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What do declining woodland birds eat? A synthesis of dietary records

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Abstract. Ground-foraging insectivores are prominent among the 26 species considered 'declining woodland birds' in southern Australia but the mechanisms driving their declines remain elusive. Nutritional factors may be critical, with larger and more structurally complex woodlands supporting greater arthropod biomass, but these differences need not translate into more arthropods actually consumed by these insectivores. We synthesised existing dietary records of a subset of the 26 declining woodland birds – 13 ground-foraging insectivorous passerines – to determine the range of arthropods consumed and to estimate the relative importance of each prey group for these birds. Declining insectivores consumed a wide array of arthropods, but diets were characteristically dominated by one or two prey groups: Coleoptera, Formicidae and Lepidoptera accounted for 58% of prey records. Coleoptera contributed the greatest proportion of records (27%) and was the dominant prey group in the diets of nine of the 13 birds. These popular prey groups likely represent core resources supporting populations of declining insectivores and measurement of their abundance may provide meaningful estimates of the availability of prey. We highlight the need to quantify the size-range and identity of those prey eaten by declining woodland birds, and propose that reliance on a small number of prey groups may underlie the sensitivity of ground-foraging insectivores to modification of habitat.

Additional keywords: arthropods, diet, ground foraging, habitat fragmentation, insectivore, prey selection.

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Introduction

Insectivorous birds are declining worldwide, manifested in reduced abundances and distributions (Bennett and Watson 2011). Various processes have been proposed to explain these declines, including loss and fragmentation of habitat (Walters *et al*. 1999; Britschgi *et al*. 2006); increased parasitism and predation of nests (Arcese *et al*. 1996; Zanette and Jenkins 2000); food limitation (Zanette *et al*. 2000; Watson 2011); and declining abundance and diversity of arthropod prey (Didham *et al*. 1996; Benton *et al*. 2002; Sinclair *et al*. 2002). With broad-scale clearance of land for agriculture, forestry and the increasing sprawl of urban infrastructure, general declines of biota are expected. However, insectivores are often recorded as declining when other foraging guilds are maintaining or increasing their population (Reid 1999; Antos and Bennett 2006; Watson 2011), indicative of a more specific underlying mechanism.

Insectivorous birds account for 20 of the 26 species considered 'declining woodland birds' in southern Australia (Watson 2011), with 14 species foraging primarily on the ground. A range of factors have been implicated in the decline of these birds, including the effects of livestock grazing and weed encroachment (Maron and Lill 2005) and the inability of some species to disperse effectively between fragments of habitat (Walters *et al*. 1999). Nutritional factors in general – and food limitation in particular – have been largely unexplored, yet there is mounting evidence that agricultural practices, habitat fragmentation and other phenomena such as drought and weed invasion can severely affect arthropod communities (Abensperg-Traun *et al*. 1996; Bromham *et al*. 1999; Benton *et al*. 2002; Dennis *et al*. 2008; Tallamy *et al*. 2010).

Insectivorous birds forage selectively (Hutto 1990; Kaspari and Joern 1993; McCarty and Winkler 1999; Hagar *et al*. 2007) and, given known variation in the nutritional content of arthropod taxa (Robel *et al*. 1995; Finke 2002; Arnold *et al*. 2010; Razeng 2011), many workers have suggested that birds may consume specific types of prey to satisfy particular nutritional needs (Arnold *et al*. 2007, 2010; Eeva *et al*. 2010) – quality may be just as important as quantity. Although there have been no studies of feeding preference of declining insectivores in southern Australia, Zanette *et al*. (2000) suggested differences in overall arthropod biomass were indicative of food shortages for Eastern Yellow Robins (*Eopsaltria australis*) in small habitat fragments relative to large fragments. Likewise, Taylor (2008) found that box–ironbark eucalypt forests in north-eastern Victoria supported a low biomass of leaf-litter invertebrates when compared with other forest habitats in Australia and elsewhere, suggestive of a lower carrying capacity for insectivores. Although these studies highlight the importance of food limitation as a distributional constraint, both used total arthropod biomass to estimate the availability of prey – an approach that assumes those arthropods

consumed are available in direct proportion to arthropods generally. This assumption has not been explicitly evaluated, however, and the effect of prey availability on the occurrence of insectivores remains unclear.

