Using diet to assess the sensitivity of northern and upland birds to climate change

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ABSTRACT: High-latitude species are predicted to be vulnerable to climate change, particularly in the UK uplands, where many are at the margins of their southern range. There is increasing evidence that climate change may have an impact on populations through reductions in prey abundance. The diet of 17 insectivorous UK upland birds, and the sensitivity of their prey to likely climate change, were quantified from the literature and combined to produce an index of climate-change sensitivity for upland birds. Coleoptera and Diptera were the 2 most important prey taxa, with Tipulidae the most widely ingested prey family. Lepidoptera, Lumbricidae and Hymenoptera also comprised > 20 % of the diet of at least one upland bird species. Of these prey taxa, existing studies suggest that Tipulidae, Chironomidae and Lumbridicae may be particularly vulnerable to rising temperatures and increased frequency of drought projected to result from climate change. Therefore, the contribution of these 3 taxa to the diets of upland birds provides an index of climate-change sensitivity, which was correlated with an index of recent upland bird population trends. Future increases in temperature and drought frequency are expected to have an impact on populations of a range of upland bird species through reductions in prey availability, although further studies are required to test this hypothesis. Many upland areas have been artificially drained using ditches. Blocking these ditches may therefore provide a potential management option for climate-change adaptation in the UK uplands.

KEY WORDS: Climate change · Upland bird · Invertebrate · Diet · Food chain · UK · Trophic interactions

1. INTRODUCTION

Climate change is one of the greatest potential threats to biodiversity (Thomas et al. 2004). The most widely used method to assess the vulnerability of species to climate change is climate envelope modelling, in which species distribution is modelled as a function of climate. This model is then used to predict the probable change in species distribution as a result of climate change, which allows the projected change in range size, and overlap between current and projected future ranges, to be estimated (e.g. Araujo et al. 2006, Thuiller et al. 2006, Huntley et al. 2008). Although this method has been subject to a number of criticisms (Beale et al. 2008), there is increasing evidence that recent changes in species range (e.g. Hickling et al. 2006) and popula-

tions (Green et al. 2008, Gregory et al. 2009) match climate envelope model predictions.

Whereas many mechanisms may underpin the link between climate and avian population trends (Mustin et al. 2007), it is probable that one of the most important of these mechanisms is through changes in food availability, which strongly determines both avian productivity (Arcese & Smith 1988, Marshall et al. 2002) and survival (Ratcliffe et al. 2002, Johnson et al. 2006). For example, in the marine environment, reductions in both seabird productivity (Frederiksen et al. 2006) and survival (Barbraud & Weimerskirch 2001) have been driven by climate-related changes in prey abundance. In woodlands, climate-related variation in caterpillar abundance contributes to the sensitivity of North American migratory birds to climate change (Sillett et

al. 2000, Anders & Post 2006), whereas changes in caterpillar availability to European woodland birds as a result of phenological mismatch have resulted in declines in breeding success (Visser et al. 2006) and abundance (Both et al. 2006).

High-latitude species, such as arctic and subarctic breeding birds, are regarded as being particularly vulnerable to future warming (Huntley et al. 2007). Many such species find their southern range margins in the uplands of the UK, where they occupy unenclosed moorland, grassland and blanket bog habitats and comprise an internationally important bird community (Thompson et al. 1995). Recent population trends of the rarest of these species indicate that they have declined as climatic suitability is reduced (Green et al. 2008), and there is evidence for others being vulnerable to climate change (Cattadori et al. 2005, Beale et al. 2006, but see Pearce-Higgins et al. 2009b). For one species, the golden plover *Pluvialis apricaria*, warming may result in population declines mediated through reductions in the abundance of tipulid prey (Pearce-Higgins et al. 2010), matching the principles outlined above for seabirds and insectivorous woodland birds. Given that cold-adapted herbivorous invertebrates, such as tipulids, are particularly vulnerable to climate change (Bale et al. 2002) and form an important component of many upland bird diets (Buchanan et al. 2006), these impacts might be expected to affect a wide range of species. In the present study, the potential link between climate impacts on invertebrate prey populations and their avian predators is investigated for this potentially sensitive UK upland bird assemblage. Specifically, quantitative estimates of both upland bird diet and the probable sensitivity of invertebrate prey to climate change from reviews of the existing literature were combined to produce an index of climate-change sensitivity for upland birds. This index is therefore based on an understanding of ecological processes, rather than the statistical association between distribution and climate that underpins climate envelope models, and provides an alternative index of sensitivity to climate change.

2. METHODS

The upland species listed in Pearce-Higgins et al. (2009a) were used to identify obligate and facultative upland insectivorous species to focus on for the present study. Raptors were therefore excluded, with the list comprising grouse, wader and passerine species, with the exception of the granivorous twite *Carduelis flavirostris*. Dietary information was extracted only for those seasons in which species occur in the uplands.

2.1. Upland bird diet

The review of upland bird diet conducted by Buchanan et al. (2006) was updated with additional material obtained by searching Web of Science and Google Scholar, and followed up with additional relevant literature from the reference lists of published papers. Dietary composition was extracted from each paper, separating results from different populations or habitats as appropriate. Because the number of studies on any one species was limited, and the methods used to estimate and summarise diet varied between studies, a modelling approach was used to correct for these varied methods and produce comparable estimates of dietary composition for each species. Given the differences in habitat utilisation and diet between adults and pulli of many upland bird species (e.g. Grant et al. 1992, Pearce-Higgins & Yalden 2003, 2004), these life stages were modelled separately. A list of the studies included is given in Supplement 1 (see www.int-res. com/articles/suppl/c045p119_suppl.pdf).

2.1.1. Variation in assessment methods between studies

Studies sampled the diet of bird species using a variety of methods, including direct observation of birds (n = 12 studies), ligatures (n = 7), examination of crop or stomach contents (n = 148), or faecal analysis (n = 92). Given the small number of cases that used direct observation or ligatures, results from these were combined with data from crop and stomach contents to provide a group describing prey intake that contrasts with faecal analysis, which is affected by digestion rates. These methods (intake or excreta) were therefore distinguished in the model, although results from both can be comparable (Pearce-Higgins & Yalden 2004).

