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What do declining woodland birds eat? A preliminary assessment

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Running head: Diet of declining insectivorous birds

Abstract. Ground-foraging insectivores are prominent among those birds identified as Declining Woodland Birds in southern Australia but, despite considerable ecological research, the mechanisms driving these declines remain unclear. Some work has suggested food limitation may be critical, with larger and structurally more complex habitat patches supporting greater arthropod biomass, but whether these differences translate into greater availability of arthropod groups that are consumed by these insectivores has not been established. We synthesise existing dietary records of a subset of the 26 declining woodland birds"—thirteen ground-foraging insectivorous passerines—to determine what range of arthropods are consumed, and estimate the relative importance of each prey group to the diet of these birds. Declining insectivores consumed a wide array of arthropods, but diets were characteristically dominated by one or two prey groups. The three most commonly occurring prey groups (Coleoptera, Formicidae, Lepidoptera) accounted for over half of all prey records (58%). Coleoptera contributed the greatest proportion of dietary records (27%), and was the dominant prey group in the diets of 9/13 birds. We suggest that these frequently occurring prey groups likely represent core resources supporting populations of declining insectivores, and propose that direct measurement of their abundance will provide meaningful estimates of prey availability, while noting that less frequently consumed groups may be important on a seasonal basis. We highlight the need for detail and consistency in prey identification, and propose that reliance on a relatively small number of prey groups may make ground-foraging insectivores particularly sensitive to changes in habitat structure.

Keywords: Declining woodland birds, insectivore, ground foraging, diet, arthropods, habitat fragmentation, prey selection

Introduction

Insectivorous birds are declining world-wide, manifested in reduced abundances and distributions (Bennett and Watson 2011). Various processes have been proposed to explain these declines, including habitat loss and fragmentation (Walters *et al*. 1999; Britschgi *et al*. 2006); increased nest parasitism and predation (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 land clearance 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 "Declining Woodland Birds" in southern Australia (Reid 1999, 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 impacts of livestock grazing and weed encroachment (Maron and Lill 2005) and inability of some species to disperse effectively among habitat fragments (Walters *et al*. 1999). Nutritional factors in general (and food limitation in particular) have been largely unexplored, despite evidence from Australia and elsewhere that agricultural practices, habitat fragmentation, and other phenomena such as drought and weed invasion can severely impact arthropod communities (Abensperg-Traun *et al*. 1996; Bromham *et al*. 1999; Benton *et al*. 2002; Dennis *et al*. 2008; Tallamy *et al*. 2009).

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 prey types to satisfy particular nutritional needs (Arnold *et al.* 2007; 2010; Eeva *et al.* 2010)—quality may be just as important as quantity.

Although no feeding preference studies have been conducted on 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 forests in north-east Victoria support a low biomass of leaf-litter invertebrates when compared to other forest habitats in Australia and elsewhere, suggestive of lower carrying capacity for insectivores. While both studies highlight the importance of food limitation at patch scales, their reliance on total arthropod biomass assumes that those arthropods consumed are available in direct proportion of arthropods generally, an assumption that has not been explicitly evaluated.

The foraging ecology of ground-foraging insectivores in southern Australia has been well studied (Ford 1986; Recher *et al*. 2002; Antos and Bennett 2006; Taylor and Paul 2006) yielding detailed information on microhabitat use, substrate selection and foraging behavior. 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 prey preferentially on some groups of arthropod, or avoid other groups altogether is unknown. 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 prey groups are eaten more frequently than others, and whether any prey groups are not consumed. Available dietary information is synthesised 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 twenty were originally identified by Reid (1999) and six others have been added as the list was expanded (see Watson 2011). Of the fourteen ground-foraging insectivores in this group, thirteen are insectivorous passerines which forage mainly on the ground and associated substrates. This group of thirteen insectivorous ground-foraging birds are the focus group 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 non-passerine and arthropods are consumed as part of a wider diet including seeds, fruit and other vegetable matter.

