

Review

The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management

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We reviewed the literature to determine the importance of invertebrates for moorland-breeding birds and considered our findings with respect to the conservation of such species in the UK. The diets of many moorland birds consist predominantly of invertebrates, with a wide range of taxa recorded in the diets of moorland birds during the breeding season. Relatively few taxa (Arachnida, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Oligochaeta) were widely taken, with Diptera and Coleoptera being the most important. Among these latter two insect orders, Carabidae, Curculionidae, Elateridae and Tipulidae were the most important families. Comparisons of the diets of bird families, treated separately according to whether data were derived from adults or chicks, showed that waders take more interstitial invertebrates than passerines, which themselves take more foliage invertebrates. Although we lack detailed experimental data with which to demonstrate the direct effect of particular moorland management prescriptions on some of these key invertebrate taxa for breeding birds, available data suggest that management regimes that create a mosaic of habitats are likely to be most beneficial. In particular, heterogeneity in vegetation structure and species composition, and the presence of wet flushes associated with the synchronized spring emergence of adults of certain insect species, are likely to increase invertebrate food resources for birds.

Moorland habitats in the UK are of international conservation importance but, despite this, have been subject to major land-use and management changes in recent decades. Most notable among these are large-scale afforestation, declines in grouse moor management and increasing numbers of sheep and, in the Scottish Highlands, Red Deer *Cervus elaphus* (Mackey *et al.* 1998, Fuller & Gough 1999, Robertson *et al.* 2001). Climate change and changes in government policies that affect upland farming practices may in time lead to further major changes in moorland habitats (Bardgett *et al.* 1995, Berry *et al.* 2001, Task Force for the Hills 2001). The UK uplands hold a

unique breeding bird assemblage, including eight species listed in Annex 1 of the EC Birds Directive and 28 others of conservation concern in the UK (Thompson *et al.* 1995, Gregory *et al.* 2002), a high proportion of which occur on moorlands. Although the broad-scale habitat associations of many of these birds are known (Haworth & Thompson 1990, Brown & Stillman 1993, Pearce-Higgins & Grant *in press*), a detailed understanding of their ecological requirements is often lacking, making it difficult to assess and predict the impact of habitat and other environmental changes upon moorland birds. Given that the UK populations of several moorland bird species appear to be declining (Gibbons *et al.* 1993, Sim *et al.* 2005), it is important to address this knowledge gap and determine the role of such changes in causing declines.

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Fundamental to understanding the ecological requirements of a species is knowledge of its diet and of the factors that affect food availability (Newton 1998). A high proportion of bird species that typically breed in moorland habitats in the UK depend upon invertebrates as a major food source for some or all of their breeding cycle (Ratcliffe 1990). Although dietary studies have been conducted on a range of these bird species during the breeding season, this information is disparate and of varying quality. Furthermore, no overall assessment has yet been made of the relative contribution of different invertebrate species or taxa to moorland bird diets. Determining the main invertebrate prey of moorland birds is an essential prerequisite to assessing the extent to which the effects of habitat (and other environmental) changes may affect bird populations through effects on food supply, and the extent to which such changes can be linked to population declines.

Here we review data on the diets of a range of bird species that are widespread breeders on UK moorlands, and for which invertebrates form a substantial component of the diet for at least part of their life history. Using data from a range of habitats and localities, we describe the prevalence of invertebrates in their diets and consider differences between avian families. On the basis of this information, we consider how different land-uses and managements may affect some of the important invertebrate prey of moorland birds.

METHODS

Study species and data collation

Data were collated for 14 bird species that are considered 'typical' UK moorland species (Red Grouse *Lagopus lagopus scoticus*, Black Grouse *Tetrao tetrix*, European Golden Plover *Pluvialis apricaria*, Northern Lapwing *Vanellus vanellus*, Dunlin *Calidris alpina*, Common Snipe *Gallinago gallinago*, Eurasian Curlew *Numenius arquata*, Common Redshank *Tringa totanus*, Sky Lark *Alauda arvensis*, Meadow Pipit *Anthus pratensis*, Northern Wheatear *Oenanthe oenanthe*, Whinchat *Saxicola rubetra*, Stonechat *Saxicola torquata*, Ring Ouzel *Turdus torquatus*), and in which either the adults or chicks (or both) rely heavily upon invertebrate prey (Table 1; Cramp & Simmons 1980, 1983, Cramp 1988, Thompson *et al.* 1995). These range from species for which virtually all the UK breeding population occurs on moorland (e.g.

Red Grouse and Ring Ouzel) to others for which moorland represents one of several major breeding habitats in the UK (e.g. Northern Lapwing and Sky Lark). We do not consider species that breed primarily on montane, as opposed to moorland, habitats, and also exclude a small number of moorland species with relatively localized distributions in the UK (e.g. Common Greenshank *Tringa nebularia* and Whimbrel *Numenius phaeopus*, which are restricted largely to the far northwest of Scotland and the Northern Isles, respectively). We consider only those age classes in which invertebrates comprise a substantial part of the diet, so that for both Red Grouse and Black Grouse, it is the earlier chick phases only that are considered (because older chicks and adults are largely herbivorous – e.g. Cramp & Simmons 1980, Kastdalen & Wegge 1985).

Breeding season data were obtained from both published and unpublished (e.g. university theses and unpublished reports) sources using a combination of literature searches (on the Web of Science search facility), contacting ecologists involved in ornithological research in the British uplands, obtaining translated material from studies pertaining to the former USSR (accessed via Zoolit – <http://my.tele2.ee/birds>), and the authors' existing knowledge of relevant studies. Prior to analysis, the data were distinguished by geographical locations (treating data separately by study area) where this information was provided, and whether they concerned adult birds or chicks, hereafter termed bird species age category (BSAC). Thus, the 14 species considered give a potential 26 BSACs (adult Red and Black Grouse being excluded as largely herbivorous), although data were unavailable for some (see below). Data from different time periods within a study area (e.g. years or months within a year) were pooled, to minimize pseudoreplication and because such data were rarely available.