Dietary composition was summarised as the percentage of samples in which a prey taxon occurs (n = 72), the percentage of total items accounted for by a taxon (n = 103) or the percentage dry weight contribution of a taxon (n = 84). The former may underestimate the abundance of commonly taken items, whereas the latter will best represent the contribution of large prey items to the diet. These 3 summary methods were also distinguished in the model.

2.1.2. Modelling diet composition

To produce a comparable percentage diet composition format across all studies for modelling, the contribution of each taxon (C) was expressed as a percentage of the summed contributions of all dietary taxa

(including non-invertebrates) from that study. Thus, true estimates of percentage composition and estimates of percentage occurrence were modelled together to calculate a conversion from one to the other. C was then modelled as follows: as a function of prey taxon, bird species, life-stage (adult or pullus), sample method (intake or excreta) and summary method (% occurrence, % items, % dry weight). An additional 2-level factor described whether data were from the UK (the primary focus of the study) or abroad.

$$C = \text{Taxon} \times \text{Bird} \times \text{Stage} + \text{Taxon} \times \text{Location} + \text{Taxon} \times \text{Sample} + \text{Taxon} \times \text{Summary}$$

Thus, significant variation in the Sample and Summary methods between studies, and how those affect the apparent importance of different prey taxa, were accounted for by the Taxon × Sample and Taxon × Summary interactions. Any significant differences in the diet of species between the UK and other localities were highlighted by the Taxon × Location interaction. This simple model contained all the terms necessary to estimate diet for each species and life stage using the Taxon × Bird × Stage interaction, but a full model containing all the single and 2-way interaction terms included within the simple model was used to properly estimate the statistical significance of each interaction term. The model was used to output comparable estimates of the diet of each species and life stage for which there were some data. A standardised output, irrespective of variation in the original study methods and location, was produced by predicting, for each species, the percentage dry weight contribution of each taxon to the diet, assuming it was from a UK intake sample.

Two levels of model were produced. The first was based on broad taxonomic divisions of prey, which formed the basic unit of diet separation presented in most studies (insect orders, Arachnida and Lumbricidae). The second further subdivided diet into families. As this finer taxonomic division was most consistently applied to Coleoptera and Diptera in the literature, this model was produced using data for these families only. To simplify the modelling process, only those taxa present in >10% of studies were included, as rarer taxa were unlikely to be important.

Models were constructed using the Genmod procedure in SAS v. 9.1 (SAS Institute 2003). These failed to fully converge and produce Type III statistics when applying a binomial error distribution (the initial choice of error structure given that diet is bounded to percentage composition), so a normal error distribution was used. As model residuals did not differ significantly between the factors in the model (all p > 0.93), this structure was regarded as appropriate for what was a relatively simple averaging of dietary composition across different factor levels. As an additional check, model performance was assessed using a simple 'jack-knife' test, in which the model was repeated with each UK study that presented percentage dry weight diet composition serially excluded (n = 15). Combined dietary predictions from each repeat were then correlated with the excluded observed diets to estimate overall predictive performance of the model.

2.2. Sensitivity of prey taxa to climate change

Invertebrate prey taxa that were estimated to form >20% of the diet of any one species by dry weight were arbitrarily regarded as important. Literature searches of the impacts of climate change on the abundance of those important taxa were conducted using Web of Science and Google Scholar, with climate, weather, temperature, rainfall, moisture or abundance and the taxonomic name as keywords. Initial results were filtered using the abstract and title to exclude irrelevant studies before obtaining the remaining references. Where web searches identified thousands of potential sources, these were sorted in order of relevance, and, where 100 consecutive sources were found to be unrelated to the subject, the remainder was not subsequently searched. For most taxa, there were relatively few studies from the UK uplands (see Section 4.2); therefore, studies from all arctic, boreal and temperate habitats were included. In many instances, the species were the same as those that occur in the UK. A list of the studies included is given in Supplement 2.

The latest climate change predictions for the UK are for an increasing trend towards warmer, drier summers and warmer, wetter winters (Defra 2009). The results of each study were accordingly synthesised into a probable beneficial (scored as 1), detrimental (–1) or neutral (0) effect of climate change in the UK on that prey taxon. Thus, species associated with warm and dry conditions in the summer, or warm and wet conditions in the winter, were regarded as likely to increase as a result of climate change, whereas those associated with low temperatures or those sensitive to summer drought were predicted to decline. Scores were averaged to create a climate sensitivity score for each taxon that ranged from –1 (all studies indicated negative effects of climate change) to 1 (all studies indicated positive effects of climate change).

2.3. Relationship between diet and upland bird population trends

There has been little systematic monitoring of upland bird populations. Since 1995, Breeding Bird Survey trends have been available for some of the

more common upland birds (Baillie et al. 2009), although for species that also occur commonly in lowland habitats, population trends may not reflect upland processes. Changes in the abundance of rarer species are monitored by dedicated surveys, although estimates of change for whimbrel *Numenius phaeopus* and snow bunting *Plectrophenax nivalis* are not comprehensive (Table 1). Additional upland-specific population change data are available for a wide range of species from 13 non-random regions surveyed once during 1980–1990, and repeated in 2000 or 2002. These data are in the form of percentage changes in the abundance of breeding birds and are only presented for regions with at least 30 ind. recorded in any one survey (Sim et al. 2005), but cannot be combined to estimate national population trends given their non-random nature. These varied trend data were combined analytically to produce a comparable change index for all species as follows.

Each regional trend from Sim et al. (2005) was scored as –1 if indicative of a >25% population decline, 1 if indicative of a >25% population increase and 0 if the

population had changed by <25%. A 25% cut-off was used as the threshold for conservation concern listing (Eaton et al. 2009) in preference to the statistical significance of regional population trends, as the latter was heavily dependent upon the spatial arrangement of sample plots. Trend scores were averaged to produce a change score that ranged from –1 (>25% decline in all regions) to 1 (>25% increase in all regions).

