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Avian foraging studies: an overlooked source of distribution data for macroecological and conservation studies

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ABSTRACT

Macroecological and biogeographical studies and their applicability for biological conservation vitally depend on distribution data. These are usually taken from distribution atlases and databases or maps found in identification guides. A previous study pointed to another little explored source of data — local faunistic studies. Here, I would like to draw attention to another potential source. Papers that analysed the food composition of some taxa (e.g. insectivorous birds) are an overlooked source of rich information on taxa distributions. These studies frequently include an 'Appendix' with a list of food items determined to the species level. These studies also contain data on abundances, number of samples, sampling time, and geographical location as a rule. Foraging birds naturally provide data on invertebrate distributions with good spatio-temporal coverage and reasonably large samples. Importantly, birds frequently collect rare and by entomological methods hardly detectable species (i.e. those living high, in tree canopies, in very dense vegetation, or with secretive lifestyle). Data from bird dietary studies may help to ameliorate one of the most serious problems in distribution studies — zero inflation. I briefly discuss pros and cons of this so far neglected source of biogeographical data.

Keywords
Data sources, diversity, foraging, macroecology, methods, species richness.

INTRODUCTION

Any macroecological and biogeographical study depends on sources of species-level distribution data. Recording databases, distribution atlases, and maps in identification guides are usually used as data sources for these studies. However, there are other sources of data that are utilized rarely or not at all. Keil and Konvicka (2005) drew attention to a huge and unused data source — published quantitative descriptions of local species assemblages. In this note I would like to point to still another source of distribution data for invertebrates that has, to my best knowledge, never been used for any distribution analyses and is not included in descriptive distribution atlases and local checklists as a rule.

APPENDICES OF AVIAN DIETARY STUDIES: OVERLOOKED DATA CORNUCOPIA FOR MACROECOLOGISTS?

There is a large body of literature on avian diet (see for example references in any standard handbook on avian biology, e.g. Cramp, 1992; del Hoyo *et al.*, 2005). The majority of bird species is insectivorous or invertebratophagous (at least those breeding in the temperate zone; Stutchbury & Morton, 2001) and there are thousands of studies providing data on composition of avian insect diet.

Among various methods for the study of diet composition in birds the neck-collar (ligature) method yields reliable estimates of diet of birds. Neck collar is a plastic coated wire placed around the nestling neck that hinders the swallowing of food but is loose enough not to strangle the chick (see, e.g. Grim & Honza, 2001). Taxonomic composition of diet obtained by a neck collar is unaffected in comparison to some other methods (e.g. use of emetics or faecal samples) that, in contrast, do not provide unbiased data on quantity and quality of avian diet (Rosenberg & Cooper, 1990). The great advantage of the neck-collar method is that arthropod prey is kept relatively intact, thus enabling precise taxonomic determination of specimens including their sexing.

Some avian dietary studies provide only rough data on taxonomic composition (i.e. food items are determined only to order or family levels, e.g. Grim & Honza, 1996, 2001). However, other dietary studies are frequently accompanied by an 'Appendix' with a complete list of diet items determined down to the species level (e.g. Torok, 1981; Bures, 1986, 1987, 1993, 1994; Kristin, 1986, 1994, 1995; Trnka, 1995; Grim & Honza, 1997; Exnerova *et al.*, 2003; Grim, 2006; and many references therein). These appendices also contain data on abundances (and sometimes frequencies,

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i.e. proportions of samples containing particular food items). As both number of samples and the duration of sampling of an individual nestling/brood are as a standard provided in this sort of papers in Methods, it is easy to calculate the total sampling time and total abundance of food items of the particular study (which is necessary for rarefaction analysis to standardize data sets gathered with unequal sampling efforts). These studies also provide geographical data (location and coordinates) of particular study locations. The same holds not only for neck-collar studies but also for those based on pellets analyses (e.g. in owls, Trejo *et al*., 2005) or stomach content analyses (e.g. in passerines, Hromada & Kristin, 1996). Thus, many avian foraging studies (including master and doctoral theses and grey literature) contain all information necessary to perform macroecological distribution studies.

QUALITATIVE DIETARY DATA: DECREASING INHERENT BIASES OF DISTRIBUTION STUDIES

Various macroecological analyses can be done — and most in fact are done — on qualitative distribution data, i.e. presence or absence of particular taxa in a particular study location or grid cell (e.g. Jetz & Rahbek, 2002; Storch *et al*., 2003; Orme *et al*., 2005). Here, avian foraging studies can act as an important additional source of distribution data that complement standard entomological censuses.