Study areas were categorized according to whether or not they were within Britain and Ireland (subsequently termed 'B&I' or 'non-B&I'), with B&I study areas being further divided according to whether they comprised moorland or non-moorland habitats. Up to ten of the 30 study areas in the moorland category included habitats other than unenclosed moorland (mainly enclosed upland grasslands and woodlands), but were classed as such because many of the dietary data appeared to derive from birds foraging on typical moorland vegetation types. Only two of the B&I study areas (both non-moorland) were from Ireland.

Table 1. The number of dietary studies for each of the 14 study species, according to broad location. The number of study areas providing compositional or frequency of occurrence data on diet, and hence contributing to the analyses in Figures 4 and 5, is also shown.

	Studies from outside Britain & Ireland			Britain & Ireland: non-moorland studies		British moorlands:		No. of studies on adults and chicks (respectively) used in analysis of invertebrates occurring as:		Sources
	Adults	Chicks	Not Stated	Adults	Chicks	Adults	Chicks	Taken	'Important**	
Red Grouse (<i>Lagopus lagopus scoticus</i>)	–	–	–	–	–	–	4	0, 4	0, 3	1
Black Grouse (<i>Tetrao tetrix</i>)	–	2	0	–	0	–	4	0, 6	0, 6	2
Golden Plover (<i>Pluvialis apricaria</i>)	6	1	0	0	0	3	3	9, 4	7, 3	3
Lapwing (<i>Vanellus vanellus</i>)	6	0	0	3	1	0	0	9, 1	8, 1	4
Dunlin (<i>Calidris alpina</i>)	10	1	0	0	0	0	1	10, 2	5, 1	5
Snipe (<i>Gallinago gallinago</i>)	3	0	1	2	0	0	0	5, 0	3, 0	6
Curlew (<i>Numenius arquata</i>)	3	0	0	0	2	0	2	3, 4	3, 4	7
Redshank (<i>Tringa totanus</i>)	4	0	0	1	0	0	0	5, 0	2, 0	8
Skylark (<i>Alauda arvensis</i>)	2	3	0	0	1	0	0	2, 3	1, 3	9
Meadow Pipit (<i>Anthus pratensis</i>)	2	5	1	0	0	1	3	3, 8	3, 7	10
Wheatear (<i>Oenanthe oenanthe</i>)	3	2	5	1	1	0	0	4, 3	4, 3	11
Whinchat (<i>Saxicola rubetra</i>)	2	2	3	0	0	0	6	2, 9	1, 6	12
Stonechat (<i>Saxicola torquata</i>)	1	2	0	0	1	0	0	1, 3	1, 3	13
Ring Ouzel (<i>Turdus torquatus</i>)	0	0	2	0	0	0	3	0, 3	0, 3	14

*See text for definition of 'importance' in diet.

Sources: 1 – Butterfield and Coulson (1975); Savory (1977); Park *et al.* (2001). 2 – Filimonova (1972); Picozzi and Hepburn (1984); Cayford *et al.* (1989); Niewold (1990); Borchtchevski (2000); Starling-Westerberg (2001). 3 – Anon (1983); Kumari (1958); Ratcliffe (1976); Baker (1977); Byrkjedal (1980); Danilov *et al.* (1984); Andreeva (1988); O'Connell *et al.* (1996); Whittingham (1996); Pearce-Higgins (1999); Pearce-Higgins and Yalden (2003, 2004). 4 – Kumari (1958); Zinov'yev (1980); Peresad'ko and Koshelev (1980); Galbraith (1989); Beintema *et al.* (1991); Linsley (1999); Bains (1990). 5 – Holmes (1966, 1970); Baker (1977); Andrusenko (1980); Peresad'ko and Koshelev (1980); Danilov *et al.* (1984); Kondrat'yev and Kondrat'yeva (1988); Nechaev (1991); O'Connell *et al.* (1996). 6 – Zinov'yev (1980); Danilov (1984); Green *et al.* (1990); Nechaev (1991). 7 – Kumari (1958); Cramp and Simmons (1983); Robson (1998); Stephen (2001); Grant, unpubl. data. 8 – Peresad'ko and Koshelev (1980); Green (1986); Beintema *et al.* (1991); Nechaev (1991). 9 – Nekrasov (1978); Mal'chevskiy and Pukinskiy (1983); Jenny (1990); Nechaev (1991); Donald *et al.* (2001). 10 – Hagvar and Ostbye (1976); Walton (1979); Prokof'yeva (1980); Coulson and Whittaker (1978); Hagvar and Ostbye (1976); Danilov *et al.* (1984); Burges (1994); Burges and Weidinger (2000); Evans, unpubl. data. 11 – Averin and Ganya (1970, as cited in Cramp 1988); Brooke (1981); Kostin (1983); Gubin and Kovshar (1985); Dorzhiev and Khertuev (1992). 12 – Artem'yev and Popov (1978); Prokof'yeva (1980); Garnett *et al.* (1988); von Labhardt (1988). 13 – Greig-Smith and Quicke (1983); Kostin (1983); Siepel (1990); Nechaev (1991); Cummins and O'Halloran (2002). 14 – Tyler and Green (1994); Burfield (2002).

Treatment of dietary data

Comparison across studies was difficult because dietary data were reported to varying taxonomic levels, with some studies identifying the main invertebrate prey to the level of family, genus or, occasionally, species, whereas others only identified prey to the level of class or order. Consequently, analyses were performed at two taxonomic levels to maximize the value of the available data. First, comparisons were undertaken at a broader taxonomic level, i.e. order for insects, class for arachnids and annelids (although all mentions of worms in diet studies referred to earthworms (Lumbricidae), we use the broader Oligochaete for consistency) and higher levels for other invertebrates. Secondly, for the subset of studies that identified the main prey items to at least the level of family for insects and order for arachnids, comparisons were made at these finer taxonomic levels, although taxa distinguished in fewer than five studies were not used (e.g. Opilione or Araneae families). Percentage composition data were summed across the relevant finer taxonomic levels to produce totals for the broader level analysis (e.g. figures for Coleopteran families would be combined to produce a total for all Coleoptera). Where frequency of occurrence data (i.e. the number or proportion of samples in which the taxa were recorded) were presented, one sample may have contained several families from a particular order. In this case, the maximum percentage occurrence figure for a finer level taxon (e.g. among Coleoptera families) was used to represent the percentage occurrence of the broader taxonomic level (e.g. all Coleoptera). Insect taxa were distinguished by life-cycle stage (adult or larval), where sufficient information was provided, but were otherwise categorized as 'unaged'.