This change score was correlated against national population trends for species with data available (Table 1) to produce a calibration from one to the other. Species with significant populations in lowland habitats (above) were excluded to avoid trends that are unrepresentative of upland areas. As this yielded only 6 species (golden plover, snipe, curlew, meadow pipit, wheatear and ring ouzel), an equivalent change index was also calculated from the regional breakdown presented in the national surveys of black grouse (Sim et al. 2008) and dotterel (Whitfield 2002). Change score was positively correlated with national trend (change score = –0.12 + 0.80 × national trend; r = 0.71, n = 8, p = 0.047); the slope was unchanged when data from black grouse and dotterel were excluded. This equation was then used to convert all population trends in Table 1 to an upland bird change index equivalent to the scores calculated from Sim et al. (2005), thus providing a single comparable measure for all species.

To explore whether the proportion of climate-change-sensitive prey taxa in species' diets may be correlated with recent population trends, the change index was regressed separately against the dietary contribution of climate-sensitive taxa of adults and pulli as an index of upland bird climate-change sensitivity. Because the change index was derived from different sources (population trends or regional patterns of change from Sim et al. 2005), Source was included as a 2-level factor. National population trends were only included for upland species, i.e those whose primary UK habitat assessed by Fuller et al. (2007) was bog, dwarf shrub heath or montane. To account for the fact that this resulted in 2 different trend estimates for some species, models were constructed within a mixed model framework, using the Mixed procedure in SAS v. 9.1 (SAS Institute 2003), with species specified as a random effect, and applying the Kenward-Rogers correction to the degrees of freedom (Littell et al. 1996).

Table 1. Recent population changes in UK upland birds. Population trends in *italics* denote species whose primary habitat is non-upland (see Section 2.3) and therefore do not contribute to the change index. The change score (derived from Sim et al. 2005) is derived from the proportion of surveyed regions in which populations increased by >25% compared with the proportion that decreased by >25%, and ranges from –1 (widespread decline) to 1 (widespread increase). nd: no data

Species	Species code	Population trend (%) (time period)	Change score
Red grouse	RG	–14 (1995–2006)[a]	nd
Ptarmigan	PT	nd	nd
Black grouse	BK	–22 (1994/95–2005)[b]	nd
Dotterel	DO	–23 (1987/88–1999)[c]	nd
Golden plover	GP	7 (1995–2006)[a]	–0.22
Dunlin	DU	nd	–0.57
Snipe	SN	31 (1995–2006)[a]	0.00
Whimbrel	WH	–50 (1985/6–2007)[d]	nd
Curlew	CU	–38 (1995–2006)[a]	–0.50
Greenshank	GK	nd	0.33
Skylark	S	*–11 (1995–2006)*[a]	–0.10
Meadow pipit	MP	–13 (1995–2006)[a]	0.20
Whinchat	WC	*–38 (1995–2006)*[a]	0.38
Stonechat	SC	*+200 (1995–2006)*[a]	1.00
Wheatear	W	–13 (1995–2006)[a]	–0.40
Ring ouzel	RO	–58 (1989/91–1999)[e]	–0.75
Snow bunting	SB	–42 (1991–2005)[f]	nd

[a]National trends from Breeding Bird Survey (Baillie et al. 2009)
[b]Unbiased estimate of change from national survey (Sim et al. 2008)
[c]Estimated change from national survey, although biases in initial site selection mean this may not fully reflect the national trend (Whitfield 2002)
[d]Estimated decline in Fetlar and Unst (Shetland, UK) stronghold, representing about 40% of the national total (Grant unpubl. data)
[e]Reanalysis of data from national survey to estimate minimum population change between Gibbons et al. (1993) and Wotton et al. (2002) by Sim (I. M. W. Sim unpubl. data)
[f]Estimated reduction from 70–100 pairs to 50 pairs (Marquiss 2007)

3. RESULTS

3.1. Upland bird diet

There were marginal effects of Location ($\chi^2_7 = 13.16$, p = 0.068) and Summary method ($\chi^2_{14} = 23.43$, p = 0.054) on estimated dietary importance, whereas the effects of Sample method were less important ($\chi^2_7 = 10.40$, p = 0.17). *Post hoc* contrasts indicate that Hymenoptera were more common in the diet of UK birds than in birds from other countries ($\chi^2_1 = 4.93$, p = 0.027), whereas faecal analysis increased the apparent importance of Lumbricidae over samples of intake ($\chi^2_1 = 5.09$, p = 0.024). The importance of Coleoptera was overestimated when summarised as percentage occurrence relative to percentage dry weight ($\chi^2_1 = 4.92$, p = 0.027), and the apparent contribution of Hymenoptera increased when summarised as percentage items rather than percentage dry weight ($\chi^2_1 = 5.59$, p = 0.018). There was a strong correlation between observed and predicted dietary composition across the taxa taken by the species covered by the 15 serially excluded studies (r = 0.78, n = 98, p < 0.0001), with a relationship close to 1:1 (slope = 0.97 ± 0.080).

Diet was modelled for 17 upland bird species, although there were no quantitative data on the diet of greenshank *Tringa nebularia*, snipe *Gallingo gallinago* or ptarmigan *Lagopus mutus* pulli. Diptera and Coleoptera were the 2 most important taxa for adult upland birds (Table 2), estimated to be important (>20% dry weight) for 9 and 8 of the 17 species, respectively, with a mean composition of 25% for both. Lepidoptera and Lumbricidae were each important for 3 species, and Hymenoptera for 1 species. Of the 14 species for which pullus diet was estimated, Diptera were important for 11 and Coleoptera for 7, with mean estimated compositions of 38 and 22%, respectively (Table 3). Hymenoptera were important for 2 species, and Arachnida, Lepidoptera and Lumbricidae for 1 species each.