These thirteen species from six families are small to medium-sized birds, ranging from ~6 g in mass for the Chestnut-rumped Thornbill, to ~75 g for the Grey-crowned Babbler (HANZAB). Time spent foraging on the ground varies seasonally within species, and estimates of percent of foraging time spent on the ground ranges from 28% for the Grey-crowned Babbler (Brooker *et al*. 1990), and 99% for the Southern Whiteface (Recher and Davis 1997) and White-browed Babbler (Taylor and Paul 2006). As a group, these birds are largely territorial and sedentary (Ford *et al.* 2001). They inhabit a wide range of wooded habitats, extending from wet eucalypt forests, grassy eucalypt woodland and Callitris woodland into acacia-dominated woodlands 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).

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; Marchant and Higgins 2001). HANZAB is the pre-eminent reference for birds in the region, compiled from exhaustive searches of the primary ornithological literature, incorporating unpublished data, university theses, museum specimens, historic accounts and personal communications, in close consultation with leading ornithological experts. Quantifying diets from existing records can be confounded by different sampling methods used to collect information on bird diets and/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 were one-off records of birds observed foraging (often recorded because the prey or foraging mode was novel or noteworthy). Setting appropriate parameters for analysis of relative frequencies of prey taxa in bird diet enables consolidation of this varied data, allowing for comparison of diet at a broad scale.

To minimize these 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. For each species, a list of 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. For each species of declining insectivore, a list of consumed prey taxa was created, and the number of references pertaining to each prey type was counted.

In the 127 studies summarised in these records, the majority of invertebrate taxa were identified to class or order with few identified to family, genus or species. Due 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 sub-class groupings were used for those taxa with no records below these levels, such as Diplopoda, Chilopoda and Oligochaeta. Ants (Hymenoptera: Formicidae) were categorised separately from the remainder of 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 orders ranked according to the relative percentage of total prey items recorded.

Results

Summary of data

The final data set contained 902 diet records from 127 sources, spanning a 95 year period (1905–2000). This data set spanned a wide range of taxonomic resolution, with one prey group identified to phylum only (Mollusca), three being identified to class / 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 4 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 widely between species, ranging from seven sources for the White-browed Treecreeper, to 55 for the White-browed Babbler (mean = 18.8 ± 6.1; Fig. 1A). The number of prey taxa recorded also varied broadly between bird species, from 18 for the White-browed Treecreeper to 55 for the White-browed Babbler (mean = 33.9 ± 12.1; Fig. 1B). However, when records were condensed to order level (and class when order was not listed), the uniformity of the diets of these bird species became more obvious (Fig. 1C), varying between 6 taxa recorded for the White-browed Treecreeper, to 13 taxa recorded for the Hooded Robin and the White-browed Babbler (mean = 9.7 ± 2.1). Dietary records for each species were characteristically dominated by 1 or 2 prey groups, with other prey groups recorded in low frequencies. Coleoptera was the most frequently recorded prey group for 8/13 species, Formicidae for 3/13 species, Lepidoptera for 1/13 species and Diptera for 1/13 species (Fig. 2).

Occurrence of arthropod taxa in the collective diet

Collective diet records for this group of 13 bird species included 15 Insect orders and two Arachnid orders, as well as records from Diplopoda, Chilopoda, Oligochaeta and a single record of a mollusk (Fig. 3). Coleoptera contributed the greatest proportion of dietary records (n = 220, 27 %), followed by Formicidae (Hymenoptera; n = 148, 18 %) and Lepidoptera (n = 100, 12 %). Eleven of the 21 groups listed here contained <10 records, and 4 groups (Mollusca, Pseudoscorpionida, Phasmatodea and Thysanoptera) were recorded only once.

The three most commonly occurring prey groups (Coleoptera, Formicidae: Hymenoptera, 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 study species (Hemiptera, Orthoptera, Araneae, Diptera, Hymenoptera (bees and wasps); Figure 4)—although consumed less frequently, they are nonetheless widely consumed by this group of birds.

