

NATURAL HISTORY

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

DOUGLAS H. BOYES¹ and OWEN T. LEWIS^{1,2} ¹Brasenose College, Oxford, U.K. and ²Department of Zoology, University of Oxford, Oxford, U.K.

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. Two hundred and twenty-four nests, from 16 bird species, were sampled from sites in mid-Wales (UK) and the moths that emerged from them were recorded.

3. Seventy eight percent of nests produced moths, with 4657 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.

Key words. commensal, detritivore, fleas, invertebrates, moths, Tineidae.

Introduction

Bird nests are an 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) listed 18 insect orders associated with bird nests. An assessment of nests from 56 bird species in Finland noted 528 different arthropods (Nordberg, 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 *et al.*, 2012); the arthropod fauna of shrike nests in Poland (Tryjanowski *et al.*, 2001); and the invertebrate fauna of bird nests in England, UK (Woodroffe & 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 *et al.*, 1994). Variations in the location, structure and materials of nests are expected to lead to opportunities for specialization 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.

Correspondence: Douglas Boyes, Brasenose College, Radcliffe Square, Oxford OX1 4AJ, U.K. E-mail: info@douglasboyes.co.uk

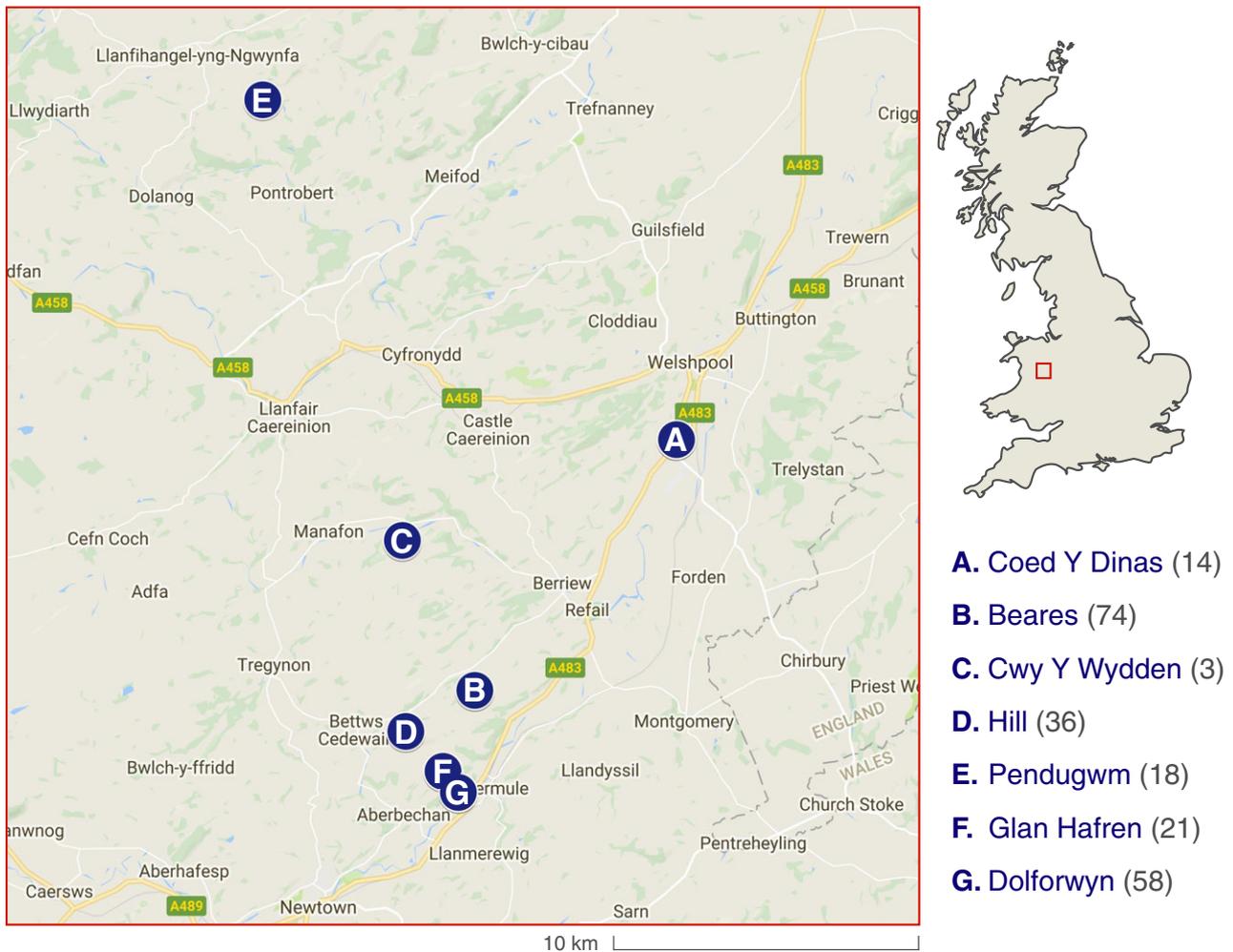


Fig. 1. The location of the seven study sites; the number of nests sampled from each is given in parentheses. Map image ©2018 Google. [Colour figure can be viewed at wileyonlinelibrary.com].

Methods

Study system

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

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 1.4 m 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 of 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 built within other structures were defined as ‘closed’. Table 1 summarizes 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 18 cm × 13 cm × 7 cm, 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

Table 1. The bird species investigated and their representation at each study site.

Species	BTO species code	Number of observations							Totals
		Beares	Coed Y Dinas	Cwy Y Wydden	Dolforwyn	Glan Hafren	Hill	Pendugwm	