The foraging ecology of ground-foraging insectivores in southern Australia has been well studied (Ford *et al*. 1986; Recher *et al*. 2002; Antos and Bennett 2006; Taylor and Paul 2006) yielding detailed information on microhabitat use, substrate selection and foraging behaviour. In contrast to this fine-grained understanding of where these species forage, our current knowledge of what these birds actually eat is limited to 'insects'. Whether these birds preferentially eat some groups of arthropods or avoid other groups altogether is not known. Likewise, the size range of prey items eaten has not been measured. Without information on dietary breadth and prey preference, realistic estimates of prey availability cannot be determined, preventing the testing of food limitation as a determinant of bird distribution.

As the first element of a broader research program examining the nutritional ecology of declining insectivorous birds, this study addresses the question: do certain arthropod taxa occur more frequently than others in the diet of ground-foraging insectivores? Rather than comparing the diets of declining insectivores with other insectivores, we examine declining insectivores in detail to determine what range of arthropods are consumed, whether some groups of prey are eaten more frequently than others, and whether any prey groups are not consumed. Rather than relating to the dietary preferences of particular species, we synthesised available dietary information for a group of ground-foraging insectivores to examine the relative contribution of arthropod groups to the diet of declining woodland birds. This information is discussed in the context of habitat change in southern Australia, and the nutritional limitation hypothesis is revisited and refined.

Methods

Study species

This study focuses on a subset of the declining woodland birds of southern Australia, of which 20 were originally identified by Reid (1999), and six others have been added as the list was expanded (see Watson 2011). Of the 14 ground-foraging insectivores in this group, 13 are insectivorous passerines that forage mainly on the ground and associated substrates. This group of 13 insectivorous ground-foraging birds are the focus of this study, hereafter referred to as 'declining insectivores' (Table 1). We did not include the Painted Button-quail (*Turnix varia*) because, although it is a ground-forager, it is a non-passerine and arthropods are consumed as part of a wider diet including seeds, fruit and other vegetable matter (Marchant and Higgins 1993).

These 13 species, from six families, are small to medium-sized birds, ranging from ~6 g (Chestnut-rumped Thornbill, *Acanthiza uropygialis*) to ~75 g (Grey-crowned Babbler, *Pomatostomus temporalis*) (Higgins *et al*. 2001). Time spent foraging on the ground varies seasonally within species, and estimates of percentage of foraging time spent on the ground ranges from 28% (Grey-crowned Babbler; Brooker *et al*. 1990) to 99% (Southern Whiteface, *Aphelocephala leucopsis*; Recher and Davis 1997; and White-browed Babbler, *Pomatostomus superciliosus*; Taylor and Paul 2006). These 13 species are largely territorial and sedentary (Ford *et al*. 2001). As a group, they inhabit a wide range of wooded habitats, extending from wet and dry eucalypt forests, to grassy eucalypt woodlands and *Callitris* woodland and *Acacia*-dominated woodlands further inland. However, the most marked declines in these birds have occurred in eucalypt woodlands in the southern parts of their range, and are less pronounced in other woodland types (Watson 2011; see Major *et al*. 2001; Antos and Bennett 2005; Maron and Lill 2005).

Table 1. List of the 13 bird species used for analysis of diet in this study
All are insectivorous passerines which are known to perform most foraging actions on or near the ground

Common name	Species name
White-browed Treecreeper	*Climacteris affinis*
Brown Treecreeper	*Climacteris picumnus*
Speckled Warbler	*Chthonicola sagittata*
Chestnut-rumped Thornbill	*Acanthiza uropygialis*
Southern Whiteface	*Aphelocephala leucopsis*
Grey-crowned Babbler	*Pomatostomus temporalis*
White-browed Babbler	*Pomatostomus superciliosus*
Crested Bellbird	*Oreoica gutturalis*
Restless Flycatcher	*Myiagra inquieta*
Jacky Winter	*Microeca fascinans*
Red-capped Robin	*Petroica goodenovii*
Hooded Robin	*Melanodryas cucullata*
Eastern Yellow Robin	*Eopsaltria australis*