The methods used to collect dietary data, and the treatment of these data, varied between studies. Different sampling methods used in these studies are each subject to biases (Moreby & Stoate 2000), preventing direct comparisons between studies. Therefore, results from the dietary studies were summarized and, for each BSAC in each study area, data on invertebrate taxa were classed according to (1) their presence or absence, and (2) whether or not they either comprised at least 5% of the diet or occurred in at least 5% of samples (for those studies quantifying composition or frequency of occurrence). Where results were presented in different forms, compositional data were used in preference to frequency of occurrence, and biomass composition used in

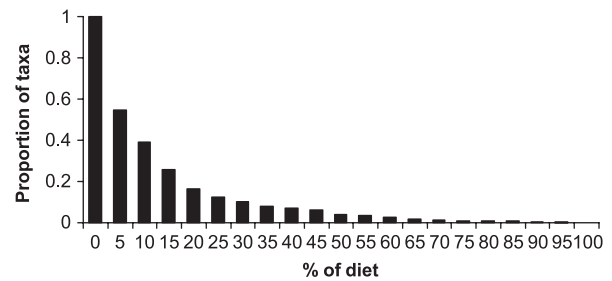


Figure 1. The decline in the proportion of broader invertebrate taxa (see text) in relation to the increasing contribution made to bird diets (i.e. all taxa comprise between 0% and 5% of the diet, but none contributes more than 90%). Data are derived from 14 bird species (with data from adults and chicks treated separately, giving 24 different categories), using studies that present dietary data either as percentage composition or as percentage occurrence in diet samples. The proportions for each taxon are calculated from the average of the mean values for the different bird species and age categories.

preference to numerical composition. The 5% level was selected to distinguish the 'important' taxa, because this represented the most marked discontinuity in the decline in the contribution of different invertebrate taxa to the bird diets (Fig. 1), and concurs with a previous review of bird diets (Wilson *et al.* 1999).

To compare the diets of different BSACs across all studies, data were summarized according to whether each invertebrate taxon was recorded in any study of that species, and whether its average percentage composition or percentage occurrence (across study areas providing data for that species) was at least 5%. This was performed at both taxonomic levels considered here.

Determining differences between diets of bird families and ages

Statistical comparisons of the diets of different age classes of different moorland bird families were undertaken (there being insufficient data for comparisons between BSACs). Analyses were performed at the broader taxonomic level only, owing to the small sample size available at the finer level. 'Unaged' invertebrates were omitted, as were data from study areas providing no information on the sampling methods, and any taxa taken by, or classed as 'important' in, fewer than 10% of BSACs in the respective analyses (Fig. 2).

Analyses were conducted using (1) the presence or absence of each invertebrate taxon, and (2) whether the taxon was classed as 'important' (based upon the 5% criterion), as dependent variables. Data were

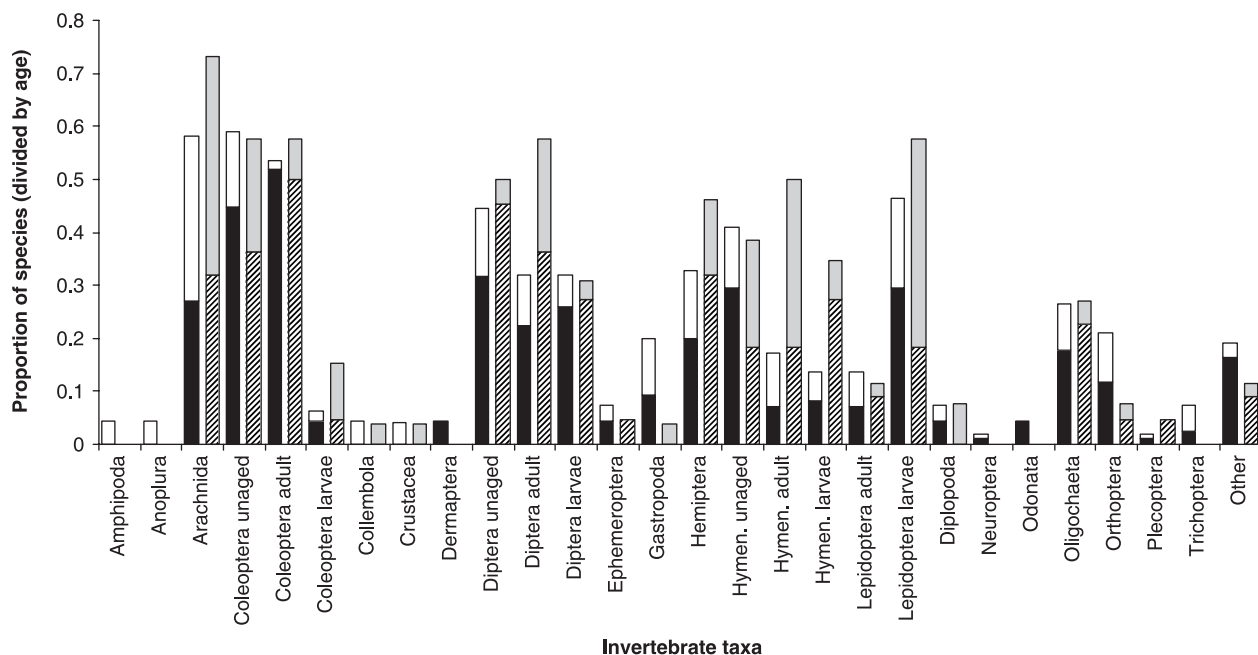


Figure 2. The number of bird species age categories (i.e. adults or chicks, or both, of 14 species) in which different broader invertebrate taxa were recorded as occurring in the diet (entire bar) and being of importance in the diet (open and thin hatched grey sections of bars only). Data are presented for studies from all locations (solid/open bars) and from British moorland studies only (hatched bars). Importance in the diet is defined as comprising $\geq 5\%$ of diet composition, or as occurring in $\geq 5\%$ of dietary samples (where the study presents frequency of occurrence, but not compositional, data).

