

Ecology of Lepidoptera associated with bird nests in mid-Wales, UK

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Abstract

1. Bird nests are ubiquitous but patchy resources in many terrestrial habitats. Nests can support diverse communities of commensal invertebrates, especially moths (Lepidoptera). However, there is a shortage of information on the moths associated with bird nests, and the factors influencing their abundance, diversity and composition.
2. 224 nests, from 16 bird species, were sampled from sites in mid-Wales (UK) and the moths that emerged from them were recorded.
3. 78% of nests produced moths, with 4,657 individuals of ten species recorded. Moth communities were dominated by generalist species rather than bird nest specialists.
4. Open nests built in undergrowth supported significantly fewer moths than nests in enclosed spaces (for example, nesting boxes). The occurrence of fleas was positively associated with the incidence and abundance of moths. There was no evidence that different nest types supported different moth communities.

Keywords: commensal, detritivore, fleas, invertebrates, moths, Tineidae

Introduction

Bird nests are a ubiquitous feature of terrestrial ecosystems. They represent concentrated resource patches and can support a diverse fauna of commensal invertebrates, which exploit nesting materials, feathers, faeces and other organic detritus. A global checklist compiled by Hicks (1959; 1962; 1971) lists eighteen insect orders associated with bird nests. An assessment of nests from 56 bird species in Finland noted 528 different arthropods (Norberg, 1936), and a study of bird nests in England identified over 120 insect species, spanning eight orders (Woodroffe, 1953).

Moths (Lepidoptera) are particularly frequent and species-rich occupants of bird nests, but remarkably little is known about the biology of moths associated with nests. The existing literature concentrates on species which also occur as pests in human habitation, but even for these species, large gaps in knowledge and some misapprehensions remain. For example, the common clothes moth *Tineola bisselliella* (Hummel, 1823) was thought to infest human habitations via bird nests, which acted as natural population reservoirs. It has recently been discovered, however, that this non-native species seldom occurs in bird nests and can be regarded as wholly synanthropic in Europe, where it was introduced from Africa around the turn of the 19th century (Plarre & Krüger-Carstensen, 2011; Plarre, 2014).

We are aware of seven papers documenting whole assemblages of moths in bird nests. These investigated moths in Japan associated with nests of insectivorous passerines (Nasu et al., 2012a) and owls (Nasu et al., 2012b); the moths of owl nests in Finland (Jalava, 1980) and Poland (Jaworski, Gryz and Krauze-Gryz, 2012); the arthropod fauna of shrike nests in Poland (Tryjanowski et al., 2001); and the invertebrate fauna of bird nests in England, UK (Woodroffe and Southgate, 1951; Woodroffe, 1953).

In constructing nests, birds act as ecosystem engineers: organisms that create new habitat and modify the resources available to other organisms (Jones, Lawton & Shachak, 1994). Variations

in the location, structure and materials of nests are expected to lead to opportunities for specialisation on particular bird species or nest types. However, we are unaware of studies that have explored the associations of these moths in a quantitative and systematic manner.

In this paper, we document the community composition and host-associations of moths from bird nests collected at a set of sites in Wales, UK, and investigate the biotic and abiotic factors structuring these assemblages. Specifically, we investigate factors affecting the occurrence and abundance of moths in bird nests, and the extent to which moth community composition is structured by nest type, location and bird species.

Methods

Study system

Nests were collected from seven sites in mid-Wales (Figure 1) in January 2016. Five of the sites are nature reserves, managed by Montgomeryshire Wildlife Trust, while the remaining two are on privately-owned land. All of the sites contain a significant area of mature oak woodland and are between 70-300m elevation.

Most nests (206 of 224) were collected from nest boxes installed for the benefit of breeding birds. Nest boxes were all fixed to mature tree trunks roughly 1.4m above ground, facing northeast. To reduce avian parasites, the contents of these boxes are removed after the breeding season each autumn or winter (most recently in the autumn and winter of 2014/2015). In addition to the nest boxes, 18 other nests were collected; these were either nests found in undergrowth (n=15) or in a sheltered location (wren nest in a tractor cab, robin nest from a wood shed, and stock dove nest in an owl box). All the nests had been monitored for the British Trust for Ornithology (BTO) breeding bird survey, providing data on occupancy and breeding outcome. Only nests where at least one chick fledged successfully were included. Nests from the undergrowth were classified as 'open' and those

build within other structures were defined as 'closed'. Table 1 summarises information on the nests collected of each species at each site.