Most importantly, as avian foraging study can only *add* new species (or localities) to qualitative macroecological analyses, it can only decrease bias inherently present in any distribution study. On the other hand, it cannot in principle increase the sampling bias.

Birds — to great surprise of experienced entomologists — frequently collect species of invertebrates that are extremely rare, i.e. are localized geographically, show unusually narrow ecological niches, and/or have very low population densities (i.e. are hardly detectable by humans; see below). Thus, birds as an effective tool able to sample rare species of insects and inaccessible habitats can help to correct one of the most serious problems in ecological studies — zero inflation. A high incidence of zero values is especially common problem in distribution data sets (Martin *et al*., 2005).

At first sight, selectivity of avian foraging behaviour (Wolda, 1990) seems to lower benefits of dietary studies as sources of distribution data. For example, some insects defend themselves by distasteful compounds or mimic other defended insect species to avoid predation (Ruxton *et al*., 2004). However, passerines routinely forage even on aposematic unpalatable insects (e.g. Kristin, 1986; Exnerova *et al*., 2003) and their Batesian mimics (e.g. Kristin, 1986; Grim, 2006). Moreover, a brief review of previously mentioned avian foraging studies from Central Europe has shown that birds included in their diet species from all insect orders distributed in that area (the best represented group was Diptera). Although there can be a relationship between bird body size and prey size, even very small passerines (e.g. reed warbler, *Acrocephalus scirpaceus*, *c*. 12 g) are ready to take relatively large insects (up to 35 mm; Cramp, 1992; Grim & Honza, 2001). From my own field experience and discussions with many experienced entomologists, I expect that the *magnitude* of selectivity of avian foraging is comparable to that of traditional entomological methods, but the two 'selectivities' may be just different. This highlights the potential of dietary studies to lower sampling biases of traditional entomological methods. Moreover, dietary selectivity cannot lead to biases if dietary data are used only as complementary sources as already stated.

Additionally, avian foraging studies could in principle be used as sources of distribution data on their own. Many bird species were sampled for their food across large continental areas, i.e. at similar scales as macroecological studies are performed (e.g. Keil & Konvicka, 2005). This provides opportunities to study qualitative composition of 'dietary taxocenes' (i.e. taxonomically related sets of species within a 'dietary community') across large geographical areas. Because foraging selectivity varies between species, researchers could control for this potential confounding factor by using data only from a particular study species across the various study sites. Moreover, the study of geographical variability of birds' foraging selectivity may help to clarify some of the trophic mechanisms behind the intensively studied geographical patterns of bird diversity (see, e.g. Jetz & Rahbek, 2002; Orme *et al*., 2005).

To my knowledge, the avian dietary studies are usually ignored when descriptive distribution atlases and local checklists are compiled. These often represent a basic reference for a macroecological analysis. Hence, bird dietary studies could improve quality of such references as well.

Importantly, birds' foraging as a method of study of taxocene composition has some advantages in comparison to traditional entomological methods (e.g. entomological net or sets of traps). Birds forage — and consequently 'sample' — all vegetation strata (and air high above the ground; Cheng & Zhou, 1987) while a human entomologist with a net is limited to lowest strata (only herbaceous and shrub strata in fact). In addition to these spatial aspects there is also temporal advantage: birds forage (and neck-collar method is applicable) even in the rain when, e.g. the entomological net performs poorly.

To sum up, avian foraging studies may provide biased data on composition of invertebrate taxocenes, but we should remember that various standard entomological methods also suffer from differing effectiveness and selectivity as mentioned by Keil and Konvicka (2005).

CONCLUSIONS

Foraging birds naturally provide data on invertebrate distributions with good spatio-temporal coverage, reasonably large samples and well intact specimens. Bird 'entomologist' can even work better than a human one, e.g. two rare species of hoverflies included in local taxon list for The Palava UNESCO Protected Landscape and Biosphere Reserve (Czech Republic) were found only by reed warbler 'collectors' despite the efforts of dozens of entomologists active in that area for several decades (Grim, 2006 and references therein). Similarly, a meta-analysis of true bugs (Heteroptera) in bird diets revealed several very rare epigeic and canopy taxa (Exnerova *et al*., 2003). Thus, the study of nestling diet in birds may provide important information on extremely rare species and/or those which may be difficult to collect by traditional entomological methods (Lauterer & Bures, 1984; Exnerova *et al*., 2003; Grim, 2006) or even lead to the discovery of new species for a particular country (Bures & Pecina, 1993; Kristin & Patocka, 1997; Grim, 2006). Both these aspects of avian foraging studies are clearly of importance for biogeography, macroecology, and conservation biology.

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