categorized according to whether they were grouse chicks, wader adults, wader chicks, passerine adults or passerine chicks. Variation due to different sampling methods and to the localities and habitats from which data were derived was taken into account before assessing differences between bird groups. In addition, the treatment of the data (e.g. percentage occurrence or numerical composition) was taken into account in the analyses of the 'importance' of taxa. Thus, logistic ANOVA was undertaken, using Proc GENMOD in SAS 8.02 (SAS Institute 2001), specifying a logit link and binomial error structure (see Endnote), first fitting sampling method, location (i.e. B&I moorland, B&I non-moorland, non-B&I) and, for analyses of 'importance', data treatment.

RESULTS

Coverage of bird species age categories: variation with location and sampling methods

Data on the 14 moorland bird species considered in this review were collated from 62 different sources. When treated separately by study area and bird

species age category, there were 115 diet studies – 31 from British moorland habitats, 12 from other habitats in B&I and 72 from outside B&I (Table 1). The extent to which data were available for adult birds and chicks varied between these three categories, with 70% of the dietary studies from outside B&I concerning adult birds, compared with 50 and 13% of those from non-moorland and moorland habitats, respectively, in B&I (Table 1; $\chi^2_2 = 9.84$, $P = 0.007$). There were also differences in the methods used to collect dietary data, with 74% of B&I studies using faecal analysis compared with 9% elsewhere, where 81% used either crop or stomach samples ($\chi^2_1 = 42.5$, $P < 0.001$). A higher proportion of the dietary studies from outside B&I reported data as presence or absence only (i.e. 33% compared with 15 and 0% for moorland and non-moorland habitats in B&I, respectively), although this difference was not statistically significant ($\chi^2_2 = 5.1$, $P = 0.08$).

Trends in the prevalence and importance of invertebrate taxa

At the broader taxonomic level (order and above), adult and unaged Coleoptera (beetles), Diptera (true

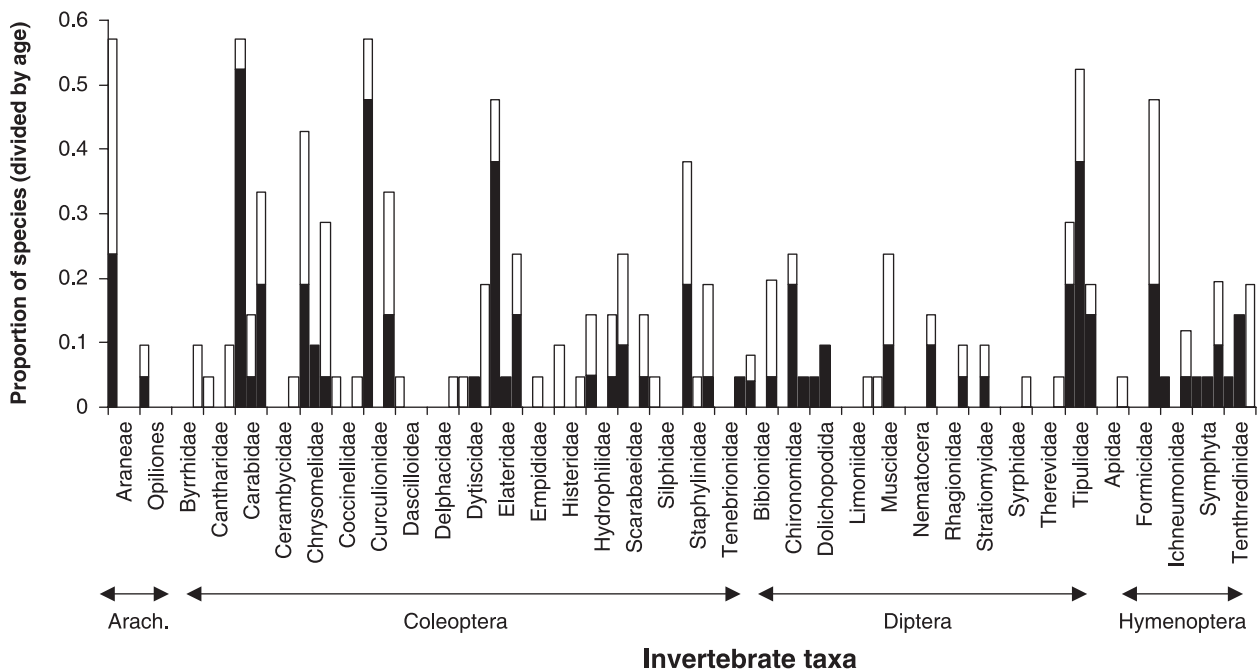


Figure 3. The number of bird species age categories (i.e. adults or chicks, or both, of 14 species) in which different finer level invertebrate taxa were recorded as occurring in the diet (filled plus open sections of bars) and being of importance in the diet (filled section only). Data are derived from studies from all locations. Importance in the diet is defined as for Figure 2. For each taxon (e.g. Carabidae) columns from left to right represent proportion of adults, larvae and unaged, except for Arachnids (Araneae and Opiliones) for which all are classed as adults.

flies), Hemiptera (bugs), Hymenoptera, Lepidoptera larvae, Arachnida (arachnids) and Oligochaeta (worms) were the most ubiquitous prey, all being taken by more than 25% of the different BSACs (Fig. 2). There was a similar pattern in the occurrence of taxa when comparisons were limited to 'important' taxa only (i.e. those comprising $\geq 5\%$ of the diet, or occurring in $\geq 5\%$ of the samples, on average for a BSAC). Arachnids, adult and unaged beetles, true flies, bugs, Hymenoptera and Lepidoptera larvae were most prevalent as 'important' taxa in the diets (Fig. 2). Differences between the frequency of occurrence of taxa and the frequency with which they occurred as 'important' taxa were most marked for arachnids and Lepidoptera larvae. Both taxa were taken by a wide range of BSACs, but often formed a relatively small part of the diet. These comparisons indicated few major differences between the data from all study areas combined and those from British moorland only. However, among the most frequently occurring prey there was a markedly greater representation of both Hymenoptera (adults and larvae) and adult true flies in the moorland diets.