Closed nests									
Blue tit, <i>Cyanistes caeruleus</i>	BT	35	13	0	31	12	17	4	112
Great tit, <i>Parus major</i>	GT	20	0	0	15	5	9	7	56
Pied flycatcher, <i>Ficedula hypoleuca</i>	PF	13	0	0	7	2	0	7	29
Redstart, <i>Phoenicurus phoenicurus</i>	RT	6	0	0	0	0	1	0	7
Coal tit, <i>Periparus ater</i>	CT	0	0	0	0	1	0	0	1
Nuthatch, <i>Sitta europaea</i>	NH	0	0	0	0	0	1	0	1
Robin, <i>Erithacus rubecula</i>	R.	0	0	0	0	0	1	0	1
Wren, <i>Troglodytes troglodytes</i>	WR	0	0	0	0	0	1	0	1
Stock dove, <i>Columba oenas</i>	SD	0	0	0	1	0	0	0	1
Open nests									
Blackbird, <i>Turdus merula</i>	B.	0	1	0	0	1	4	0	6
Blackcap, <i>Sylvia atricapilla</i>	BC	0	0	0	3	0	0	0	3
Wood warbler, <i>Phylloscopus sibilatrix</i>	WO	0	0	2	0	0	0	0	2
Garden warbler, <i>Sylvia borin</i>	GW	0	0	0	0	0	1	0	1
Chiffchaff, <i>Phylloscopus collybita</i>	CC	0	0	0	1	0	0	0	1
Goldcrest, <i>Regulus regulus</i>	GC	0	0	1	0	0	0	0	1
Goldfinch, <i>Carduelis carduelis</i>	GO	0	0	0	0	0	1	0	1
	Totals	74	14	3	58	21	36	18	224

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 and Emmet (1985) and Bengtsson and Johansson (2011). For families other than Tineidae, Emmet and Langmaid (2002), Riley and Prior (2003) and Sterling *et al.* (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 of the material had dried to a constant mass, which was recorded to the nearest 0.01 g using digital scales. The composition of the nests was quantified by visually estimating the percentage makeup of grass, leaves, hair, moss and feathers. Because nest moisture can influence the moth fauna within a nest (Woodroffe, 1953), nests were categorized 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, whereas the remainder leaked very little moisture. The abundance of fleas (Siphonaptera) was categorized 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 v3.3.1 (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 specialization index d' was calculated for each moth species, using the bipartite package (Dormann *et al.*, 2008). The d' index provides an unbiased estimate of specialization, 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 level 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 of 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 of 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