Nest collection, storage and inspection

Nest contents were collected into paper bags for transportation and later transferred to plastic takeaway boxes with dimensions approximately 18cm x 13cm x 7cm, with bulkier nests split between multiple containers. The central part of the lid of each box was cut away to form a window, and the lid was then used to secure a sheet of muslin, providing ventilation while preventing insects from escaping. The boxes were kept out of direct sunlight and stored in an unheated shed. They were inspected every few days from the start of May until the end of July 2016, and any emerging moths were counted and removed. The contents of each container were then searched for any dead adults. Many of the species can be identified without close examination; however, if there was any doubt over the identification, specimens were collected. Difficult species were dissected for genitalia determination. The moths were identified using Heath & Emmet (1985) and Bengtsson & Johansson (2011). For families other than Tineidae, Emmet & Langmaid (2002), Riley & Prior (2003) and Sterling, Parsons & Lewington (2012) were consulted.

Variables recorded

Information on the bird species responsible for each nest was available from BTO's breeding bird survey data. In late July, once all the moths had emerged, the nests were left in a closed greenhouse for several hot days until all the material had dried to a constant mass, which was recorded to the nearest 0.01g using digital scales. The composition of the nests was quantified by visually estimating the percentage makeup of grass, leaves, hair, moss and feathers. Since nest moisture can influence the moth fauna within a nest (Woodroffe, 1953), nests were categorised as either 'wet' or 'dry' depending on the condition of the paper bags following transport. Roughly half of the nests were wet enough to cause the paper bags to become saturated during transport, while

the remainder leaked very little moisture. The abundance of fleas (Siphonaptera) was categorised with three levels: 0 (no fleas apparent), 1 (≤ 20 fleas present) or 2 (fleas abundant; > 20 and often several hundred present).

Data analysis

Statistical analyses used R 3.3.1 (R Core Team, 2016). To assess sampling completeness, species accumulation curves were drawn using the 'vegan' package (Oksanen et al., 2016). Interaction networks were drawn to represent host-associations, and the specialisation index d' was calculated for each moth species, using the bipartite package (Dormann et al., 2008). The d' index provides an unbiased estimate of specialisation, based on the degree of deviation from null expectation (i.e., a random assortment of interactions; Blüthgen et al., 2006). Mann-Whitney U -test and Fisher's exact test were used to compare mean moth abundance, presence and species richness between nest types (closed and open).

The response variables were the presence of any moths, total moth abundance, overall moth species richness, presence of each species, and abundance of each species. Explanatory variables were bird species, site, nest dry mass, % nest composition, moisture (binomial: 'wet' or 'dry') and the levels of flea infestation (ordinal: 0, 1 or 2). Because sample sizes were small for open nests, analyses investigating explanatory variables that might influence the structure of moth communities were restricted to the four most common box-dwelling bird species (blue tit, great tit, pied flycatcher and redstart). For moth presence, GLMs were specified with a binomial distribution and logit link; for species richness and abundance, GLMs with a Poisson distribution and log link were used. All the GLMs for abundance were overdispersed, as quantified using the AER package (Kleiber & Zeileis, 2009) and thus violated the assumption of equal variance. Two potential solutions were applied: a negative binomial GLM with log link, and a quasi-poisson GLM with log link (Ver Hoef & Boveng, 2007). Both approaches yielded similar results and thus only the results of negative binomial GLMs (using the MASS package: Ripley et al., (2013)) are reported. All the explanatory

variables were entered initially into the GLMs and the dredge function from the package 'MuMIn' (Bartoń, 2014) was used to rank the top models by Akaike weight. McFadden's R was estimated for the top 10 models using the 'pscl' package (Jackman, 2017). When categorical variables were significant, *post-hoc* Tukey's pair-wise comparisons were made using the package 'multcomp' (Hothorn et al., 2013). Linear models were also used to test for differences in nest composition and nest mass between bird species.

Differences in moth community composition between bird species and across sites were visualised using non-metric multidimensional scaling (NMDS) in 'vegan', based on Bray-Curtis dissimilarity. Points representing bird species or sites with similar moth communities will cluster together on the NMDS plot.