Discussion

The declining insectivores 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 insect groups (beetles, ants and moths/butterflies) made up the majority of diet records, as well as being dominant in the diet of most bird species examined. Although the contribution of arthropod taxa at finer taxonomic levels could not be assessed, this preliminary analysis nonetheless provides new insights into the nutritional ecology of this declining group of birds.

The three most frequently consumed prey groups (Coleoptera, Formicidae and Lepidoptera) were the only groups to occur in the diet of all thirteen species of declining insectivore. Although dietary profiles of declining insectivores vary among species, there is a tendency to have a wide prey base, with a select few groups of insect forming the majority of their diet. Coleoptera, which made up twenty-seven per cent of total prey records, are the most frequently recorded prey group in nine of the thirteen bird species examined here, with Formicidae and Lepidoptera also prevailing. Only the Restless Flycatcher had a diet that was dominated by a low-ranking prey group—living up to its name by frequently consuming flies (Diptera). Therefore, despite variation between species, the congruence in dominant dietary components suggests that a small number of key prey groups may 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 diets of moorland birds in the United Kingdom and farmland birds in northern Europe, respectively. 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 (Hymenoptera: Formicidae). The importance of Lepidoptera in bird diet is less prevalent in the aforementioned 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 declining insectivores, they were nonetheless consumed widely. There is some evidence that arthropods consumed less often by birds are integral to providing specific nutrients which more frequently consumed arthropods may not contain. Ramsay and Houston (2003) argued that Blue Tits (*Cyanistes caeruleus*) and other woodland passerines select lycosid spiders for provisioning of chicks during the rearing period due to the high content of taurine, an amino acid considered essential for growth and development of chicks. Interestingly, we found only one record of a mollusc being consumed (by the Crested Bellbird). Passerine species 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 spiders are generally known to be low in calcium, these birds may acquire calcium via occasional consumption of these taxa or via non-food items such as carbonaceous stones or calcareous grit.

Assessment of diet literature

While commonly consumed 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 prey identification meant it was not possible to discern whether taxonomic differences at family level 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 review of diet literature performed here (Curculionidae, Carabidae, Chrysomelidae and Scarabaeidae; Razeng 2011), closely reflect those found by Buchanan *et al*. (2006) and Wilson *et al*. (1999) to be important parts of the diets of moorland birds in the United Kingdom, and farmland birds in northern Europe respectively. Thus it is possible that particular beetle families may be of world-wide significance to insectivorous birds.

Our analysis indicated that some prey types appear far more frequently than others within the collective diet of declining insectivores. However, the assessment performed here focused on the frequency of prey groups in dietary records, and did not quantify the abundance of 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, both under controlled conditions (Krebs *et al*. 1977) and as 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, and represent those arthropods most frequently consumed by these birds of conservation concern.

Implications for fragmented 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 or food availablity to declining insectivores. While 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 numerous 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 lead to further simplification of microhabitat structure (Watson 2011). It has previously been shown that simplification of habitat structure leads to reduced diversity within arthropod communities (Dennis *et al*. 1998; Bromham *et al*. 1999; Maron and Lill 2005). If declining insectivores prefer particular prey groups or combination of prey groups, simplification of habitat structure may compromise the ability of insectivores to find and consume their preferred prey.

Prospect

The interactions between predators, their prey and the environment are complex and often difficult to distinguish. Whilst the commonality of insectivory in declining woodland birds has been noted by several authors (Reid 1999; Ford *et al*. 2001; Watson 2011), prey preference has not previously been investigated. This preliminary study highlights the issue of preference for specific prey groups in ground-foraging, declining insectivores, and also raises a number of 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 diversity of arthropod communities are likely to differ between higher and lower quality patches, it is also possible that diet composition of declining insectivores reflects this. Diet composition, and therefore diet 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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Table 1. List of the thirteen 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 layer.