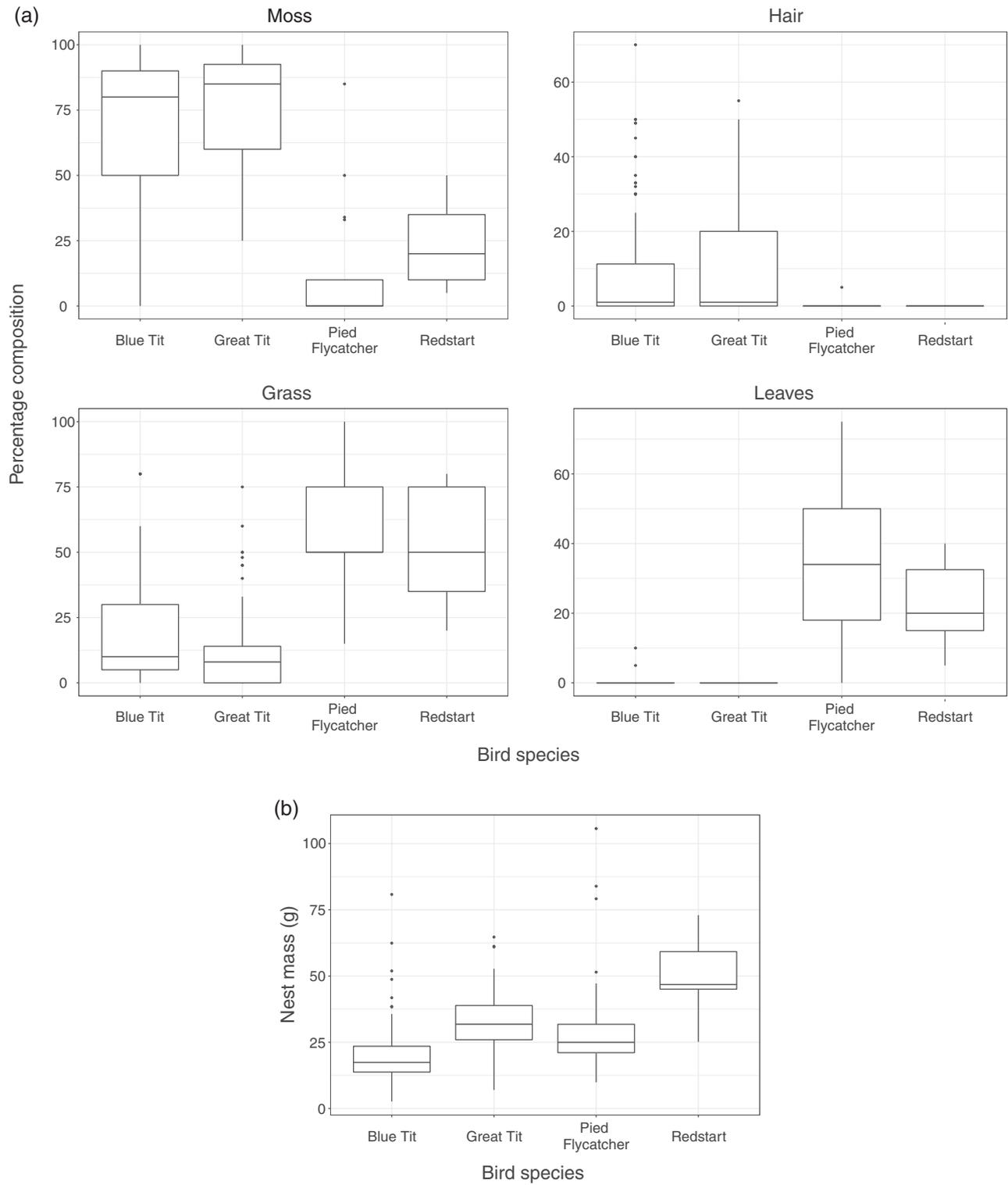


Fig. 2. Boxplots showing (a) nest materials used by the bird species, and (b) nest mass variation between bird species. The horizontal lines represent the median; the boxes denote the interquartile range; the whiskers extend from the box to the minimum and maximum data point, provided these are within 1.5 times the interquartile range; any values outside of this are outliers and are plotted separately.

Table 2. The moth species that emerged across all nests. The fourth column indicates associations with bird species (BTO codes are given in Table 1).

Species	Combined count	Total nests occupied (% of nests)	Bird species (BTO codes)
<i>Endrosis sarcitrella</i> (Linnaeus, 1758)	1907	128 (57)	BT, GT, PF, R., CT, NH, B., GW, CC
<i>Monopis laevigella</i> ([Denis & Schiffermuller], 1775)	1871	87 (39)	BT, GT, PF, R., CT, NH, B.
<i>Hofmannophila pseudospretella</i> (Stainton, 1849)	509	52 (23)	BT, GT, PF, R., CT, R., B., WR, SD
<i>Niditinea striolella</i> (Matsumura, 1931)	138	11 (5)	BT, GT, PF, CT,
<i>Tinea semifulvella</i> Haworth, 1828	57	7 (3)	BT, GT, B., WO
<i>Eupithecia vulgata</i> *(Haworth, 1809)	3	3 (1)	BT, GT
<i>Nemapogon cloacella</i> (Haworth, 1828)	4	2 (<1)	BT
<i>Aphomia sociella</i> *(Linnaeus, 1758)	166	2 (<1)	BT
<i>Tinea trinotella</i> Thunberg, 1794	1	1 (<1)	GT
<i>Agonopterix heracliata</i> *(Linnaeus, 1758)	1	1 (<1)	BT

*Indicates species whose occurrence in bird nests is considered to be merely incidental; these species have been excluded from further analysis.