Data collection

To determine the relative contribution of arthropod taxa to the diet of declining insectivores, data were collected using the comprehensive sources listed in the *Handbook of Australian, New Zealand and Antarctic Birds* (*HANZAB*; Higgins *et al*. 2001, 2006; Higgins and Peter 2002). *HANZAB* is the pre-eminent reference for birds in the region, drawn from exhaustive searches of the primary ornithological literature, incorporating, unpublished data, university theses, museum specimens, historical accounts and personal communications, compiled in close consultation with leading ornithological experts. Quantifying diets from existing records can be confounded by different sampling methods used to collect information on avian diets or prey availability (Buchanan *et al*. 2006) and methods for quantifying prey (typically compositional comparisons, frequency of occurrence or biomass composition). In *HANZAB*, many sources are simple lists of items found in stomach samples, whereas others are one-off records of birds observed foraging (often recorded because the prey or foraging mode was novel or noteworthy). By establishing clear criteria for including dietary records and minimum levels of taxonomic resolution, analysis of relative frequencies of prey taxa can be performed, revealing generalised dietary preferences of this group of declining woodland birds.

To minimise confounding effects while incorporating all available information, a simple count of the number of sources citing each prey taxon listed was used to compile dietary composition for this group of 13 species. An instance of a species eating a particular arthropod, or a report of the presence of a particular arthropod in the gut contents of multiple individuals are both treated as single records. For each species, a list of the food items that have been recorded in *HANZAB* as being eaten by that species is provided. For each food item recorded, a reference is

given for all original sources which list that particular food item. Thus, if five sources noted that Eastern Yellow Robins consume ants, these five sources were individually referenced. Using *HANZAB*, for each species of declining insectivore we created a list of prey taxa consumed and counted the number of references pertaining to each prey type.

In the 127 sources summarised in these records, most invertebrate taxa were identified to class or order, with few identified to family, genus or species. Owing to this inconsistent resolution, grouping prey taxa at the ordinal level (or lowest available level where order was not specified) was considered most appropriate for analysis, reflecting a compromise between distinguishing between different prey types and errors in identification associated with finer taxonomic resolution. Class or subclass groupings were used for those taxa with no records below these levels, such as Diplopoda, Chilopoda and Oligochaeta. Ants (Hymenoptera :