Fewer data were available for the comparisons at the finer taxonomic level, with 66 dietary studies

from 14 bird species (nine adult, 11 chick) providing sufficient data at this level (Fig. 3).

These comparisons suggested that Araneae (spiders) are more prevalent than Opiliones (harvestmen), and that although a wide range of beetle and true fly families are taken, only a few occur frequently. Carabidae (carabids), Chrysomelidae (chrysomelids), Curculionidae (curculionids), Elateridae (elaterids) and Staphylinidae (staphylinids) were the most frequently taken adult beetles, being recorded in more than 35% of the BSACs (Fig. 3). Beetle larvae were recorded relatively rarely. True fly families tended to be less prevalent in bird diets, with only Chironomidae (chironomid), Bibionidae (bibionid) and Tipulidae (tipulid) adults recorded in more than 20% of the diets, and each recorded in less than 30%. However, larval tipulids and Muscidae (muscid) were recorded in 52 and 24% of the diets, respectively. Of the Hymenoptera, Formicidae (formicids) (unaged) were the only group that were relatively prevalent in the diets. When classifying diet in terms of the 'important' taxa, the decrease in occurrence was most marked for Araneae (spiders), chrysomelids, staphylinids, bibionids, muscids and formicids. Comparisons of the prevalence of

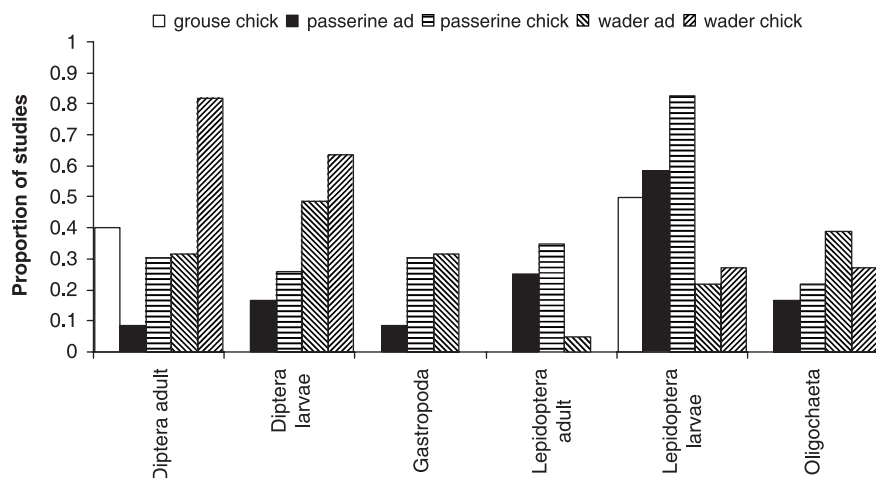


Figure 4. The proportion of dietary studies of each of five moorland bird groups in which different broader level invertebrate taxa were recorded in the diet. Data are shown only for those invertebrate taxa for which statistically significant differences occurred between bird groups. Details of the statistics are as follows (with the significant pair-wise differences given in parentheses): Diptera adults, $\chi^2_4 = 17.29$, $P < 0.01$ (wader chicks > wader adults; passerine adults < passerine chicks, wader chicks). Diptera larvae, $\chi^2_4 = 17.00$, $P < 0.01$ (wader chicks > passerine adults). Gastropoda, $\chi^2_4 = 21.21$, $P < 0.001$ (passerine chicks > passerine adults). Lepidoptera adults, $\chi^2_4 = 28.52$, $P < 0.001$ (passerine chicks > wader adults). Lepidoptera larvae, $\chi^2_4 = 30.52$, $P < 0.001$ (passerine adults > wader adults; passerine chicks > grouse chicks, wader adults and chicks). Oligochaeta, $\chi^2_4 = 26.77$, $P < 0.001$ (wader adults > passerine adults).

invertebrates from studies on British moorlands only were not made at this taxonomic level because few studies provided such data (16 compared with 30 in Fig. 2) and few BSACs were represented (eight compared with 15 in Fig. 2).

Differences between bird families and age categories

Significant differences in the prevalence of invertebrates were detected between the different sampling methods for arachnids, worms and Hymenoptera larvae and, between locations, for adult beetles, Hymenoptera adults and Lepidoptera larvae ($\chi^2_2 > 11.7$, $P < 0.01$ in all cases). Among invertebrate taxa that were classed as 'important', significant differences occurred between sampling methods for worms, locations for adult beetles and the method of data treatment for larval true flies, Gastropoda, bugs and Hymenoptera adults ($\chi^2_2 > 7.8$, $P < 0.05$ in all cases). Owing to the high degree of association between these different effects (particularly sampling method and location – see above), these differences have to be interpreted with caution.