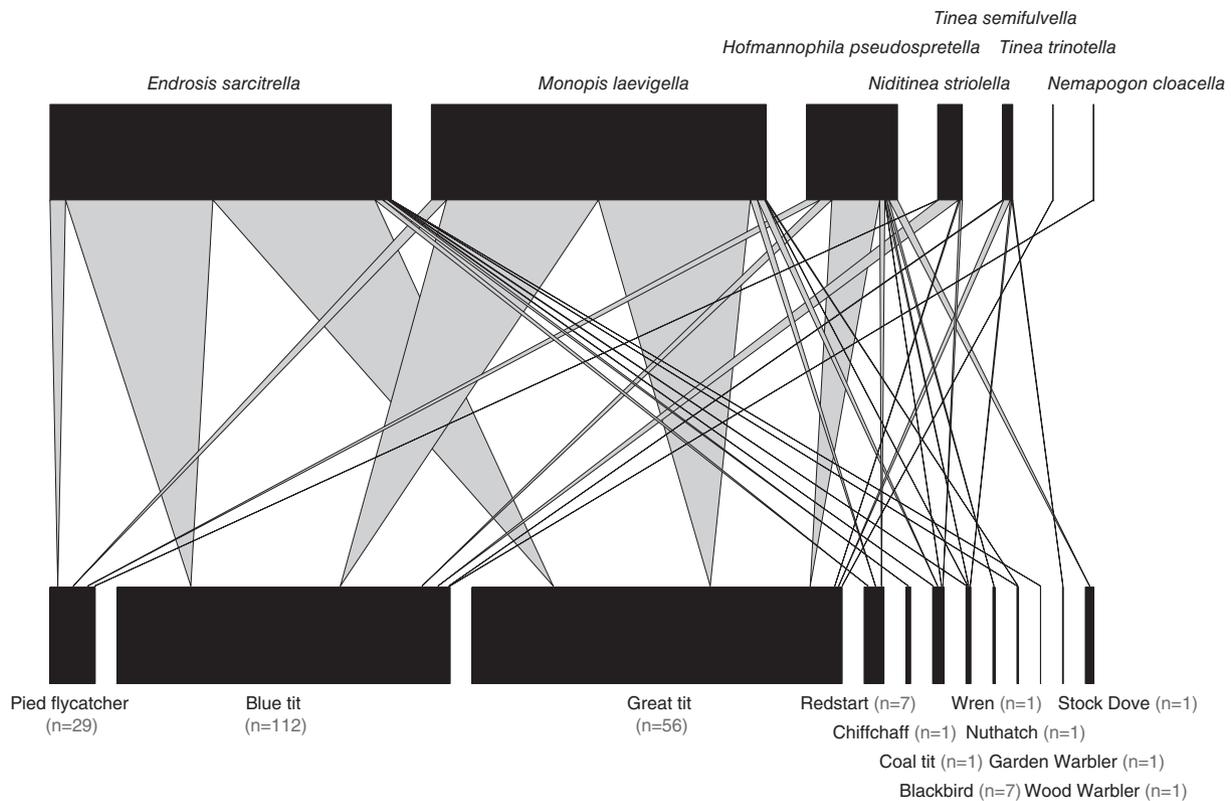


Fig. 3. Interaction network showing the frequency of interactions between moth species and the nests of different bird species. The widths of the bars are proportional to moth abundance. The widths of the linkages indicate the fraction of each moth species associated with nests of each bird species.

by Akaike weight. McFadden's R^2 was estimated for the top ten models using the `pscl` package (Jackman, 2017). When categorical variables were significant, post-hoc Tukey's pairwise 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 visualized 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 (Fig. 2a). For

Table 3. Values of the specialization index d' for the five commonest moth species.

Species	Occurrence (% of nests)	d'
<i>Endrosis sarcitrella</i>	57	0.58
<i>Monopis laevigella</i>	39	0.56
<i>Hofmannophila pseudospretella</i>	23	0.56
<i>Niditinea striolella</i>	5	0.80
<i>Tinea semifulvella</i>	3	0.69

Values of 1 indicate a perfect specialist; the lower the value, the more generalist a species. Species appearing in a very small number of nests are excluded from these calculations as they may have high or low specialization index values as an artefact of sample size.