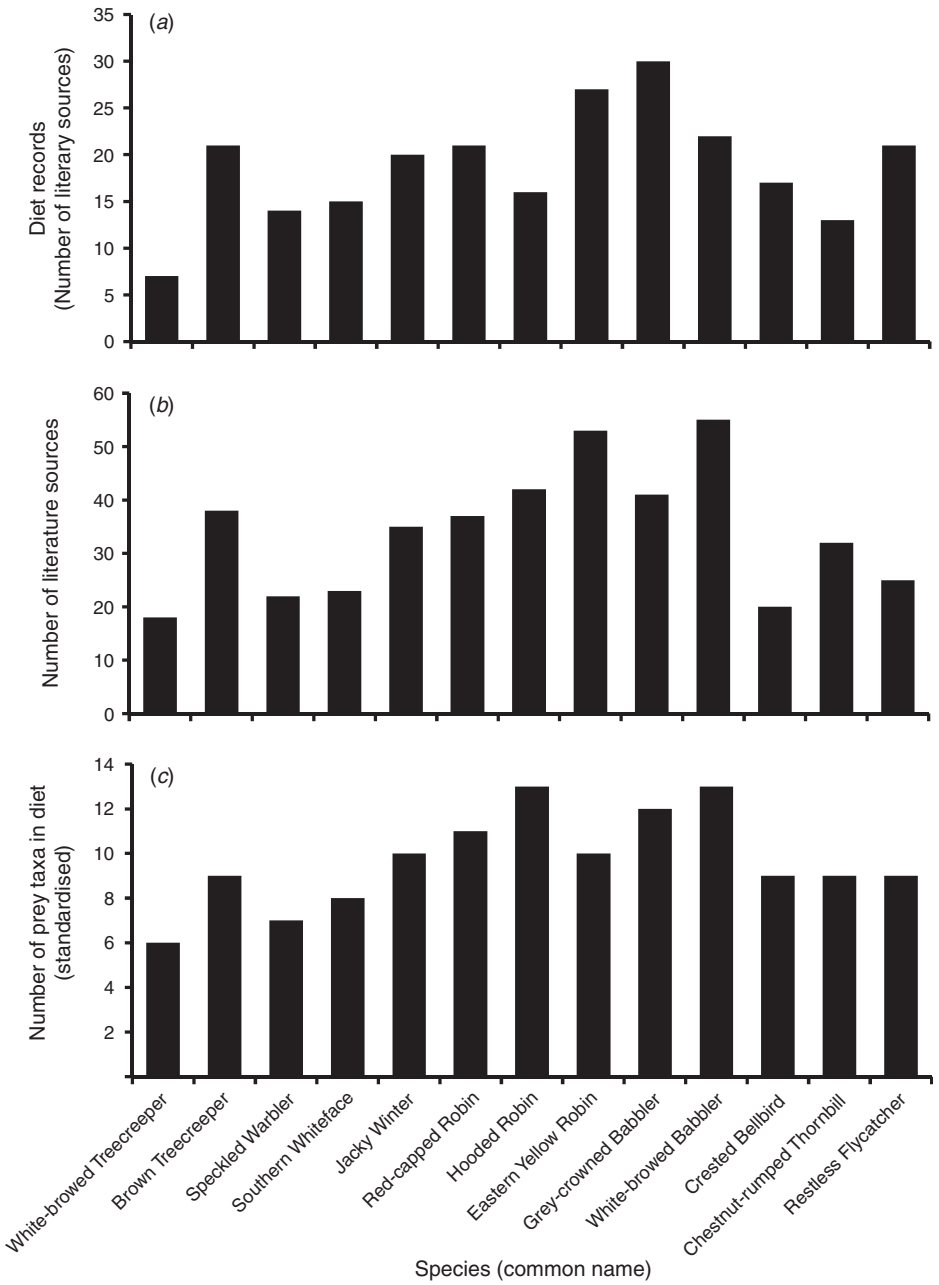

Fig. 1. (*a*) Number of literary sources providing dietary data; (*b*) total number of prey taxa recorded (all taxonomic levels); and (*c*) number of 'standardised prey taxa' recorded for each of the 13 species of ground-foraging birds in the study group, obtained via a comprehensive review of dietary records (see methods). 'Standardised prey taxa' is the number of prey taxa standardised by grouping into the highest comparable taxonomic level (order for insects and arachnids, and class or subclass where order was not available).

Formicidae) were categorised separately from other Hymenoptera (bees and wasps) – ants occur in high densities on Australian soil-surface habitats (Shattuck 1999) and tend to be a more accessible and frequently recorded food source for ground-foraging birds than bees or wasps. This is the only instance in which an order was subdivided in this analysis. The total number of records for each prey group was then calculated across all bird species being studied, and the prey groups ranked according to the relative percentage of total prey items recorded.

Results

Summary of data

The final dataset contained 902 records of diet from 127 sources, spanning a period of 95 years (1905–2000). This dataset spanned a wide range of taxonomic resolution, with one prey group identified to phylum only (Mollusca), three being identified to class or sub-class (Diplopoda ($n = 7$), Chilopoda ($n = 4$) and Oligochaeta ($n = 2$)) and eight prey taxa identified to species ($n = 22$). Invertebrates identified in the diets of these birds were predominantly arthropods, the only non-arthropod records being from the phyla Annelida ($n = 2$) and Mollusca ($n = 1$). Arthropods from four classes, 24 orders, 69 families and 37 genera have been identified in the diets of these birds (see Razeng 2011), with most records belonging to class Insecta (740 records listed to order and below, and 88 records identified only as 'insects' which were not included in the final analysis).