After taking the effects of sampling method, location and data treatment into account, significant differences between bird families and age categories were found in both prevalence and importance for

adult and larval true flies, adult and larval Lepidoptera, and worms. There were also significant differences in prevalence between bird families and age categories for Gastropoda and in importance for bugs (Figs 4 & 5). These analyses suggested that adult true flies were of greater importance to wader chicks than to the other bird groups (although the difference with grouse chicks was non-significant), whereas larval true flies tended to be more important to both wader adults and chicks than to other groups. By contrast, adult and larval Lepidoptera were of most importance to both passerine adults and chicks, but of little importance to the waders and grouse. Worms were of greatest importance to wader adults. Although frequently present in the diets of wader chicks, they were never recorded as an 'important' taxon and were absent from the diets of grouse chicks. Gastropods were most prevalent in diets of adult passerines and waders, whereas bugs occurred as an 'important' taxon most frequently in the diets of adult passerines and grouse chicks. When interpreting these results it must be remembered that certain of the bird groups were heavily influenced by data from one or two species; for example, for adult waders data from ten of the 40 studies were from Dunlin, but only five were from Common Redshank (Table 1). Thus, certain comparisons may reflect differences attributable to one or two species

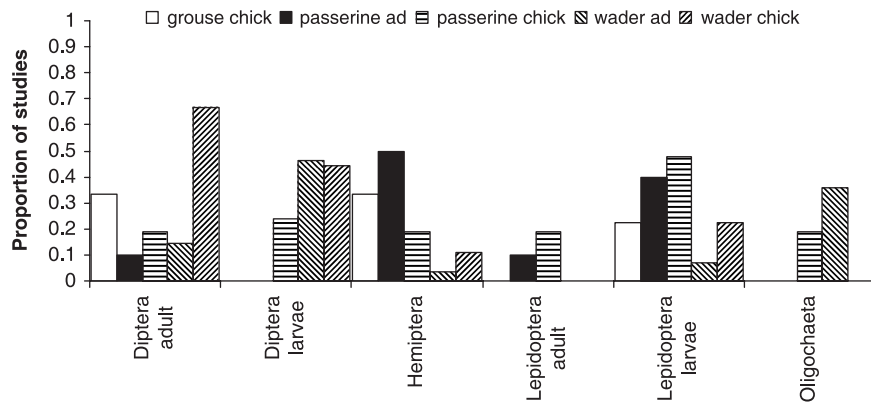


Figure 5. The proportion of dietary studies of each of five moorland bird groups in which different broader level invertebrate taxa were recorded as being important in the diet. Importance in the diet is defined as for Figure 2. Data are shown only for those invertebrate taxa for which statistically significant differences occurred between bird groups. Details of the statistics are as follows (with the significant pairwise differences given in parentheses): Diptera adults, $\chi^2_4 = 13.89$, $P < 0.01$ (wader chicks > wader adults, passerine adults and chicks). Diptera larvae, $\chi^2_4 = 21.30$, $P < 0.001$ (wader adults > passerine chicks). Hemiptera, $\chi^2_4 = 11.78$, $P < 0.05$ (grouse chicks > wader adults; passerine adults > passerine chicks, wader adults). Lepidoptera adults, $\chi^2_4 = 17.14$, $P < 0.01$ (passerine chicks > passerine adults). Lepidoptera larvae, $\chi^2_4 = 12.54$, $P < 0.05$ (wader adults < passerine adults and chicks). Oligochaeta, $\chi^2_4 = 31.85$, $P < 0.001$ (wader adults > passerine chicks).

as opposed to being more widely representative of the relevant bird groups.

DISCUSSION

The contribution of invertebrates to moorland bird diets

A wide range of invertebrates are consumed by moorland birds, but only a small number of the broader level taxonomic groups are particularly prevalent (i.e. arachnids, beetles, true flies, bugs, Hymenoptera, Lepidoptera and worms). With the exception of Hymenoptera and earthworms, Coulson (1988) found that these taxa were among the most abundant on moorland in northern England, suggesting that birds are generally exploiting the most available prey on moorlands. The absence of Collembola and enchytraeid worms from diets, despite also being numerous, is almost certainly due to their small size and, hence, lack of profitability as prey. This diverse range of prey will partly reflect variation in diet between BSACs resulting from their different foraging strategies (discussed below). However, spatial and temporal differences in prey availability within and between studies will also influence diet composition, as indicated by within-species dietary differences associated with different study locations and the few studies that have examined diet in relation to seasonal and between-habitat variation in invertebrate abundance (Picozzi & Hepburn 1984, Starling-

Westerberg 2001, Whittingham *et al.* 2001, Pearce-Higgins & Yalden 2004).

Twelve studies presenting detailed compositional dietary data for eight BSACs on British moorlands (Walton 1979, Picozzi & Hepburn 1984, Garnett *et al.* 1988, Cayford *et al.* 1989, Whittingham 1996, Starling-Westerberg 2001, Stephen 2001, Burfield 2002, Pearce-Higgins & Yalden 2003, 2004) generally support the results of our wider analysis. These studies showed that beetles formed the most important item for five of the BSACs considered, comprising over 15% of the diet of four cases. True flies were most important in four cases, comprising over 15% of the total diet in five. The prevalence of adult true flies in moorland bird diets, especially among waders and Red Grouse, reflects in part the high abundance of tipulids on some moorland areas following their highly synchronized emergences (Coulson 1962). Less important in this subset of more detailed moorland studies were earthworms, which were taken mainly by adult waders foraging on nearby improved grasslands, but were also the most important item for Ring Ouzel chicks. As in our wider analysis, arachnids, bugs, Hymenoptera and Lepidoptera were also important and frequently occurring prey items in these studies, albeit less so than true flies and beetles. Thus, Hymenoptera were the most important prey in one case, and accounted for more than 15% of the diet of three cases. Arachnids, bugs and Lepidoptera were never dominant, possibly because of the relatively low biomass and small prey size of some of these

taxa (Coulson 1988). Arachnid prevalence in these studies supports the trend in our wider analyses that although widespread in the bird diets, they often form a relatively small part of the total prey intake.