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 comparison 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 4657 individuals, comprising ten species (Table 2). Seven of these were probably using the nests as a resource for larval development, whereas 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 (Figure S1), suggesting that sufficient nest sampling was undertaken to provide a reasonable

characterization 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' specialization 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 Fig. 4. Post-hoc pairwise comparisons revealed that great tit nests supported a larger number of moths than blue tit nests, and that pied flycatcher nests had fewer moths than the nests of great tits. Table 5 summarizes the GLM results. McFadden R^2

Table 4. Comparison of closed and open nests.

Variable	Sample mean		U	Odds ratio	P -value
	Open nests	Closed nests			
Presence of any moths	0.33	<u>0.80</u>	n/a	7.85	2.47×10^{-4}
Species richness	0.47	<u>1.33</u>	30 036	n/a	1.86×10^{-5}
Total moth abundance	4.07	<u>21.16</u>	37 246	n/a	2.20×10^{-16}
Presence of individual species:					
<i>Endrosis sarcitrella</i>	0.2	<u>0.60</u>	n/a	6.91	0.0051
<i>Monopis laevigella</i>	0.067	<u>0.41</u>	n/a	9.73	0.011
<i>Hofmannophila pseudospretella</i>	0.067	<u>0.24</u>	n/a	4.50	0.20
<i>Tinea semifulvella</i>	<u>0.13</u>	0.024	n/a	0.16	0.072
Abundance of individual species:					
<i>Endrosis sarcitrella</i>	2.47	<u>8.95</u>	27 511	n/a	0.056
<i>Monopis laevigella</i>	0.13	<u>8.94</u>	19 575	n/a	1.22×10^{-5}
<i>Hofmannophila pseudospretella</i>	0.6	<u>2.39</u>	11 475	n/a	2.20×10^{-16}
<i>Tinea semifulvella</i>	<u>0.87</u>	0.21	2986.5	n/a	2.20×10^{-16}

For species-specific analyses, only the four commonest moth species were analysed as sample sizes were too small for the other species to allow meaningful comparison. The higher mean for each variable is underlined. For presence variables, the P -value is from a Fisher's exact test (testing for a difference in the proportion of occupied nests). For continuous variables, the P -value is from a Mann–Whitney U -test (testing for a difference in the median).

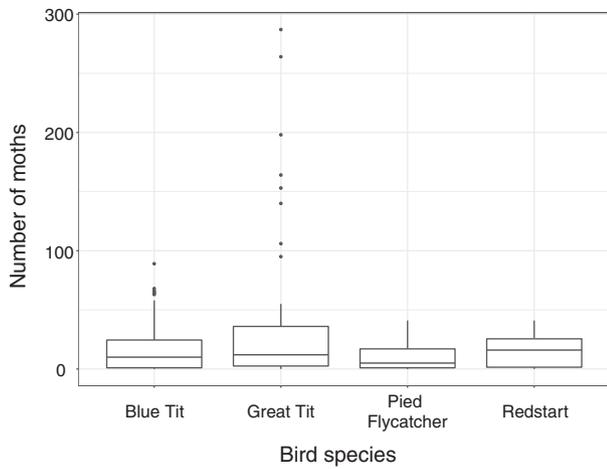


Fig. 4. Boxplot showing how the total number of individuals emerging from each nest varies for different bird species. See Fig. 2 caption for boxplot explanation.

values for the best model were typically low (ranging between 0.012 and 0.086) (see supplementary information for tables summarizing model outputs in File S1).

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 (Fig. 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. Although 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

Table 5. Summary of the GLM results, where each model is represented by a row.