Coleoptera and Diptera were the 2 most widely represented insect orders in upland bird diets. The above analysis was therefore replicated for specific Coleoptera and Diptera families using only those studies where a finer taxonomic breakdown was available. There were significant interactions between Taxon and both Sample ($\chi^2_5 = 18.14$, p = 0.0028) and Summary ($\chi^2_{10} = 24.35$, p = 0.0067), whereas diet differed less with Location ($\chi^2_5 = 10.97$, p = 0.052). *Post hoc* contrasts indicated that Chrysomelidae were less important in the diet of UK birds than elsewhere ($\chi^2_1 = 4.82$, p = 0.028). Faecal analysis appeared to increase the apparent importance of Tipulidae ($\chi^2_1 = 10.56$, p = 0.0012), but decrease the estimated contribution of Chironomidae ($\chi^2_1 = 5.45$, p = 0.020), relative to intake samples. The contribution of Tipulidae was also estimated to be greatest when summarised as percentage

Table 2. Modelled percentage dietary composition for adult upland birds (predicted mean dry weight composition ± SD). **Bold**: taxa that form >20% of the diet. Values with an estimated composition of <0.1% are coded as 0.0. Letters refer to species codes given in Table 1

	RG	PT	BG	DO	GP	DN	SN	WH	CU	GK	S	MP	WC	SC	W	RZ	SB
Arachnida	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 4.2	2.9 ± 5.1	0.0 ± 5.1	0.0 ± 5.1	1.5 ± 5.6	8.1 ± 12.9	0.0 ± 7.0	0.0 ± 0.0	16.3 ± 9.4	15.6 ± 7.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 7.0	0.0 ± 0.0	1.1 ± 4.6
Coleoptera	0.0 ± 0.0	0.0 ± 0.0	2.1 ± 4.2	**60.0 ± 5.1**	**35.6 ± 5.1**	2.4 ± 5.0	16.5 ± 5.6	17.6 ± 13	**24.1 ± 7.0**	**97.0 ± 12.9**	**28.5 ± 5.1**	5.7 ± 7.7	**51.2 ± 9.4**	**22.7 ± 12.8**	**42.3 ± 7.0**	10.0 ± 9.2	7.1 ± 4.5
Byhrridae	0.0 ± 0.0		0.0 ± 0.0	18.9 ± 5.3	4.1 ± 4.7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 8.5	0.0 ± 0.0	12.4 ± 8.4	0.0 ± 0.0	0.0 ± 0.0		0.0 ± 0.0		5.0 ± 4.5
Carabidae	0.0 ± 0.0		0.0 ± 0.0	13.3 ± 5.3	5.9 ± 4.7	0.0 ± 5.1	2.3 ± 5.5	0.0 ± 0.0	1.1 ± 8.5	12.7 ± 11.5	0.0 ± 0.0	1.5 ± 11.3	11.5 ± 8.4		4.2 ± 7.1		0.6 ± 4.5
Chrysomelidae	0.0 ± 0.0		0.0 ± 0.0	0.0 ± 5.3	8.3 ± 4.7	0.0 ± 5.1	0.0 ± 5.5	0.0 ± 0.0	8.9 ± 8.5	**72.5 ± 11.5**	0.0 ± 0.0	0.0 ± 11.3	5.6 ± 8.4		0.0 ± 0.0		0.0 ± 0.0
Curculionidae	0.0 ± 0.0		19.4 ± 11.3[a]	**31.0 ± 5.3**	8.3 ± 4.7	0.0 ± 0.0	4.1 ± 5.5	0.0 ± 0.0	3.1 ± 8.5	0.0 ± 0.0	10.9 ± 8.4	13.0 ± 11.3	17.9 ± 8.4		18.7 ± 7.1		4.0 ± 4.5
Diptera	16.4 ± 7.3	0.0 ± 0.0	6.5 ± 4.2	**30.3 ± 5.0**	**37.3 ± 5.1**	**87.3 ± 5.0**	**24.7 ± 5.6**	**45.4 ± 9.2**	**24.8 ± 7.0**	2.1 ± 12.9	17.7 ± 9.4	**35.4 ± 7.8**	17.7 ± 9.4	0.0 ± 0.0	10.3 ± 7.0	**27.8 ± 9.2**	**41.0 ± 4.6**
Chironomidae	0.0 ± 0.0		0.0 ± 0.0	0.0 ± 0.0	2.0 ± 4.7	**25.9 ± 5.1**	10.5 ± 5.5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		0.0 ± 0.0		9.2 ± 4.5
Tipulidae	11.5 ± 5.4		0.0 ± 0.0	**25.2 ± 5.2**	**36.4 ± 4.7**	**41.7 ± 5.1**	14.7 ± 5.4	**45.9 ± 8.1**	**23.0 ± 8.4**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		11.6 ± 7.0		**35.8 ± 4.4**
Hemiptera	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 5.5	0.0 ± 5.4	0.0 ± 0.0	0.0 ± 5.6	0.0 ± 13	0.0 ± 7.3	0.0 ± 13.2	0.0 ± 0.0	7.6 ± 8.0	1.9 ± 9.7	3.4 ± 13.0	0.0 ± 7.3	0.0 ± 0.0	0.3 ± 5.0
Hymenoptera	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 4.3	1.8 ± 5.1	1.1 ± 5.2	0.0 ± 0.0	0.0 ± 5.6	0.0 ± 13	0.0 ± 7.1	0.0 ± 0.0	13.4 ± 9.5	11.2 ± 7.8	10.9 ± 9.5	0.0 ± 0.0	**26.2 ± 7.1**	0.0 ± 0.0	0.0 ± 4.7
Lepidoptera	0.0 ± 0.0	0.0 ± 0.0	3.2 ± 4.3	1.0 ± 5.1	7.6 ± 5.2	0.0 ± 0.0	1.9 ± 5.6	10.4 ± 13	**26.5 ± 7.1**	0.0 ± 0.0	**20.9 ± 9.5**	6.7 ± 7.8	9.4 ± 9.5	**67.4 ± 12.8**	7.9 ± 7.1	11.0 ± 9.3	7.7 ± 4.7
Lumbricidae	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 6.4	9.9 ± 5.7	6.8 ± 5.7	**30.1 ± 6.1**	**29.4 ± 9.5**	14.3 ± 7.4	0.0 ± 0.0	0.0 ± 0.0	6.2 ± 8.3	15.2 ± 9.8	0.0 ± 0.0	0.0 ± 0.0	**25.5 ± 9.5**	0.0 ± 0.0
Orthoptera	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 7.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 9.3	0.0 ± 0.0	5.2 ± 11.6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 9.5	0.0 ± 0.0	0.0 ± 0.0

[a]Estimate greater than the 95% confidence intervals of Coleoptera and, given the error bars, an overestimate, resulting from the fact that only 1 study presented a fine taxonomic breakdown of invertebrates in black grouse diet