Prey size is likely to be important in determining the extent to which birds take different invertebrates, but few studies have identified the main prey to the level of species, or even genus, and considerable size variation exists within insect families and other invertebrate orders. Of the insect families identified as important in the current review, several include a large number of relatively large species (e.g. carabids, staphylinids, and adult and larval tipulids), but others tend to comprise relatively small species, such as chironomids (e.g. Chinery 1986). The evidence suggests that moorland birds often prey upon relatively large, and presumably more profitable, invertebrates, especially in the case of adult waders foraging for soil invertebrates on nearby grasslands. Existing data prevent any detailed assessment of the prey sizes that are most often taken or selected, although in European Golden Plover, the mean prey size taken by chicks foraging on blanket bog habitats increased with chick age, from 3.12 mg (1- to 8-day-old chicks) to 8.34 mg (over 32 days), with this increase being at least partly due to the greater exploitation of tipulid larvae by older chicks (Pearce-Higgins & Yalden 2004). Beintema *et al.* (1991) found that wader chicks (including Northern Lapwing and Common Redshank) foraging on agricultural grasslands tended to select invertebrate taxa in the largest size class (4–20 mm), rather than taxa in smaller size classes (0–4 and 2–6 mm), relative to measures of their abundance. However, in some instances, relatively small prey can be important (e.g. Red Grouse chicks and *Molophilus ater* – Savory 1977).

The comparison of diets between bird families and age classes highlights some broad differences, related largely to differing foraging strategies: surface and subsurface feeders vs. foliage gleaners and aerial salliers. Waders, comprising mainly the former grouping, tended to take higher proportions of interstitial invertebrates such as true fly larvae and worms than did most passerines, which took more foliar invertebrates, such as Lepidoptera and bugs. Ring Ouzels were an exception among the passerines in taking earthworms. This is presumably associated with their strong preferences for foraging on short grass (Burfield 2002).

Dietary differences between wader adults and chicks reflect the fact that during the prelaying and incubation periods, at least, adult Eurasian Curlew

and European Golden Plover forage off moorland on improved pastures and other grasslands where they exploit soil invertebrates while chicks generally remain on moorland where they exploit surface-active invertebrates (Whittingham *et al.* 2000, 2001, Robson *et al.* 2002, Pearce-Higgins & Yalden 2003, 2004). Differences in the diets of passerine adults and chicks are less readily explained, given that adult passerines provision their chicks in the nest and would be expected to have similar diets. However, variation in nutritional value between invertebrate taxa could be important in this respect (e.g. Gosler 1993, Ramsay & Houston 2003), or there may be seasonal differences in the times at which adult and chick diets have been studied.

Invertebrate habitat associations

As indicated above, a relatively small range of invertebrates tend to be important components of moorland bird diets, although a wide range of invertebrates are taken, reflecting the pattern found in lowland farmland birds (Wilson *et al.* 1999). Thus, it is likely that the abundance and distribution of some moorland bird species are influenced by factors affecting habitat suitability for these key invertebrate taxa. The diversity and abundance of many invertebrate taxa are heavily dependent on soil type and moisture content. For example, beetles (which often have interstitial larvae) display strong associations with both characteristics (Butterfield & Coulson 1983, Dennis *et al.* 1997, Gardner *et al.* 1997), with, specifically, the abundance of carabids being greatest on sites with a mix of both wet and dry habitats (Butterfield & Coulson 1983). Among the true flies, tipulid larvae are most abundant on peaty soils, especially where annual rainfall is high (Butterfield & Coulson 1975, Coulson 1988), probably due to their vulnerability to desiccation (Coulson 1962). There are no strong, general, associations with physical characteristics of soil among two of the three remaining taxa (spiders and Lepidoptera) that formed a substantial proportion of bird diets (Downie *et al.* 1995), but given that soil type can determine the distribution of the vegetation, it can indirectly affect bug distribution, and probably that of other, less well-studied, taxa as well (Sanderson *et al.* 1995, Hartley *et al.* 2003). Despite being prevalent in the diets of some moorland birds, worms are virtually absent from peat soils. However, they are abundant on mineral soils, especially pastures, near moorland edges, where the adults of some species forage regularly (e.g.

Whittingham *et al.* 2000, Burfield 2002, Pearce-Higgins & Yalden 2003).

Moorland vegetation composition is also an important determinant of the invertebrate community (e.g. Butterfield & Coulson 1983, Coulson & Butterfield 1986, Gardner 1991, Gardner *et al.* 1997). On sedge-dominated blanket bogs, true flies, especially tipulids, tend to predominate, although this may also reflect the wet, peaty, substrate. Conversely, drier heath communities dominated by dwarf shrubs such as Heather *Calluna vulgaris* are characterized by a high Lepidoptera biomass (Coulson 1988), and can support more beetles than graminoid-dominated habitats (Gardner *et al.* 1997). The differing habitat associations of invertebrates mean that sites with a mosaic of habitat types are liable to support a greater diversity and abundance of invertebrates than homogeneous sites (Coulson & Butterfield 1985, Usher & Thompson 1993), potentially resulting in a greater diversity and abundance of moorland birds.

The effects of moorland management

Vegetation and management are important determinants of bird abundance (e.g. Tharme *et al.* 2001, Calladine *et al.* 2002, Pearce-Higgins & Grant in press). Changes in vegetation, or management affecting vegetation, may affect bird populations through altering invertebrate abundance. Large-scale changes in moorland habitats will alter invertebrate community composition (Coulson 1988, Usher & Thompson 1993), while smaller-scale changes in vegetation composition and structure can have major impacts on both species richness and abundance of the major invertebrate groups (Southwood *et al.* 1979, Gimingham 1985). Trends in moorland management since the middle of the last century will have changed the soil conditions, vegetation structure and composition on moorlands, and hence affected invertebrate abundance and community composition. Notable trends are:

(1) Increases in sheep and Red Deer numbers, affecting moorland vegetation across many upland areas, particularly in causing the expansion of grassland into heather moorland (Mackey *et al.* 1998, Fuller & Gough 1999).

(2) Declines in grouse moor management (e.g. Robertson *et al.* 2001) may have reduced the extent and frequency of muirburn, so reducing spatial variation in vegetation composition and height (although specific evidence for declines in muirburn extent is lacking – Hester & Sydes 1992).