Response variables	Explanatory variables									
	Bird species	Site	Leaves	Grass	Moss	Feather	Hair	Moisture	Fleas	Mass
Presence of any moths	-	-	-	-	-	-	-	-	-	-
Species richness	-	-	-	-	-	-	-	-	-	-
Total moth abundance	-	-	-	-	-	-	-	-	-	-
<i>Endrosis sarcitrella</i>	Positive effect	-	-	Positive effect	Positive effect (ns)	-	-	-	Positive effect	Positive effect (ns)
<i>Monopis laevigella</i>	Abundance	-	-	Negative effect (ns)	Negative effect	-	-	-	Positive effect	Positive effect (ns)
<i>Hofmannophila pseudospretella</i>	Presence	-	-	Negative effect (ns)	Positive effect	-	Negative effect	-	-	-
	Abundance	-	-	Positive effect (ns)	-	-	Negative effect	-	-	-
	Presence	-	-	-	-	-	Positive effect	-	-	-
	Abundance	-	-	-	-	-	-	-	-	-
	Abundance	Negative effect	-	-	-	-	-	Negative effect	-	-

Shaded boxes indicate the explanatory variables that were included in the final model; unless indicated by 'ns', the effect was statistically significant ($P < 0.05$). The direction of the effect is shown where applicable. The highest ranked model by AIC weight is shown; see File S1 for the top model tables.

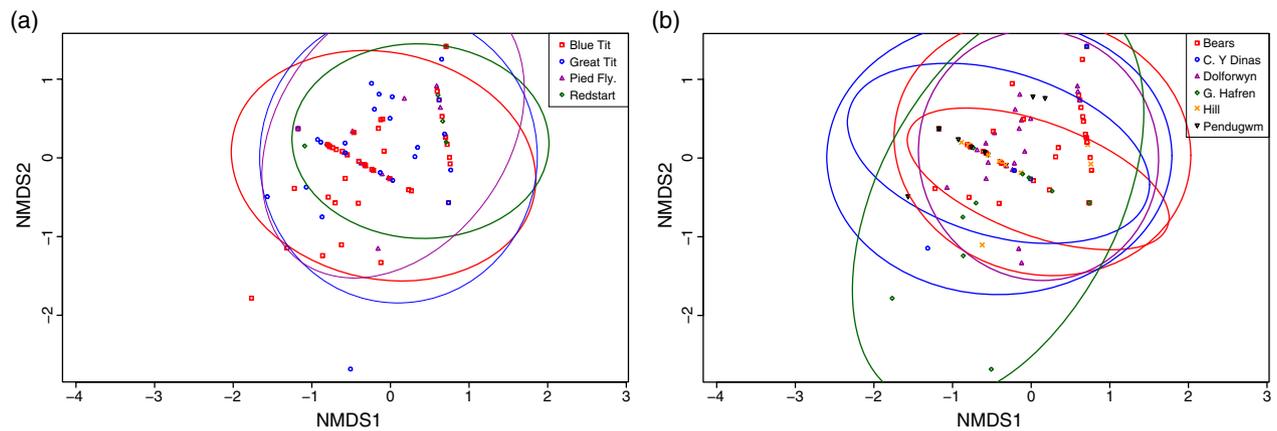


Fig. 5. NMDS plots to examine community composition. Each point represents a nest and these are colour-coded according to bird species (a) and sampling location (b). The plots have a stress value of 0.0713, indicating they constitute a robust representation of the community composition dissimilarity. Ellipses show 95% confidence intervals. The narrow clustering of points along two axes, forming a 'V' shape is an artefact of the low species richness and limited number of species combinations within the dataset. [Colour figure can be viewed at wileyonlinelibrary.com].

preferable to measure nest volume in addition to nest mass to account for the differing density of nest materials and the 3D 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 that 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 *et al.*, 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 that fleas are prey for some nest-dwelling invertebrates (Hanmer *et al.*, 2017).

The small sample sizes for most of the 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. Third, and finally, improved retention and preservation of organic debris in closed nests, along with lower rates of decomposition (Woodroffe & 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 *et al.*, 2017; Maziarz *et al.*, 2017) mean that the two habitats are unlikely to support identical invertebrate faunas.

Species richness, community composition and specialization

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. Although 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 (Fig. 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 also may contribute to the differing results. The absence of a site effect also is not surprising; all of 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 *et al.*, 2011).

The absence of species richness and composition differences across bird species is consistent with the results of the quantitative network analysis and calculated specialization index values. Moths are highly generalized with no suggestion of host specialization at the level of bird species. This is perhaps unsurprising.

Detritivores are expected in general to be unspecialized 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 *et al.*, 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 categorization 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 is 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 the present 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, for example, 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 BTO. 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 specialization, might become apparent.

Acknowledgements

We are grateful to three anonymous reviewers for their thoughtful and constructive feedback. We thank Ada Grabowska-Zhang and Natasja van Gestel for advice on data analysis and Paul Roughley for help in locating and collecting nests. Montgomeryshire Wildlife Trust gave permission to collect nests

from their reserves. Clare and Simon Boyes provided patient support, even in the face of the unexpected flea infestation of their house.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Smoothed species accumulation curves showing the number of moth species expected as a function of sampling effort for (a) all moths, and (b) excluding species not linked to bird nests through their natural history (these are indicated with an asterisk in Table 3).

