2.4. Assessment of over-winter survival

Finally, chapter 3 in this thesis identified a negative association between hard winters and abundance of Grey Wagtail and Dippers in the following season. These findings are consistent with theorised drivers of decline in both species, but it is unclear whether this is related to survival rates of adults, or first-year birds. This may be resolvable through an intensive monitoring program over multiple sites and years, and utilising colour rings to enable identification of individuals without recapture; data could be directly compared against indices of climate conditions to identify possible causal mechanisms.

5.5. Conclusion

Despite their crucial significance for life, rivers and streams are exposed to a broad range of threats globally, including pollution, habitat, and flow modification, which have resulted in significant ecological degradation, observed through decline in vertebrate taxa and decelerating trajectories in improvement of invertebrates. Understanding how lotic ecosystems respond to, and recover from multiple often integrated stressors is challenging, but essential to ensure that watercourses are improved, restored, and protected as resources for nature and humans alike. The findings in this thesis broadly demonstrate the multiple direct and indirect pressures that act on breeding riverine birds, and highlight some key similarities and differences between the focal species, likely due to their varying life history strategies. These divergent ecologies strongly reflect their dependence on the riverine environment, thus Dipper and Grey Wagtail are likely suitable indicators of riverine ecosystem health, whereas Common Sandpiper strong association with adjacent terrestrial environments limits their utility. These results support the application of multiple existing policies and practical initiatives (e.g. buffer strips, restoration of riparian

woodland or herbaceous vegetation, whole scale floodplain restoration) at channel, riparian and catchment scales, which are widely advocated for pollution control, climate mitigation and/or natural flood management. These approaches provide benefits to taxa across multiple trophic levels, from single-celled organisms to vertebrate predators, with subsequent improvements to overall riverine health and ecological status, but management will likely need to be contextually bespoke and adaptive.

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