(3) The widespread construction of drainage ditches (grips) between the 1960s and 1990s changed soil conditions and vegetation composition (Coulson *et al.* 1990).

Where relationships between moorland management, vegetation and invertebrates have been investigated by experimental manipulation, focus has been on the impacts of relatively short-term changes in vegetation structure, mediated through differential grazing regimes (e.g. McFerran *et al.* 1994a, 1994b; Dennis *et al.* 1997, 1998, 2001, 2005) or muirburn management (Gardner 1991, Haysom & Coulson 1998). Few experimental studies have investigated the impacts of different management regimes over longer periods (decades), replicated across several different sites. In particular, relatively few experimental studies have focused on the effects of moorland management on the true flies, especially tipulids, which are a key component in the diet of many bird species. However, their general ecology has been well studied, allowing some management impacts to be inferred (Coulson & Butterfield 1985, Coulson *et al.* 1990).

The effects of mixed grazing regimes (sheep and cattle) on invertebrates appear to vary. Sheep and cattle grazing reduce beetle abundance through trampling and dunging by cattle, while increased grazing can reduce overall arthropod abundance on *Nardus*-dominated grasslands by damaging the tussocks where invertebrates shelter (Dennis *et al.* 1998). Increased dunging may, however, also benefit invertebrates by providing food for larvae (e.g. McCracken & Foster 1993). Overall invertebrate biomass may increase at lower grazing intensities, with the biomass of surface-dwelling invertebrates (as sampled by suction sampling) doubling after a 66% decrease in stocking (Dennis *et al.* 2005). However, reduced grazing did not benefit all invertebrates in that study, and larval tipulid biomass decreased under the reduced stocking levels. There is also evidence of an interaction between cattle grazing and Heather Beetle *Lochmaea suturalis* on dry heaths in the Netherlands (Bokdam 2001). Patches of defoliated heather are vulnerable to invasion by grasses (especially *Molinia* on wet heaths, and *Deschampsia* on dry heaths), although cattle grazing of the grass leads to more rapid heather recovery.

Among the invertebrates that are key components of moorland bird diets, changes in vegetation structure can produce rapid responses in the abundance of spiders, which favour tall, complex swards (Coulson & Butterfield 1986, McFerran *et al.* 1994b, Dennis *et al.* 1998, 2004, Bell *et al.* 2001) and some bugs

(Gimingham 1985), which increased after a reduction in grazing pressure (Dennis *et al.* 2005). Similarly, beetles, especially staphylinids, increased with a decrease in grazing pressure (Dennis *et al.* 2005). Hymenoptera and Lepidoptera larvae both increase in abundance with increased vegetation height or structural complexity (Haysom & Coulson 1998). The short, open, vegetation patches produced by muirburn benefit mobile predatory and scavenging species, and pioneer species that colonize the new growth of vegetation (Gardner & Usher 1989, Gardner 1991, Bell *et al.* 2001). Moorland drainage schemes were formerly used to improve heather growth, and hence provide better habitats for grouse and sheep, although the wet areas affected by such drainage may provide important food for grouse chicks (Coulson & Butterfield 1985). The impacts of drainage appear to be relatively minor in areas with heavy rainfall, but on drier areas it may remove small pockets of wet peat, reducing the overall invertebrate diversity and, perhaps more importantly in the context of bird diets, depressing the spring emergence of insects, especially tipulids (Coulson & Butterfield 1985, Coulson *et al.* 1990).

Overall, these studies suggest that management regimes that create habitats characterized by a mosaic of vegetation communities and structures are likely to support the greatest invertebrate diversity and abundance (Coulson & Butterfield 1985, Usher & Thompson 1993), potentially benefiting the moorland birds. Thus, the generally positive effects of increasing vegetation structure on overall arthropod abundance are likely to benefit foliage gleaners and aerial salliers such as Whinchat and Stonechat that associate with taller, denser vegetation (e.g. Allen 1995, Pearce-Higgins & Grant *in press*). Conversely, short, open, vegetation can be associated with a greater abundance of important subsurface invertebrate prey, and can also increase the availability of surface invertebrates, so benefiting such birds as European Golden Plover and Ring Ouzel, which tend to require short, open vegetation (Burfield 2002, Pearce-Higgins & Yalden 2003).

In conclusion, we have summarized the importance of different invertebrate taxa in the diets of moorland birds, highlighting the most important taxa and, based upon current knowledge, summarized how moorland management may affect their abundance. We have also identified gaps in current knowledge. For example, diets remain poorly described for the majority of moorland bird species. Furthermore, to maximize the potential use of such data, we recom-

mend that future studies quantify diet in terms of numerical or, preferably, biomass composition to as fine a taxonomic level as possible (at least family), assess prey-size selection, and target bird species for which dietary data are scarce. To understand the effects of management on invertebrate prey, experimental studies are required, particularly on the effects of burning or cutting moorland vegetation and on grip blocking. Fundamentally, investigations of relationships between the diversity and abundance of invertebrates and the abundance of moorland birds are required to determine the extent to which habitat change affects these bird populations, via effects on their invertebrate prey.

ENDNOTE

Analyses were performed by first fitting sampling method (i.e. stomach or crop, faecal, neck collar, feeding observation), location (i.e. B&I moorland, B&I non-moorland, non-B&I) and, for analyses of 'importance', data treatment (i.e. biomass composition, numerical composition, percentage occurrence). A step-down procedure was used, deleting the factor with the lowest significance level at each stage, until only the significant ($P < 0.05$) factors remained. Effects of bird families and age were assessed at this stage by testing whether the addition of this factor produced a further significant change in model deviance. Statistical significance was determined by treating the change in residual deviance associated with each term as χ^2 with the appropriate degrees of freedom (Crawley 1993, SAS Institute 2001). Changing the order in which the levels of the factor (bird family and age) were entered allowed the standard errors around each estimated mean to be compared, and hence which categories differed significantly from the others (Crawley 1993, SAS Institute 2001).

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