Comparison of diet between bird species

The number of original sources of dietary records varied greatly between species, ranging from seven sources for the White-browed Treecreeper (*Climacteris affinis*) to 30 for the White-browed Babbler, with the overall mean (± s.d.) of 18.8 ± 6.1 records (Fig. 1*a*). The number of prey taxa recorded also varied greatly between species, from 18 for the White-browed Treecreeper to 55 for the White-browed Babbler, with an overall mean of 33.9 ± 12.1 prey taxa per species (Fig. 1*b*). However, when records were condensed to the level of order (and class when order was not listed), the uniformity of the diets of these bird species became more apparent (Fig. 1*c*), ranging from six taxa recorded for the White-browed Treecreeper to 13 taxa for the Hooded Robin (*Melanodryas cucullata*) and the White-browed Babbler, with an overall mean of 9.7 ± 2.1 taxa per species. Dietary records for each species were characteristically dominated by one or two prey groups, with other prey groups recorded in low frequencies. Coleoptera was the most frequently recorded prey group for eight of the 13 species, Formicidae for three species, Lepidoptera for one species and Diptera for one species (Fig. 2).

Occurrence of arthropod taxa in the collective diet

Collective dietary records for this group of 13 bird species included 15 insect orders and two arachnid orders, as well as records of Diplopoda, Chilopoda, Oligochaeta and a single record of a mollusc (Fig. 3). Coleoptera contributed the greatest proportion of dietary records ($n = 220$, 27%), followed by Formicidae ($n = 148$, 18%) and Lepidoptera ($n = 100$, 12%). Eleven of the 21 groups listed here contained <10 records, and four groups (Mollusca, Pseudoscorpionida, Phasmatodea and Thysanoptera) were recorded only once.

The three most commonly occurring prey groups (Coleoptera, Formicidae, and Lepidoptera) collectively accounted for 58% of prey records. These three groups were also the only groups recorded in the diets of all 13 bird species. However, five more groups appeared in the diets of at least 11 of the 13 species (Hemiptera, Orthoptera, Araneae, Diptera, Hymenoptera (bees and wasps); Fig. 4); although consumed less frequently, they are nonetheless widely consumed by this group of birds.

Discussion

The declining insectivorous birds assessed here were found to consume a diverse array of arthropods, including insects, spiders, millipedes and centipedes, as well as earthworms and molluscs. Despite this dietary breadth, three groups of insects (beetles, ants, and moths and butterflies) made up the majority of dietary records, as well as being dominant in the diets of most of the bird species examined. Although the contribution of arthropod taxa at finer taxonomic levels was not assessed, this preliminary analysis nonetheless provides new insights into the nutritional ecology of this group of declining birds.

The three most frequently consumed prey groups (Coleoptera, Formicidae and Lepidoptera) were the only groups to occur in the diet of all 13 species of declining insectivore. Although dietary profiles of declining insectivores varied among species, there was a tendency to have a wide prey base, with a select few groups of insects forming the majority of their diet. Coleoptera, which made up 27% of total prey records, were the most frequently recorded prey group in nine of the 13 bird species examined here, with Formicidae and Lepidoptera also dominant. Only the Restless Flycatcher (*Myiagra inquieta*) had a diet that was dominated by an otherwise infrequently recorded prey group, living up to its name by frequently consuming flies (Diptera). Therefore, despite variation between species, the congruence in dominant components of the diet suggests that a small number of key prey groups represent core food resources supporting populations of all of these bird species.

Coleoptera and Formicidae were the most frequently recorded prey types within this group of declining insectivores, a result that concurs with similar studies from other regions. Both Buchanan *et al*. (2006) and Wilson *et al*. (1999) found Coleoptera to be most commonly reported as 'important' in the respective diets of moorland birds in the United Kingdom and farmland birds in northern Europe. Poulin *et al*. (1994), who conducted empirical investigations into the diets of land birds in Venezuela, also found Coleoptera to be the most commonly consumed prey group, followed by ants (Formicidae). Lepidoptera were not found to be important in avian diets in these studies. However, Lepidoptera and their larvae are known to be important on a seasonal basis to many passerines, especially during the breeding season (Perrins 1991; Naef-Daenzer and Keller 1999; Arnold *et al*. 2010).