Results

Comparison of nest variables among bird species

Blue tit and great tit nests were constructed from similar materials: moss, hair and grass. Pied flycatcher and redstart nests were predominantly built using grass and leaves (Figure 2a). For these nest material variables (percentage makeup of moss, hair, grass and leaves), Tukey's tests showed that there were significant differences between these bird species pairs (blue tit-great tit compared to pied flycatcher-redstart), but no significant differences within the species pairs. Redstart nests were heaviest and blue tit nests were lightest. Figure 2b illustrates the nest mass for each species; each pairwise comparisons showed significant differences ($p < 0.05$), except for the great tit-pied flycatcher comparison.

Summary of moths recorded and network structure

Most nests contained moths (172 of 224; 78%) yielding a total of 4,657 individuals, comprising ten species (Table 2). Seven of these were probably using the nests as a resource for larval development, while the remaining three species should be classed as incidentally associated

with the nests. Detailed natural histories of each species are discussed elsewhere (Boyes, 2018). The species accumulation curve approaches an asymptote (Supplementary information; Figure S1), suggesting that sufficient nest sampling was undertaken to provide a reasonable characterisation of the moth community and that additional sampling effort would be unlikely to increase the list of species recorded greatly. Figure 3 illustrates how frequently interactions occurred between moth species and the nests of each bird species. Table 3 provides the d' specialisation index values for each species.

Comparison between nest types

Moth presence, species richness and the abundance of individual species tended to differ significantly between closed and open nests (Table 4). Higher values were recorded for closed nests, with the exception of *Tinea semifulvella*, which showed the opposite effect: overall mean abundance and presence were higher for open nests.

Factors affecting moth communities

For the overall presence of any moths, only the flea variable was included in the top model. Nests with fleas were slightly more likely to support moths than nests without fleas. For species richness, there was no significant relationship with any of the explanatory variables; the model with the lowest AIC contained no variables.

The highest ranked model for explaining the variation in total moth abundance included bird species, flea, grass and moss variables. Nests with a higher abundance of fleas tended to have a high abundance of moths. Grass and moss both had a positive effect but this was only statistically significant for the former. The effect on abundance from bird species is illustrated in Figure 4. *Post-hoc* pairwise comparisons revealed that great tit nests supported a larger number of moths than blue tit nests and pied flycatcher nests had fewer moths than the nests of great tits. Table 5

summarises the GLM results. McFadden R^2 values for the best model was typically low (ranging between 0.012-0.086); see supplementary information for tables summarising model outputs.

No clusters are apparent in the NMDS plots for either bird species or site, indicating that the moth communities are extremely similar across bird species and sites (Figure 5).

Discussion

Our study represents the first systematic assessment of ecological factors structuring moth communities in bird nests. Ten moth species were recorded, of which seven have life histories truly associated with bird nests. Most moth individuals were generalist detritivore species (which can use resources other than bird nests), although bird nest specialists were present.

Factors affecting the overall occurrence and abundance of moths

Most nests (78%) contained moths, but there was large variation among nests in the number of individuals, with one nest supporting 287 moths, 6% of the total. Bird species proved to be a significant factor influencing overall moth abundance, with nests of great tits supporting a higher abundance of moths than those of blue tits or pied flycatchers. The data suggest this may be a consequence of a combination of nesting material and nest mass. While pied flycatcher and redstart nests comprised mainly grass and leaves, blue tits and great tit nests were constructed largely from moss and hair. Great tit nests were heavier than those of blue tits, perhaps supporting a greater number of moths as a consequence of larger clutch sizes laid by egg-laying moths, or lower intraspecific and interspecific competition for resources. It would be helpful to extend similar studies to a wider range of bird species to explore in more detail the effects of nest size and nesting materials. It might also be preferable to measure nest volume in addition to nest mass to account for the differing density of nest materials and the three-dimensional space available to moth larvae within nests.

Nests with high flea abundance had a greater abundance of moths, and the presence of fleas was positively associated with overall moth presence. It is possible these are causal relationships; for example, fleas might cause the birds to shed more feathers, increasing resources available to moth larvae. However, it seems more likely that the apparent association with fleas is indirect, with conditions that favour fleas also favouring developing moth larvae. Bird fleas are most abundant on cavity-nesting species (Tripet & Richner, 1997) and have been found to elevate humidity in nests (Heeb, Kölliker & Richner, 2000). This positive relationship may not extend to other invertebrate groups; a negative relationship between flea abundance and arthropod diversity in tit nests has been demonstrated, possibly reflecting the fact some nest-dwelling invertebrates predate fleas (Hanmer et al., 2017).