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

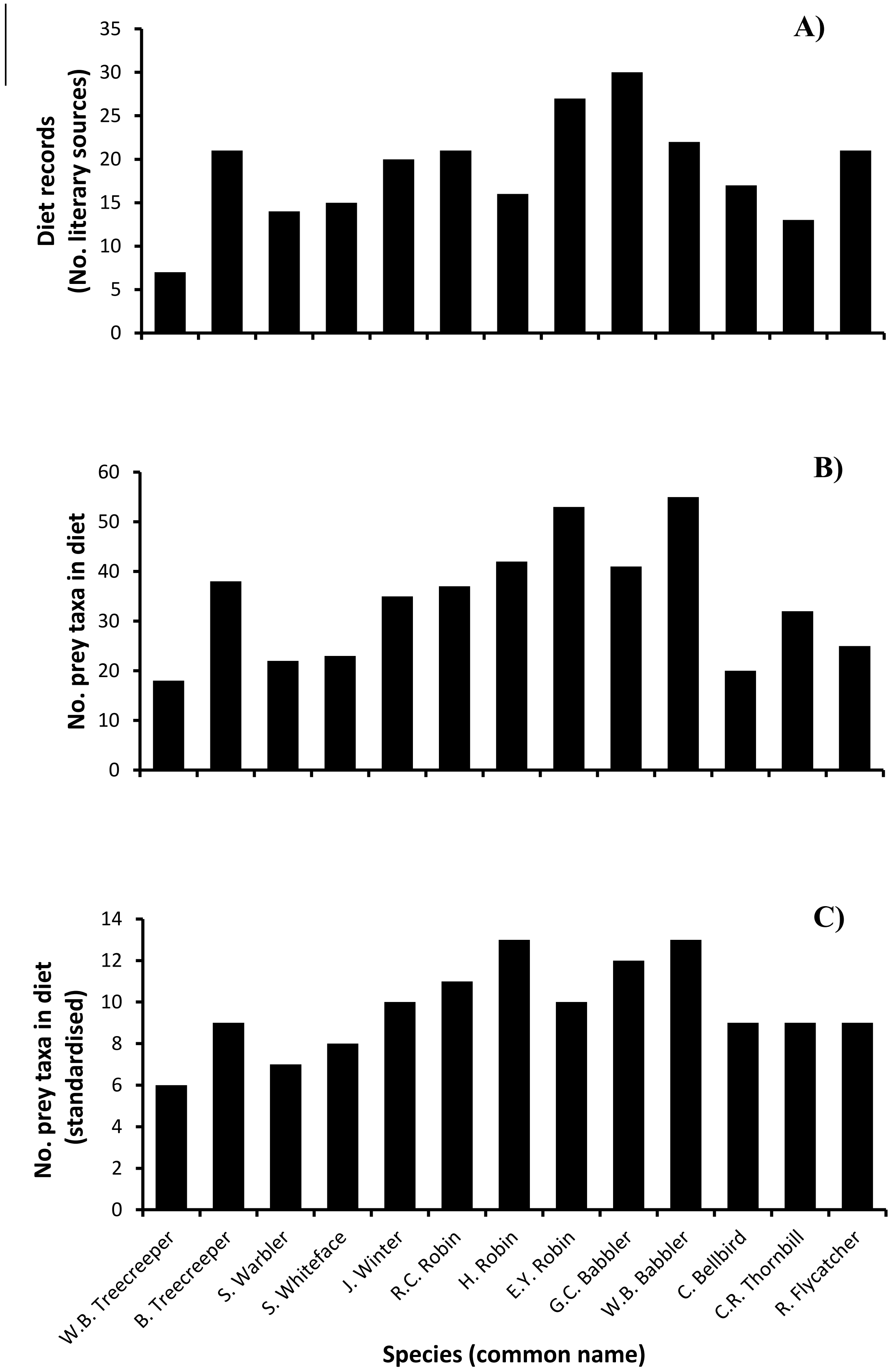

Figure 1. A). Number of literary sources of diet data, B). Total number of prey taxa recorded (all taxonomic levels), and C). number of 'standardised prey taxa' recorded for each ground foraging bird species in the study group, obtained via a comprehensive review of diet records. 'Standardised prey taxa' is the number of prey taxa standardised by grouping into the highest comparable taxonomic level (order for insects and arachnids, and class/sub-class where order was not available).