Although some prey groups were consumed less frequently by the declining insectivores, they were nonetheless consumed widely. There is some evidence that arthropods consumed less often by birds are integral to providing specific nutrients that more-frequently consumed arthropods may not contain. Ramsay and Houston (2003) argued that Blue Tits (*Cyanistes caeruleus*)

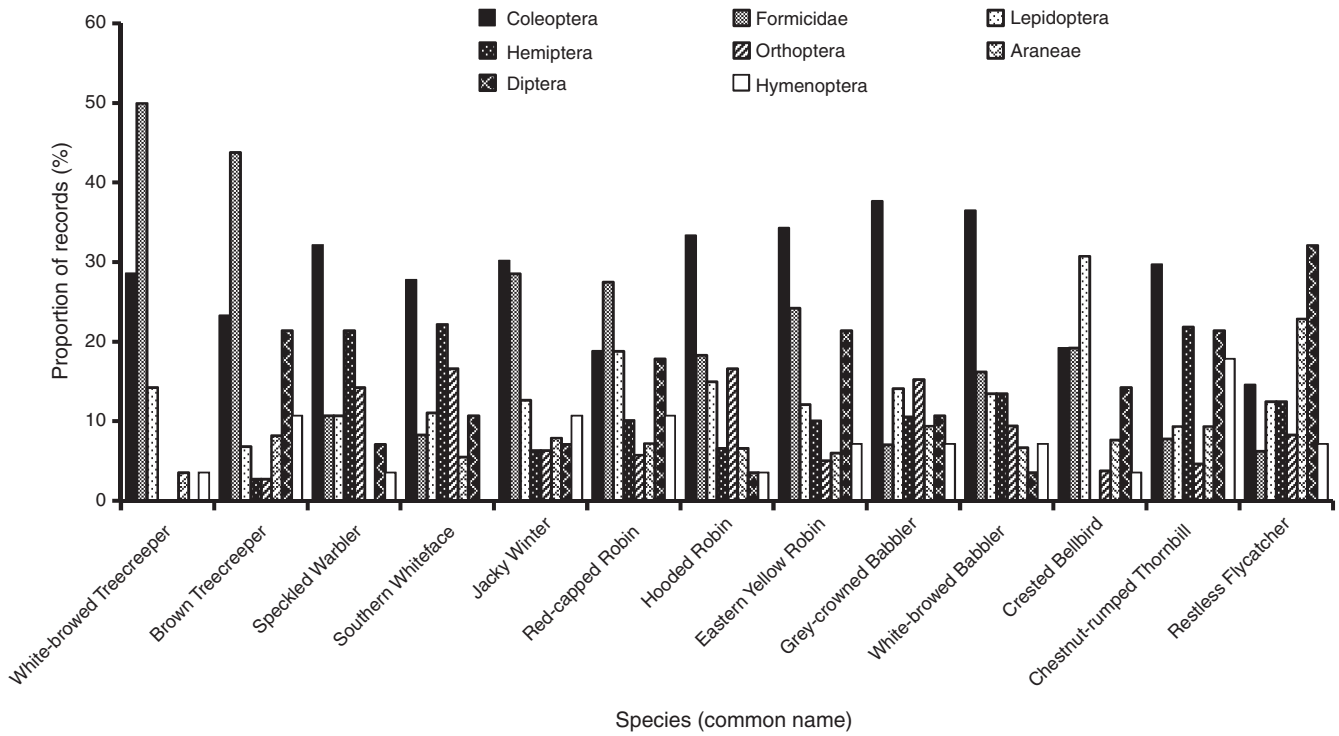

Fig. 2. Relative proportions of prey groups contributing to the diet of each of the 13 species of declining insectivorous birds. The eight most-frequently occurring prey groups are represented, all of which were found to contribute to the diets of ≥11 species of bird.