The small sample size for most of open nests excluded the possibility of detailed statistical analyses, except for broad comparisons with closed nests. The results of these tests were, however, compelling. Nests within prebuilt structures were significantly more likely to support moths, and had higher abundance. With one exception, the means for individual species all followed the same trend. There are at least three possible explanations for these patterns. First, nest boxes are sheltered and this may provide abiotic conditions that are more conducive for successful larval and pupal development. Second, moth larvae in open nests may be more vulnerable to predators. Finally, improved retention and preservation of organic debris in closed nests, along with lower rates of decomposition (Woodroffe and Southgate, 1951), may increase resources for moth larvae. The significant differences in microclimate and decomposition rates between nests in artificial nest boxes and natural cavities (Hebda, Kandziora, and Mitrus, 2017; Maziarz, Broughton and Wesołowski, 2017) means the two habitats are unlikely to support identical invertebrate faunas.

Species richness, community composition and specialisation

Closed nests had significantly higher moth species richness than open nests. This is likely to be for similar reasons to those discussed above with respect to moth abundance. However, within

the subset of the data for box-nesting moths, none of the variables investigated helped explain species richness across nests. While the number of moths developing successfully within a nest seems likely to respond strongly to nest conditions, nest discovery by ovipositing female moths may be a largely stochastic process. Thus, all that might be needed for a species to be present in a given nest is for a single gravid female of that species to locate it.

The NMDS analysis revealed that the moth communities were very similar across species and sites (Figure 5). Woodroffe (1953) reported a very different community of moth species in his study, with only three species of moths common to both studies: *Monopis laevigella*, *Endrosis sarcitrella* and *Hofmannophila pseudospretella*. The contrast between the two studies is most likely because very different bird species were considered: Woodroffe's data were mostly for pigeon and sparrow nests in an urban setting, whereas box-dwelling passerines were the focus of this study. The contrasting habitats and perhaps changes in moth communities over the past 60 years may also contribute to the differing results. The absence of a site effect is also not surprising; all the sites are in similar habitats and they are separated by no more than 25 km. Further exploration of the moth communities associated with the nests of different guilds of birds in Britain is needed. For example, studies elsewhere in Europe have reported distinctive communities from the nests of birds of prey, where tineid larvae may consume animal remains (Jalava, 1980; Jaworski, Gryz & Buszko, 2011).

The absence of species richness and composition differences across bird species is consistent with the results of the quantitative network analysis and calculated specialisation index values. Moths are highly generalised with no suggestion of host-specialisation at the level of bird species. This is perhaps unsurprising. Detritivores are expected in general to be unspecialised feeders, in comparison to co-evolved interaction networks such as those for insect herbivores and their host plants (Novotny et al., 2010). Furthermore, bird nests are a clear example of a patchy and unpredictable resource for moths, something which will tend to select for generalist life history strategies (Southwood, 1977).

The importance of nest material

The favoured nesting materials reported here are typical for the focal bird species (Del Hoyo, Elliott, & Christie, 2005; 2006; 2007), but there was no evidence that nest composition explained moth communities. In contrast, Nasu et al. (2012a) found that the moth fauna associated with nests was predicted by nest materials and debris. In the current study we assessed nest composition using a categorisation into five broad material types, whereas Nasu et al. (2012a) undertook a more detailed assessment, separating out the sources of keratin and chitin in each nest, for example. It unclear at what stage Nasu et al. (2012a) recorded the nest materials, but if done early during larval development, this could be another reason for the contrasting results. In this study, it was not possible to measure nest composition until after the larvae had developed. By this time, larvae may have consumed most of their favoured nest materials, concealing any relationship between their occurrence and nest composition. In future, it would be preferable to quantify nest materials as soon as possible after the breeding birds have vacated the nest. In addition, it would be advantageous to describe the nest materials at the highest possible resolution, e.g. quantities of keratin and chitin resources.

Conclusions

In this study, the nests sampled were heavily skewed towards those of box-dwelling bird species. Nest boxes can be erected and occupied at high densities and their use by breeding birds is readily monitored, allowing a large dataset to be collected with relative ease. In contrast, open nests can be difficult and time-consuming to locate. One approach that might allow nests of a wider selection of species to be sampled would be to 'crowd source' nests, for example through the nest recording scheme run by the British Trust for Ornithology. Such an investigation, generating data from a much larger range of bird species that use a diverse range of nest strategies and habitats, would most likely provide greater variation in microhabitat structure, resources and abiotic

conditions. As a result, moth community composition differences among bird species, and perhaps greater evidence of specialisation, might become apparent.

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