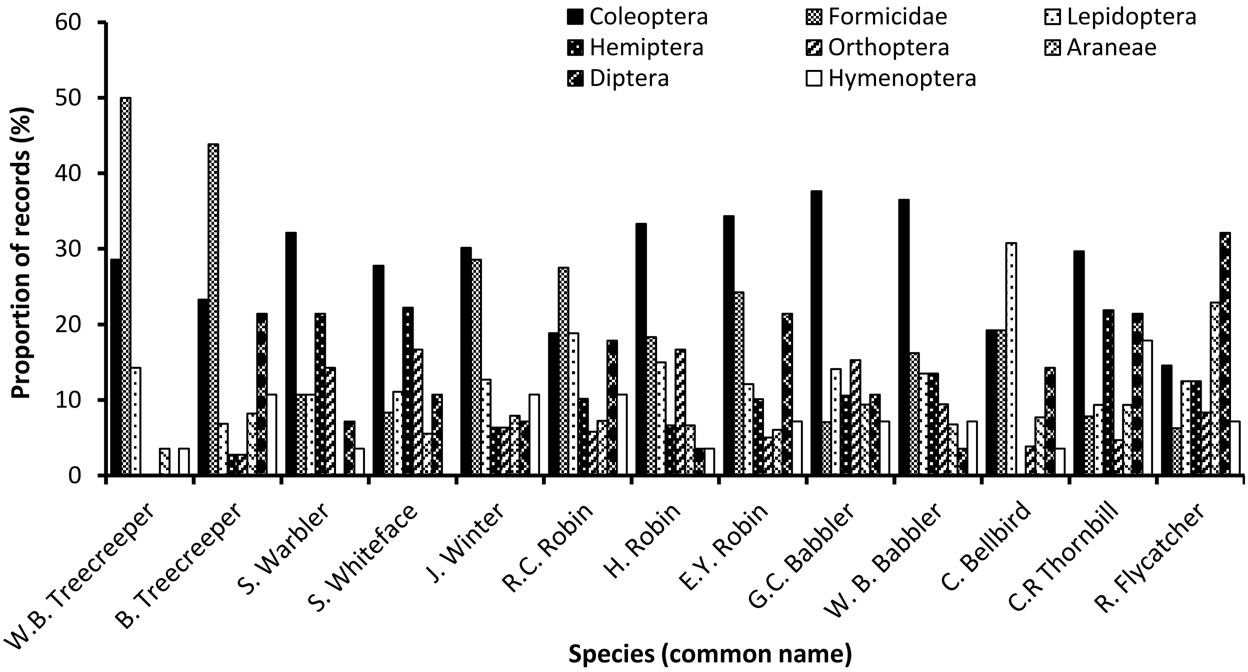

Figure 2. Relative proportions of prey groups contributing to the diet of each species of declining insectivorous bird examined. The eight most frequently occurring prey groups are represented, all of which were found to contribute to the diets of eleven or more bird species.