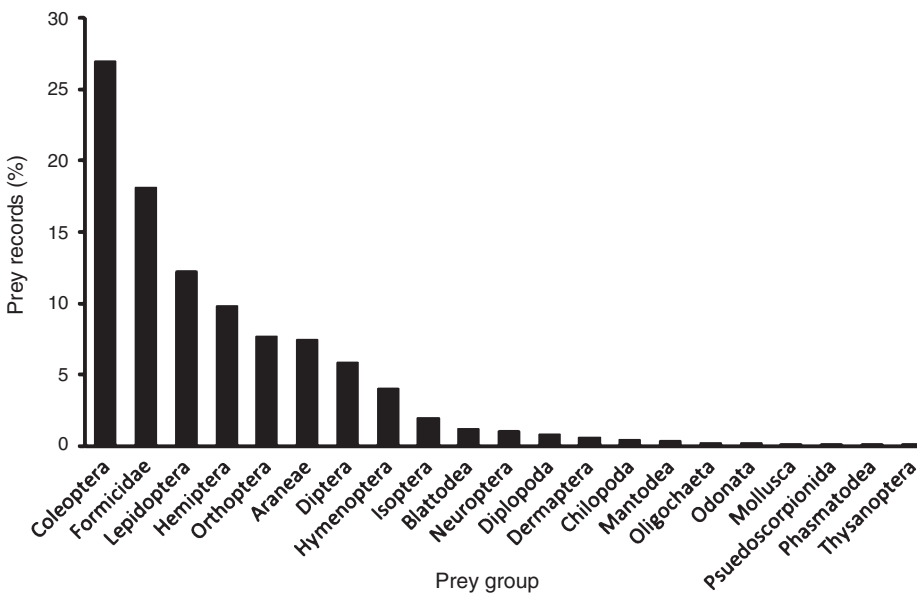

Fig. 3. Proportion of dietary records of each prey taxa, standardised to order for insects and arachnids, and class or sub-class when data to order level was not available.

and other woodland passerines select lycosid spiders for provisioning chicks during the chick-rearing period owing to the high content of taurine, an amino acid considered essential for growth and development of avian chicks. Interestingly, we found only one record of a mollusc being consumed (by the Crested Bellbird, *Oreoica gutturalis*). Passerines in other regions of the world have been shown to rely on snail shells to satisfy increased calcium demands during the breeding season (Graveland *et al*. 1994; Graveland and Van Der Wal 1996; Tilgar *et al*. 1999). Other calcium-rich prey types, such as millipedes and isopods (Ziegler *et al*. 2005), occurred infrequently or were absent in the diets of the declining insectivores assessed here. As insects and

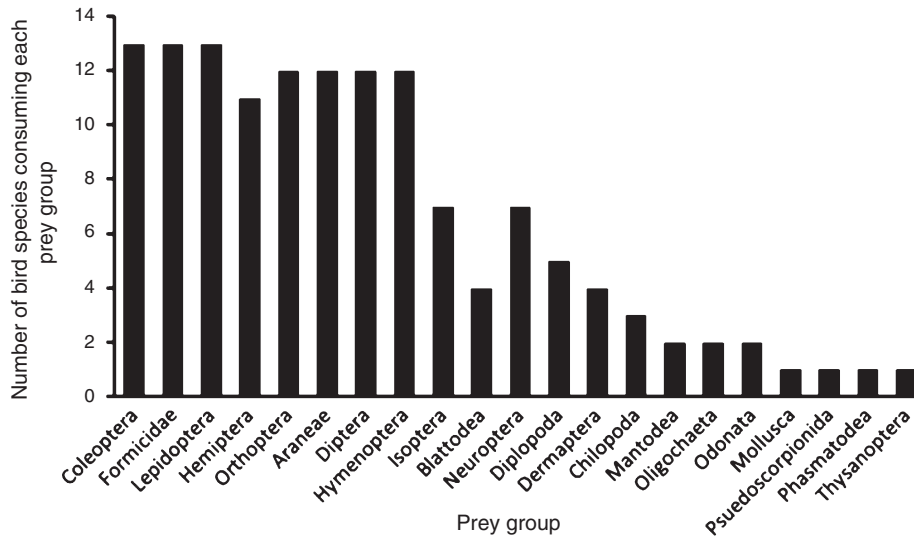

Fig. 4. Number of species of declining insectivorous birds (of the 13 species examined herein) consuming each prey group recorded in the collective diet.

spiders are generally known to be low in calcium, these birds may acquire calcium via occasional consumption of Calcium-rich prey or via non-food items such as carbonaceous stones or calcareous grit.