Table 3. Modelled percentage dietary composition for pullus upland birds (predicted mean dry weight composition ± SD). **Bold**: taxa that form >20% of the diet. Values with an estimated composition of <0.1% are coded as 0.0. Ptarmigan, snipe and greenshank are omitted due to a lack of quantitative information. Letters refer to species codes given in Table 1

	RG	BG	DO	GP	DN	WH	CU	S	MP	WC	SC	W	RZ	SB
Arachnida	2.0 ± 6.5	1.9 ± 5.5	6.7 ± 5.8	5.0 ± 7.5	4.5 ± 8.3	16.3 ± 14.0	6.7 ± 7.4	**21.3 ± 8.7**	6.1 ± 5.2	3.8 ± 7	3.9 ± 5.4	1.9 ± 7.6	0.1 ± 6.9	15.2 ± 7.9
Coleoptera	11.5 ± 6.5	6.5 ± 5.5	**58.7 ± 5.8**	**32.5 ± 7.6**	10.7 ± 8.3	14.5 ± 14.1	**44.1 ± 7.4**	**25.1 ± 8.7**	0.3 ± 5.2	**20.6 ± 7.1**	18.8 ± 5.4	**30.8 ± 7.7**	**29.0 ± 6.9**	0.0 ± 13.8
Byhrridae	3.2 ± 5.4	0.0 ± 0.0	**20.4 ± 5.4**	5.1 ± 6.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Carabidae	2.1 ± 5.4	0.8 ± 7.6	14.4 ± 5.4	4.0 ± 6.4	0.0 ± 0.0	0.0 ± 0.0	6.1 ± 7.3	19.7 ± 11.6	0.0 ± 0.0	0.0 ± 7.2	5.7 ± 6.8	0.0 ± 0.0	**23.7 ± 6.1**	0.0 ± 0.0
Chrysomelidae	0.0 ± 0.0	0.0 ± 7.6	0.0 ± 5.4	0.0 ± 6.4	0.0 ± 6.8	0.0 ± 0.0	0.0 ± 7.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 7.2	0.0 ± 6.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Curculionidae	3.6 ± 5.4	6.3 ± 7.6	**26.3 ± 5.4**	11.6 ± 6.4	0.0 ± 0.0	0.0 ± 0.0	12.6 ± 7.3	0.0 ± 0.0	1.3 ± 5.1	1.4 ± 7.2	9.8 ± 6.8	0.0 ± 0.0	4.6 ± 6.1	0.0 ± 0.0
Diptera	**39.2 ± 6.5**	10.1 ± 5.4	**26.9 ± 5.7**	**54.8 ± 7.5**	**83.5 ± 8.3**	**33.9 ± 14.0**	**38.0 ± 7.4**	**25.7 ± 8.6**	**55.2 ± 5.2**	**26.2 ± 7**	15.9 ± 5.4	**21.2 ± 7.6**	7.2 ± 6.8	**87.6 ± 7.9**
Chironomidae	0.9 ± 5.4	6.9 ± 7.6	7.2 ± 5.4	0.0 ± 0.0	**35.0 ± 6.8**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	7.4 ± 5.1	0.7 ± 7.2	0.3 ± 6.8	0.0 ± 0.0	0.0 ± 0.0	**29.5 ± 7.5**
Tipulidae	**33.4 ± 5.3**	0.0 ± 0.0	19.8 ± 5.2	**44.3 ± 6.3**	**40.0 ± 6.8**	16.6 ± 11.4	16.6 ± 7.2	0.0 ± 0.0	**48.9 ± 5.0**	16.5 ± 7.1	11.2 ± 6.7	**24.6 ± 11.4**	1.0 ± 5.9	**53.4 ± 7.4**
Hemiptera	0.0 ± 6.7	0.0 ± 5.8	0.0 ± 6.3	0.0 ± 7.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 7.7	0.0 ± 9.2	7.5 ± 5.5	0.0 ± 7.3	5.9 ± 5.7	0.0 ± 7.9	0.0 ± 0.0	0.0 ± 14.0
Hymenoptera	0.0 ± 6.5	**26.0 ± 5.5**	8.4 ± 5.8	0.0 ± 7.6	0.0 ± 0.0	7.9 ± 14.1	0.0 ± 7.4	6.1 ± 8.7	1.7 ± 5.2	**27.6 ± 7.1**	10.0 ± 5.5	8.1 ± 7.7	0.3 ± 6.9	0.0 ± 8.0
Lepidoptera	3.5 ± 6.5	16.2 ± 5.5	0.4 ± 5.8	5.1 ± 7.6	2.2 ± 8.6	15.8 ± 14.1	6.0 ± 7.4	10.6 ± 8.7	19.6 ± 5.2	17.3 ± 7.1	**24.7 ± 5.5**	16.7 ± 7.7	3.4 ± 6.9	7.9 ± 8.0
Lumbricidae	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 8.1	0.0 ± 0.0	0.0 ± 14.5	0.0 ± 7.9	0.0 ± 0.0	3.2 ± 5.9	0.0 ± 0.0	4.2 ± 5.9	0.0 ± 0.0	**50.7 ± 7.6**	0.0 ± 0.0
Orthoptera	0.0 ± 0.0	11.1 ± 8.6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	8.2 ± 9.0	16.2 ± 13	0.0 ± 0.0	8.0 ± 10.1	11.5 ± 8.1	11.8 ± 10.5	0.0 ± 0.0	0.0 ± 0.0

dry weight rather than the percentage of items (χ^2_1 = 17.29, p < 0.0001) or percentage occurrence (χ^2_1 = 16.07, p < 0.0001). There was a strong correlation between observed and predicted estimates of the contribution of Coleoptera and Diptera families across the 15 serially excluded studies (r = 0.70, n = 90, p < 0.0001), although composition was slightly underestimated by the model (slope = 0.89 ± 0.098).

The dietary importance of Diptera and Coleoptera families were estimated for 14 upland bird species, with no data at this taxonomic level for adult ptarmigan (which was largely herbivorous), ring ouzel *Turdus torquatus* or stonechat *Saxicola torquata*, and pullus greenshank, ptarmigan or snipe (Table 2). Tipulidae were important for 6 of the 14 species, and averaged 18% of dry weight composition, whereas Chrysomelidae, Curculionidae and Chironomidae were important for 1 species each. Tipulidae were similarly the most important family for upland pulli, again important for 6 species, averaging 23% of dry weight composition (Table 3). Chironomidae were important for 2 species, and Byhrridae, Carabidae and Curculionidae important for 1 each.