File S1. Top 10 models, ranked by AIC weight, for each response variable.

Bibliography

- Bartoń, K. (2014) *MuMin: multi-model inference. Version 1.10.0* [WWW document]. URL <http://CRAN.R-project.org/package=MuMin> [accessed 15 October 2016].
- Bengtsson, B.Å. & Johansson, R. (2011) Nationalnyckeln till Sveriges flora och fauna. *Fjärilar: Bronsmalar-rullvingemalar. Lepidoptera: Roeslerstammiidae-Lyonetiidae*. ArtDatabanken, SLU, Uppsala [In Swedish].
- Blüthgen, N., Menzel, F. & Blüthgen, N. (2006) Measuring specialization in species interaction networks. *BMC Ecology*, **6**, 9.
- Boyes, D.H. (2018). *Natural history of Lepidoptera associated with bird nests in mid-Wales*. The Entomologist's Record and Journal of Variation. [manuscript in review].
- Del Hoyo, J., Elliott, A. & Christie, D.A. (2005) *Handbook of the Birds of the World, Vol. 10. Cuckoo-shrikes to Thrushes*, Lynx Edicions, Barcelona, Spain.
- Del Hoyo, J., Elliott, A. & Christie, D.A. (2006) *Handbook of the Birds of the World. Vol. 11. Old World Flycatchers to Old World Warblers*. Lynx Edicions, Barcelona, Spain.
- Del Hoyo, J., Elliott, A. & Christie, D.A. (2007) *Handbook of the Birds of the World. Vol. 12. Picarthartes to Tits and Chickadees*. Lynx Edicions, Barcelona, Spain.
- Dormann, C.F., Gruber, B. & Fründ, J. (2008) Introducing the bipartite package: analysing ecological networks. *R News*, **8**, 8–11.
- Emmet, A. M. & Langmaid, J. R. (eds) (2002) *The Moths and Butterflies of Great Britain and Ireland. Vol. 4 (Part 1). Oecophoridae-Scythridida*. Harley Books, Colchester, U.K.
- Hanmer, H.J., Thomas, R.L., Beswick, G.J., Collins, B.P. & Fellowes, M.D. (2017) Use of anthropogenic material affects bird nest arthropod community structure: influence of urbanisation, and consequences for ectoparasites and fledging success. *Journal of Ornithology*, **158**, 1045–1059.
- Heath, J. & Emmet, A. M. (eds) (1985) *The Moths and Butterflies of Great Britain and Ireland. Vol. 2. Cossidae-Helioidinidae*. Harley Books, Colchester, U.K.
- Hebda, G.A., Kandziora, A. & Mitrus, S. (2017) Decomposition of nest material in tree holes and nest-boxes occupied by European Starlings *Sturnus vulgaris*: an experimental study. *Acta Ornithologica*, **52**, 119–125.
- Heeb, P., Kölliker, M. & Richner, H. (2000) Bird–ectoparasite interactions, nest humidity, and ectoparasite community structure. *Ecology*, **81**, 958–968.

