



Differences in the niches of keratin/chitin feeding moths (Lepidoptera: Tineidae) in bird nests in central Japan

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Abstract. Some moth larvae feed not on plants but on keratin and/or chitin produced by animals. These substances are polymers and are commonly found in bird nests as feathers and raptor pellets. Many qualitative studies have examined the association of keratin/chitin feeding moths with bird nests. However, few studies have quantified the species composition with respect to type of nest and habitat. Hence, we have studied the degree to which the niches of these moths differ in terms of type of nest and habitat. We set-up open-top nest boxes for the Ural owl *Strix uralensis* (damp exposed nests from which owl chicks were fledged successfully) and artificial bird nests (mesh bags filled with duck down to imitate dry exposed nests) in a deciduous forest and artificial bird nests in an urban setting in Aichi Prefecture, central Japan, and collected the contents of the nests every two months from June to December 2014. We recorded 592 individuals of five keratin/chitin feeding moth species (Tineidae, Tineinae) from the contents. Using non-metric multidimensional scaling and cluster analysis of the relative abundances of individual species in each type of nest in forest and urban settings, these species were classified into three groups: (1) *Monopis longella* and *M. congestella* inhabiting forest, (2) *M. flavidorsalis* and *Niditinea tuguralis* mainly in damp exposed nests in forest and (3) *N. piercella* mainly in dry exposed nests in urban areas. This classification was compared with findings of other studies. As a result, these moths probably have different niches with respect to nest type (damp or dry), keratin/chitin as a source of food (raptor pellets or feathers), and habitat (forest or urban area). Furthermore, we suggest that the evolution of larviparity in *M. congestella* might be related to its preference for feathers as a source of food for the development of its larvae.

INTRODUCTION

Bird nests harbour highly diverse insects including Hemiptera, Diptera, Siphonaptera, Coleoptera, Hymenoptera and Lepidoptera (Nordberg, 1936; Woodroffe, 1953; Hicks, 1959, 1962, 1971; Křiššosík et al., 1994). Of these insect orders, the relationship of Lepidoptera (moths) with bird nests has been comparatively well studied because moths tend to be noticeable and abundant in nests (Jalava, 1980; Jaworski et al., 2012; Nasu et al., 2012a, c; Boyes & Lewis, 2019). Moth larvae in nests are classified mainly into plant- and animal-material feeders (Robinson, 2004; Nasu et al., 2012a, c). The former feed on dead leaves, grass, fibres, moss and liverwort (albeit not plants), while the latter feed on faeces, raptor pellets, hair and feathers, which contain keratin and chitin. Hence, it seems likely that the moth fauna in bird nests depends on the composition of the nest contents (Nasu et al., 2012a, c). However, Boyes & Lewis' (2019) recent comparison of moth assemblages

in concealed nests of five passerine species in mature oak woodland in mid-Wales, UK, revealed no evidence of the occurrence and abundance of species of moths in nests depending on nest contents. They offer two possible explanations. First, nest discovery by ovipositing female moths may be largely a matter of chance. Second, detritovores may be unspecialized feeders. This study focused on keratin/chitin feeding moths (animal-material feeders) in order to clarify the association of moths with bird nests.

According to Robinson (2004), keratin/chitin feeding moths belong to the subfamilies Tineinae and Hieroxestinae of the family Tineidae. Most species of Tineinae are keratin and/or chitin feeders, while only a few of the Hieroxestinae feed on chitin. Of the keratin and/or chitin feeding species of Tineinae, *Monopis*, *Niditinea* and *Tinea* are chiefly associated with bird nests. Robinson (2004) also shows that keratin/chitin feeding moths are likely to occupy different niches with respect to nest type, i.e., damp

concealed, dry concealed, damp exposed, or dry exposed; concealed nests are those in holes in trees (including nest boxes), while exposed nests are constructed in trees and hedges. For example, the *Monopis congestella*-group and *M. monachella*-group are found in damp exposed and dry exposed nests, respectively, while the *Niditinea fuscella*-group are found in nests of both types. The *Niditinea piercella*-group occur only in concealed nests. However, Robinson (2004) does not provide quantitative data supporting these conclusions.