3.2. Sensitivity of prey taxa to climate change

Taxa that form a mean contribution of >20% for any bird species and life stage were regarded as potentially important, and are focused on here. These include Coleoptera (specifically Carabidae, Chrysomelidae and Curculionidae), Diptera (specifically Chironomidae and Tipulidae), Lepidoptera, Hymenoptera and Lumbricidae.

There was little information available on the effects of climate on non-carabid beetle families; therefore, data on all beetle groups (mainly carabids) were aggregated (Table 4). Overall, the distribution of studies showing likely negative and positive effects of climate change differed significantly from expected (χ^2_5 = 24.24, p = 0.0002). This was due to the fact that Lumbricidae, Chironomidae and Tipulidae showed a general tendency for negative effects of climate change across all studies (χ^2_2 = 18.73, p < 0.0001). The results of studies on Coleoptera, Hymenoptera and Lepidoptera showed weak differences (χ^2_2 = 5.52, p = 0.06), with a tendency towards generally positive effects of climate change predicted for Hymenoptera, but neutral or mixed effects for Coleoptera and Lepidoptera.

3.3. Relationship between diet and upland bird population trends

Following the results outlined in Section 3.2, the climate-change sensitivity of each bird species was

Table 4. Review of the likely effects of climate change on different invertebrate taxa. The results of each study were summarised as indicating probable detrimental, neutral or beneficial effects of climate change. Where individual studies present differing results from different sites, habitats or taxa, those results were divided accordingly (hence the non-integer scores). These results were then combined to produce an overall assessment of likely climate-change impacts (climate score) that ranged from –1 (all detrimental) to 1 (all beneficial)

Taxa	No. studies			Climate score	UK upland studies
	Negative	Neutral	Positive		
Lumbricidae	7	2		–0.78	0
Chironomidae	7.66	3.5	0.83	–0.57	0
Tipulidae	11		2	–0.69	5
Hymenoptera	0.5	1.5	6	0.61	1
Coleoptera	2.5		2.5	0.00	2
Lepidoptera	13.4	0.7	9.90	–0.15	3
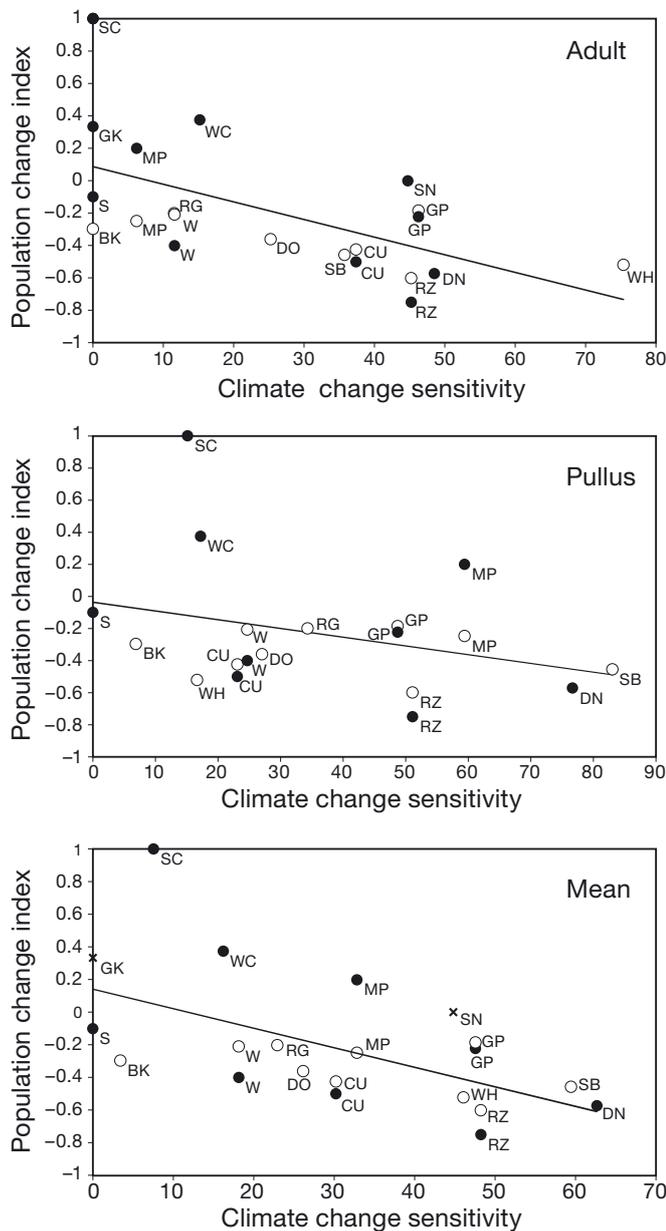
estimated separately for pullus and adult stages from the summed estimated diet contributions of Lumbricidae, Chironimidae and Tipulidae, and correlated with the population change index. For ring ouzel and stonechat, where there were no detailed studies that provided data on the contribution of Tipulidae and Chironomidae in adult diet, the strong correlation between the contribution of all Diptera (x), and that of the Tipulidae and Chironomidae contribution combined (y) (r = 0.87, n = 14, p < 0.001, $y = -3.54 + 0.86x$), was used to estimate the dietary contribution of these families for ring ouzel (19.7%) and stonechat (0.0%) adults to produce a correct estimate of climate sensitivity for those 2 species. There were no studies of pullus diet for greenshank, ptarmigan or snipe. However, given the lack of consistent correlation in the contribution of Tipulidae (r = 0.42, n = 12, p = 0.18), Chironomidae (r = 0.89, n = 12, p < 0.001) and Lumbricidae (r = 0.38, n = 15, p = 0.17) to the diet of adults and pulli, it was not possible to correct for this discrepancy. These species were therefore omitted from the analyses based on pullus and mean diet.