- Hicks, E.A. (1959) *Check-list and Bibliography on the Occurrence of Insects in Bird Nests*. Iowa State College Press, Ames, IA.
- Hicks, E.A. (1962) Check-list and bibliography on the occurrence of insects in bird nest: supplement 1. *Iowa State Journal of Science*, **36**, 233–348.
- Hicks, E.A. (1971) Check-list and bibliography on the occurrence of insects in bird nest: supplement 2. *Iowa State Journal of Science*, **46**, 123–338.
- Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A. & Scheibe, S. (2013). multcomp: simultaneous inference in general parametric models. Version 1.3-0. [WWW document]. URL <https://cran.r-project.org/package=multcomp> [accessed 15 October 2016].
- Jackman, S. (2017). *pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory*, United States Studies Centre, University of Sydney, Sydney, Australia. Version 1.5.2. [WWW document]. URL <https://github.com/atahk/pscl/> [accessed 15 October 2016].
- Jalava, J. (1980) Tineidae (Lepidoptera) from nests of the Ural owl (*Strix uralensis* Pall.). *Notulae entomologicae*, **60**, 96–100.
- Jaworski, T., Gryz, J. & Buszko, J. (2011) *Monopis fenestratella* (Heyden, 1863)(Lepidoptera, Tineidae) - new records from Poland, with notes on species biology. *Fragmenta Faunistica*, **54**, 149–151.
- Jaworski, T., Gryz, J. & Krauze-Gryz, D. (2012) Tawny owl *Strix aluco* L. nest boxes as a habitat for some moths (Lepidoptera). *Wiadomości Entomologiczne*, **31**, 17–22 [In polish; English summary].
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.
- Kleiber, C. & Zeileis, A. (2009). *AER: Applied Econometrics with R R Package. Version 1.1*. [WWW document]. URL <https://cran.r-project.org/web/packages/AER/AER.pdf> [accessed 15 October 2016].
- Maziarz, M., Broughton, R.K. & Wesołowski, T. (2017) Microclimate in tree cavities and nest-boxes: implications for hole-nesting birds. *Forest Ecology and Management*, **389**, 306–313.
- Nasu, Y., Murahama, S., Matsumuro, H., Ueda, K. & Hirowataris, T. (2012a) Lepidoptera from nests of four insectivorous bird species. *Lepidoptera Science*, **63**, 87–93 [In Japanese with English summary].
- Nasu, Y., Murahama, S., Matsumuro, H., Ueda, K., Hirowatari, T. & Yoshiyasu, Y. (2012b) Relationships between nest-dwelling Lepidoptera and their owl hosts. *Ornithological Science*, **11**, 77–85.
- Nordberg, S. (1936) Biologisch-ökologische Untersuchungen über die Vogel-nidieolen. *Acta Zoologica Fennica*, **21**, 1–168 [In German].
- Novotny, V., Miller, S.E., Baje, L. *et al.* (2010). Guild-specific patterns of species richness and host specialization in plant–herbivore food webs from a tropical forest. *Journal of Animal Ecology*, **79**, 1193–1203.
- Oksanen, J., Blanchet, F.G., Kindt, R., *et al.* (2016). *Vegan: community ecology package. Version 2.3-5* [WWW document]. URL <https://cran.r-project.org/web/packages/vegan/vegan.pdf> [accessed 15 October 2016].
- Plarre, R. (2014). Likelihood of infestations by *Tineola bisselliella* (Lepidoptera: Tineidae) from natural reservoirs. *Proceedings of the Eighth International Conference on Urban Pests*, 20–23 July, 2014, Zürich (ed. by G. Müller, R. Pospischil, and W. H. Robinson). Executive Committee of the International Conference on Urban Pests.
- Plarre, R. & Krüger-Carstensen, B. (2011) An attempt to reconstruct the natural and cultural history of the webbing clothes moth *Tineola bisselliella* Hummel (Lepidoptera: Tineidae). *Journal of Entomological and Acarological Research*, **43**, 83–93.
- R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.
- Riley, A.M. & Prior, G. (2003) *British and Irish Pug Moths (Lepidoptera: Geometridae, Larentiinae, Eupitheciini): A Guide to their Identification and Biology*. Harley Books, Colchester, U.K.
- Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D. and Ripley, M.B. (2013) *Package 'MASS'*. CRAN Repository [WWW document]. URL <http://cran.r-project.org/web/packages/MASS/MASS.pdf> [accessed 15 October 2016].
- Southwood, T.R.E. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 337–365.
- Sterling, P., Parsons, M. & Lewington, R. (2012) *Field Guide to the Micro-moths of Great Britain and Ireland*. British Wildlife Publishing, Gillingham, U.K.
- Triplet, F. & Richner, H. (1997) The coevolutionary potential of a 'generalist' parasite, the hen flea *Ceratophyllus gallinae*. *Parasitology*, **115**, 419–427.
- Tryjanowski, P., Baraniak, E., Bajaczyk, R., Gwiazdowicz, D.J., Konwerski, S., Olszanowski, Z. *et al.* (2001) Arthropods in nests of the red-backed shrike (*Lanius collurio*) in Poland. *Belgian Journal of Zoology*, **131**, 69–74.
- Ver Hoef, J.M. & Boveng, P.L. (2007) Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology*, **88**, 2766–2772.
- Woodroffe, G.E. (1953) An ecological study of the insects and mites in the nests of certain birds in Britain. *Bulletin of Entomological Research*, **44**, 739–772.
- Woodroffe, G.E. & Southgate, B.J. (1951) Birds' nests as a source of domestic pests. *Journal of Zoology*, **121**, 55–62.

Accepted 11 July 2018

First published online 27 August 2018

Associate Editor: Toomas Tammaru