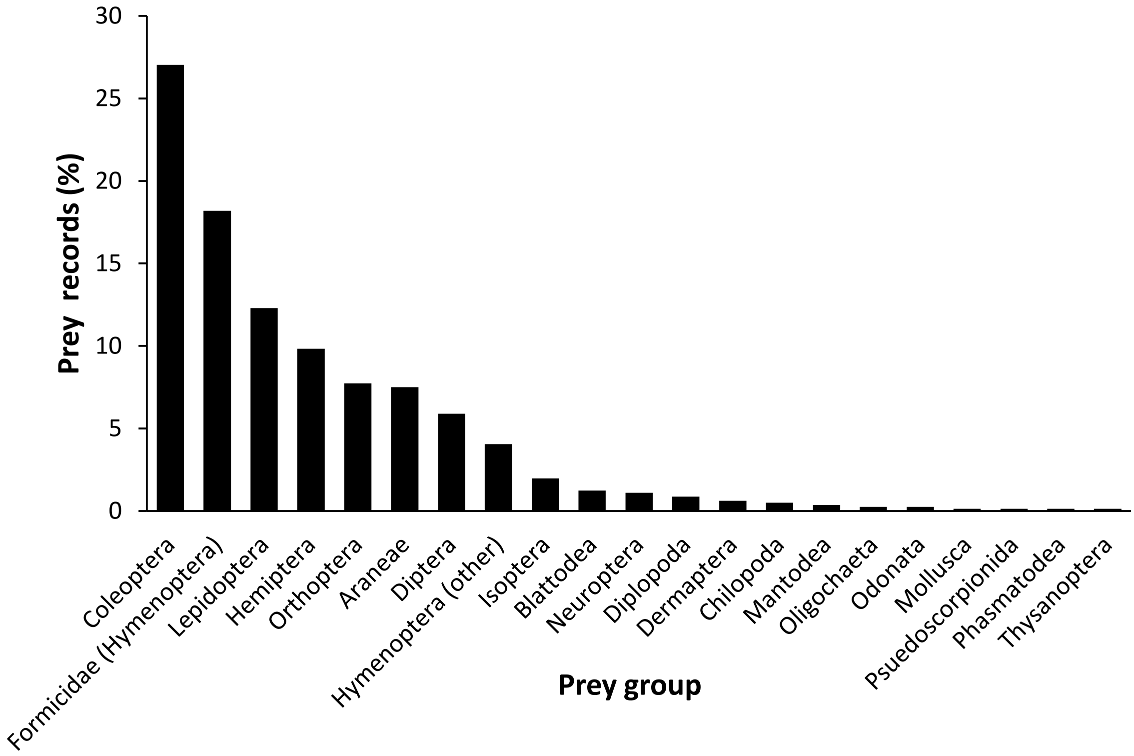

Figure 3. Proportion of diet records made up by each prey taxa, standardised to taxonomic order for insects and arachnids, and class/sub-class when data to order level was not available.

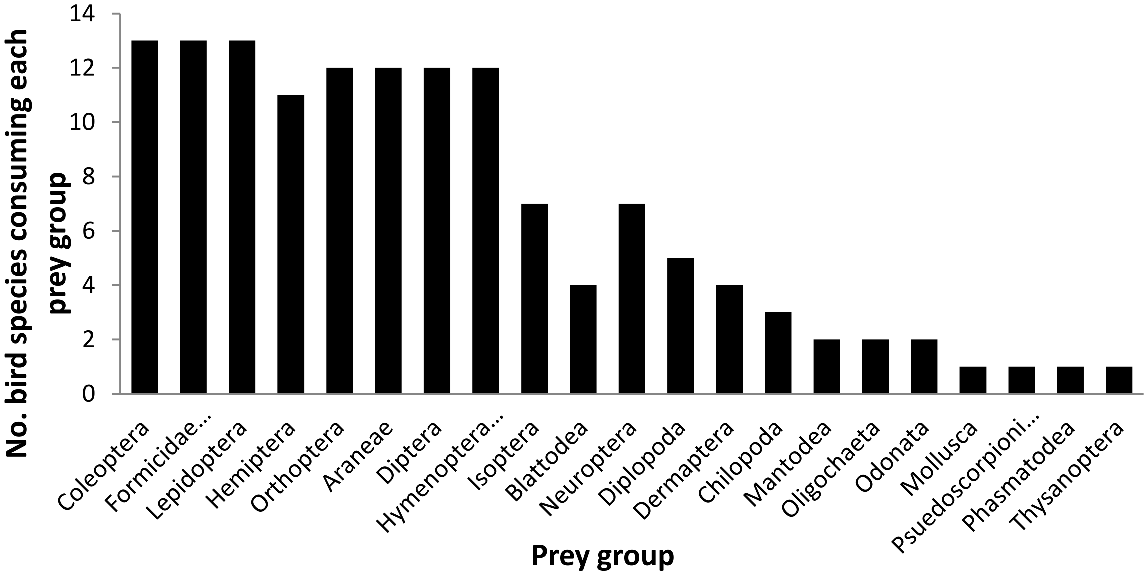

Figure 4. Number of species of declining insectivorous birds consuming each prey group recorded in the collective diet.