Adult sensitivity to climate change was significantly correlated with upland bird population change. Although climate-change sensitivity of pulli was not, the 2 slopes between climate-change sensitivity and population change did not differ significantly from each other (Fig. 1), suggesting that there was little meaningful difference in the relative importance of the sensitivity of adults and pulli (Table 5). Because of this similarity, the analysis was repeated using a single mean climate-change sensitivity score for each species, based on the average of the adult and pullus climate-change sensitivity scores (x-axis, Fig. 1c). This measure suggests that dunlin and snow bunting are likely to be the 2 most sensitive species to such

Fig. 1. Correlation between population change and adult, pullus and mean climate-change sensitivity of upland bird species assessed from diet. Filled circles indicate where the change index is derived from Sim et al. (2005) and open circles from national population estimates (Table 1). Crosses indicate species for which there were no quantitative data on pullus diet, making it impossible to calculate mean sensitivity. Therefore, these did not contribute to the fitted line, but are plotted for information. Fitted lines have an r^2 of 0.34, 0.10 and 0.30 for adult, pullus and mean climate-change sensitivity, respectively. Letters refer to species codes given in Table 1

Table 5. Relationship between the climate-change sensitivity of each bird species, based on the diet of adults, pulli or the two combined (mean), and the upland bird population change index. Data source accounts for potential variation in the change index depending upon its derivation from either Sim et al. (2005) or population trends. Parameter estimates for data source apply to estimates derived from population trends

	Estimate	SE	df	F	p
Intercept	0.16	0.13			
Data source	−0.14	0.14	1,4.61	0.93	0.38
Adult climate-change sensitivity	−0.011	0.0037	1,11.6	7.82	0.017
Intercept	0.055	0.20			
Data source	−0.083	0.13	1,4.51	0.43	0.54
Pullus climate-change sensitivity	−0.0062	0.0044	1,11.3	2.01	0.18
Intercept	0.21	0.18			
Data source	−0.088	0.13	1,4.73	0.48	0.52
Mean climate-change sensitivity	−0.012	0.0049	1,11.4	6.14	0.030

changes, followed by golden plover, whimbrel, snipe (depending upon pullus diet) and ring ouzel.

As expected from the previous correlations, species that prey most upon climate-sensitive prey were those most likely to have declined recently (Table 5, Fig. 1c).

4. DISCUSSION

4.1. Upland bird diet

Despite being based on data from a wide range of studies that employed a variety of methods, the model describing UK upland bird diets had significant retrodictive ability. Although specific estimates for some species and prey taxa had relatively high uncertainty, reflecting the variable nature of the contributing dietary studies, overall, the results highlight the general importance of both Coleoptera and Diptera prey to a wide range of species, with Tipulidae the most dominant family for both adults and pulli. Other prey taxa, particularly Lumbricidae and Lepidoptera, are also important for a number of species. Upland bird diet therefore differs from that of woodland and scrub birds, where Lepidoptera are the most important prey group, although Coleoptera, Hymenoptera and Hemiptera are widely taken (Krištín & Patočka 1997). Upland bird diet has greater similarity to that of lowland farmland birds, for which Coleoptera — particularly Curculionidae, Orthoptera, Diptera, Lepidoptera and Hymenoptera — are all important (Wilson et al. 1999). As avian breeding success is strongly dependent upon food availability (Arcese & Smith 1988, Marshall et al. 2002, Pearce-Higgins & Yalden 2004), this approach is likely to have identified many of the key prey groups whose abundance is likely to have a strong effect on avian demography.

4.2. Sensitivity of prey taxa to climate change

There is a considerable and increasing body of literature regarding the effects of climate change on invertebrates. However, most of the studies on abundance or demography have focused on species of economic importance, so that much of the literature concerns a relatively small number of reviewed species. For example, many of the reviewed studies of Lepidoptera were of boreal forest pest species, although for other groups, such as Tipulidae, most studies were on UK upland species. Literature searches also identified relatively few studies of Coleoptera, which were widely taken. These limitations emphasise the need for an urgent expansion of monitoring of key prey taxa within the UK upland environment, although, given that many of the studies from elsewhere were of the same species, or ecological analogues of UK species, the results of these studies remain relevant to the UK uplands.

Tipulidae are the most important prey group for the studied insectivorous upland bird species. As a group whose abundance is already linked to golden plover breeding success and population size (Pearce-Higgins & Yalden 2004, Pearce-Higgins et al. 2010), similar effects are likely to be widespread across the other upland bird species for which tipulids are important, such as red grouse *Lagopus lagopus scoticus* (Savory 1977, Park et al. 2001). Tipulid populations may be particularly sensitive to climate change. Summer drought can result in high mortality of young larval *Tipula subnodicornis* instars, the most common insect species in unenclosed moorland and blanket bog habitats (Coulson 1959, 1962, Coulson et al. 1976). As a result, the abundance of emerged adults is reduced after hot summers (Pearce-Higgins et al. 2010). Although the extent to which the high altitude *T. montana* might also be susceptible to drought is unclear, increasing temperatures are likely to result in a switch from a biennial to annual life cycle in this species (Todd 1996), which may have population consequences for the high-altitude birds (Holt et al. 2002).

Many upland waders commute to feed in areas of enclosed pasture that contain high densities of tipulid larvae (Grant et al. 1992, Robson et al. 2002, Pearce-Higgins & Yalden 2003, Hoodless et al. 2007). Although these are generally later-emerging species such as *Tipula pagana* and *T. paludosa* (Coulson 1959, McCracken et al. 1995), their eggs and early larval instars also appear susceptible to drought (Meats

1967a,b), and populations fluctuate in response to late summer–autumn soil moisture levels (Milne et al. 1965, Mayor & Davies 1976, McCracken et al. 1995, Blackshaw & Petrovskii 2007). Therefore, there is consistent evidence from both unenclosed and enclosed upland farmland habitats that the abundance of tipulid species is likely to be reduced by the increasing summer and autumn temperatures and decreasing rainfall predicted for the UK as a result of climate change (Defra 2009).

Chironomids are the other main dipteran family important to upland birds, and their abundance may also be reduced by warming. Evidence from subfossil remains in lake sediments indicate chironomid declines have occurred in lakes in Iceland (Axford et al. 2007) and Spain (Granados & Toro 2000) in response to warming, although such patterns are not ubiquitous (e.g. Brodersen & Anderson 2002, Woodward & Shulmeister 2006). More powerful are experimental results that show reductions in chironomid abundance following warming of both lake and river systems (Hogg & Williams 1996, Tixier et al. 2009). Overall, more studies suggest negative effects of warming than not (Table 2), but few relate to the UK. In upland peatland and moorland systems, it is likely that chironomids will originate primarily from shallow pools that might dry out in response to increasing temperatures, making the physical loss of water bodies of greater importance than the physiological tolerances of the insects themselves (Boulton 2003).