Assessment of dietary literature

Whereas commonly eaten prey types, such as Coleoptera and Formicidae, were often identified to family, genus or, sometimes, species, other orders were poorly described, with most entries listed to family or order only. These inconsistencies in the identification of prey meant it was not possible to discern whether taxonomic differences at the level of family or below are of any importance to prey choice in declining insectivores. It should be noted, however, that the most frequently recorded families of beetles in the synthesis of dietary records performed here (Curculionidae, Carabidae, Chrysomelidae and Scarabaeidae; Razeng 2011), closely reflect those found to be important parts of the diets of moorland birds in the United Kingdom and farmland birds in northern Europe (Wilson *et al*. 1999; Buchanan *et al*. 2006). Thus it is possible that particular beetle families may be of worldwide significance to insectivorous birds.

Our analysis indicated that some types of prey appear far more frequently than others within the collective diet of declining insectivores. However, the assessment performed here focussed on the frequency of prey groups in dietary records, and did not evaluate the relative abundance of prey groups in avian diets nor the abundance of available arthropod taxa in the habitat. Therefore, the varying frequencies of prey groups represented here may be indicative of active preference, or may merely reflect the abundance of those prey groups in the environment. Studies of insectivorous passerines elsewhere have demonstrated that insectivorous passerines typically forage selectively on particular sizes and species of arthropod, both under controlled conditions (Krebs *et al*. 1977) and in the field (Davies 1977; Kaspari and Joern 1993; Poulin *et al*. 1994; Naef-Daenzer *et al*. 2000; Hagar *et al*. 2007), with frequency of arthropods in the diet rarely reflecting their frequency of occurrence in the habitat. Thus, although provisional, we suggest that our results are indicative of favoured prey groups, representing those arthropods most frequently consumed by these birds of conservation concern and highlighting those arthropod groups that should be the focus of estimates of prey availability.

Implications for modified habitats

If we accept that some arthropod groups are more important than others to insectivores, it follows that total arthropod biomass is neither an accurate nor an appropriate measure of habitat quality of, or food availability for, declining insectivores. Although these conclusions seem intuitive, they have far-reaching implications for designing management strategies to arrest declines in woodland birds and the many co-occurring woodland species threatened by ongoing habitat fragmentation and land degradation. Conversion of woodlands to agricultural land has caused many changes to habitat structure and functioning. Grazing by livestock has caused a simplification of vegetation structure, towards more exotic annual grasses, more exotic woody weeds and lower abundance and diversity of native herbs, forbs and grasses. Other processes, such as soil compaction, desiccation within small fragments and removal of fallen timber, has led to further simplification of microhabitat structure (Watson 2011). It has previously been shown that simplification of habitat structure leads to reduced arthropod diversity and altered community composition (Dennis *et al*. 1998; Bromham *et al*. 1999; Maron and Lill 2005). If declining insectivores prefer particular prey groups or combinations of prey groups, simplification of habitat structure may compromise the ability of insectivores to find and consume their preferred prey.

Prospect

Interactions between predators, their prey and the environment are complex and often difficult to determine. Although the commonality of insectivory in declining woodland birds has

been noted before (Reid 1999; Ford *et al*. 2001; Watson 2011), quantitative analyses of the diet of these species has not been conducted and detailed prey preferences have not been investigated. This preliminary study highlights the issue of preference for specific prey groups in ground-foraging, declining insectivores, and also raises several questions: does access to specific prey groups affect birds' fitness? Are preferred prey types depleted in small fragments? Do habitats with greater structural heterogeneity support a higher quality prey base? As the abundance and diversity of arthropod communities are likely to differ between higher and lower quality patches, it is also possible that dietary composition of declining insectivores reflects this. Dietary composition, and therefore dietary quality, may be directly related to habitat quality. Further investigation into this issue may lead to a clearer understanding of the mechanisms driving declines in these birds.

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