The third invertebrate group regarded as important to upland birds and susceptible to climate change is Lumbricidae (earthworms). Earthworm populations are strongly affected by both temperature and soil moisture (Pelosi et al. 2008). Laboratory manipulations have shown that the growth and survival of individuals is positively related to soil moisture, whereas temperature effects vary between species (Lance Presley et al. 1996, Whalen & Parmelee 1999, Berry & Jordon 2001, Wever et al. 2001). In the field, significant mortality may occur during periods of high temperatures and summer drought (Gerard 1967, Phillipson et al. 1976), with earthworm abundance positively correlated with soil moisture on farmland (Sheldon et al. 2002). Further, drought conditions cause earthworms to burrow and aestivate (Curry 2004), potentially reducing their short-term availability to birds and affecting avian demography (e.g. Peach et al. 2004). Conversely, earthworms may drown because of flooding, although sensitivity to flooding differs considerably between species (Zorn et al. 2005). However, it is unclear whether upland earthworm populations, occupying cooler and wetter soils than the lowland environments where many of these studies have occurred, respond to variation in temperature and rainfall in the same way.

The abundance of other invertebrates taken by upland birds appears to be less negatively affected by climate change. There were mixed effects of variation in soil moisture and temperature upon both Coleoptera and Lepidoptera abundance, whereas effects on Hymenoptera were generally positive. The most detailed literature was available for Lepidoptera, illustrating the complexities of such responses. For example, *Lymantria dispar* abundance is negatively correlated with winter and spring temperature (Miller et al. 1989, Williams & Liebhold 1995), but milder winters increase the survival of *Epirrita autumnata* (Tenow & Nilssen 1990, Virtanen & Neuvonen 1999) and, similarly, the survival of sawfly (Hymenoptera: Symphata) pupae (Aebischer 1990, Barker & Reynolds 2004). Increasing temperatures may improve caterpillar development (Williams et al. 2000), but risk phenological mismatch between bud-burst and caterpillar emergence (Visser & Holleman 2001, Forkner et al. 2008), and increase parasitoid infection rates (Kerslake et al. 1996, Virtanen & Neuvonen 1999). Warming may therefore increase the abundance of some Lepidoptera and Coleoptera species, but decrease the abundance of others (Butterfield 1996, Frampton et al. 2000, Morecroft et al. 2002, Wilson et al. 2005, Franco et al. 2006), which is likely to result in species replacements northward and upward. This contrasts with the predicted negative responses of the invertebrate groups associated with wet soils or aquatic habitats (Chironomidae, Lumbricidae and Tipulidae), which appear to be consistently and negatively affected by rising temperatures and drought.

4.3. Relationship between diet and upland bird population trends

Birds which prey most on Lumbricidae, Chironomidae and Tipulidae may therefore suffer most as a result of climate change. The contribution of these 3 taxa to upland bird diet therefore provides a potential index of species sensitivity to future climate change. On this basis, snow bunting and dunlin may be more sensitive to climate change than golden plover, in which this mechanism was first described (Pearce-Higgins et al. 2010), whereas whimbrel, ring ouzel and snipe may be of similar sensitivity (Fig. 1c). With the exception of ring ouzel, this results from the dietary contribution of Tipulidae, although, if the primary mechanism of such sensitivity is through food availability for chicks (Pearce-Higgins et al. 2010), then whimbrel may be more robust to warming than Fig. 1c suggests, as whimbrel pulli feed upon a wider range of invertebrate groups than the other species (Grant et al. 1992), whereas meadow pipits and red grouse might be more sensitive.

Despite the lack of systematic monitoring of upland bird population trends, the varied nature of the dietary data and the relatively crude assessment of the sensitivity of prey taxa to climate change, there was a significant correlation between the index of climate-change sensitivity and recent trends in upland bird populations (Fig. 1). The fact that this relationship remained significant despite these caveats, and the lack of accounting for other processes known to affect upland birds (Pearce-Higgins et al. 2009a), suggests that it is worthy of further investigation. The negative correlation between ring ouzel population change and summer temperature (Beale et al. 2006), and limiting effects of tipulid abundance on the survival of first-year chough *Pyrrhocora pyrrhocorax*, another tipulid specialist, supports this contention (Reid et al. 2008). Detailed work replicating the approach of Pearce-Higgins et al. (2010) on a wider range of species — particularly, dunlin *Calidris alpina*, whimbrel, ring ouzel and snow bunting, which are all declining — should therefore be conducted to test whether this correlation is causative.

4.4. CONCLUSIONS

Given the sensitivity of bird populations to variation in prey abundance, quantitative assessments of the probable impacts of climate change upon prey populations may provide a useful alternative way to assess climate-change sensitivity. Applying this approach to UK upland birds suggests that species that prey upon Chironomidae, Lumbricidae and Tipulidae may be most sensitive to projected climate change, as indicated by a significant correlation between an index of upland bird climate-change sensitivity based on the dietary contribution of these prey taxa and recent bird population trends. However, this assessment is based upon limited invertebrate monitoring data from the UK uplands, and further research into the likely impacts of climate change on the abundance of keystone invertebrates should be a high priority. Research should also quantify potential links between prey abundance and avian demography more widely. Understanding the likely mechanisms by which climate change will impact upon biodiversity is a precursor to developing appropriate adaptation management to increase the resilience of vulnerable populations to change. Management to reduce drought risk, such as blocking drainage ditches, which were created to lower water tables and increase vegetation productivity across large areas of the UK uplands (Holden et al. 2004), may be the most effective option, but this requires testing (Pearce-Higgins et al. 2010). Given the predicted changes in distribution and abundance of UK upland bird species

as a result of climate change, and increasing evidence for these effects being detectable (Beale et al. 2006, Huntley et al. 2007, Green et al. 2008, Pearce-Higgins et al. 2010), addressing these research gaps should be a high priority.

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