Since Robinson (2004), much information has been collected about keratin/chitin feeding moths in bird nests, especially in Japan (e.g., Nasu et al., 2007a, b, 2008a, b, 2012a, b, c). In these studies moths were reared on the organic contents of concealed and exposed nests of 16 species of birds in forests and urban areas and *Monopis longella* (Walker) [= *pavlovskii* (Zagulyaev)], *M. congestella* (Walker), *M. flavidorsalis* (Matsumura), *Niditinea tugurialis* Meyrick [= *baryspilas* (Meyrick)], *N. striolella* (Matsumura), *Tinea translucens* Meyrick and *Tineola bisselliella* (Hummel) fed on the keratin/chitin in the nests of these birds. Nasu (2012) summarizes the associations of these moths with bird nests in terms of type of nest and habitat as follows: *M. longella* and *M. congestella* occur in concealed and exposed nests in forests, while *M. flavidorsalis* and *N. striolella* are found only in concealed nests in forests; in contrast, *Tinea translucens* and *Tineola bisselliella* only occur in concealed and exposed nests in urban areas. However, the studies by Nasu and colleagues did not quantitatively or systematically assess the degree to which these moths depend on concealed and exposed nests. Furthermore, the specimens identified as *N. tugurialis* probably included *N. piercella* Benthinck, so information on the occurrence of this species in bird nests is unreliable (Nasu & Sato, 2016).

Larviparity, or laying fully developed first-instar larvae instead of eggs, is very rare in Lepidoptera (Hinton, 1981; Heppner, 2009). However, it is relatively common in *Monopis*, a keratin/chitin feeding genus with 90 species worldwide (Robinson, 2019), 12 of which are known to be larviparous (Xiao & Li, 2006). Three species of *Monopis* are recorded in Japan (see above; Sakai, 2013), and one, *M. congestella*, is larviparous (Robinson, 1988, 2004; Nasu et al., 2008a). Robinson (2004) has hypothesized that larviparity in *Monopis* evolved due to (1) high mortality of eggs and neonates due to intense predation by mites in bird nests, and (2) high cost of finding more than one oviposition site, or bird's nest. If there is a difference in nests exploited by larviparous and oviparous *Monopis* moths, then there could be another reason.

This study determines the degree to which keratin/chitin feeding moths have different niches in terms of the types of nests or habitats in which they are constructed. This involved sampling moths quantitatively and systematically in a deciduous forest and an urban area using nest boxes and artificial bird nests. The open-top nest boxes were designed for the Ural owl *Strix uralensis* Pallas, while the artificial bird nests were made from duck-down stuffed

into a plastic mesh bag (Robinson & Nielsen, 1993). The owl nest boxes and artificial bird nests were categorized as damp exposed type and dry exposed type, respectively, following Robinson's (2004) classification. We compared the composition of keratin/chitin feeding species of moth in the two types of nests in different habitats.

MATERIALS AND METHODS

Ecology of the Ural owl

Paired Ural owls usually nest in cavities in tree trunks. Females lay two to four eggs in March to April and incubate them for 27 to 32 days (Nakamura & Nakamura, 1995). Prey for chicks are small mammals, birds, frogs, newts, lizards and centipedes (our unpublished data). Chicks leave the nest 30 to 34 days after hatching.

Collection of the organic contents of owl nest boxes

Nine open-top plastic boxes (26 cm wide, 26 cm long, 30 cm deep) were installed in trees 2 to 3 m above ground level in a secondary deciduous forest (80 to 360 m a.s.l.) extending across Toyota and Okazaki Cities, Aichi Prefecture, central Japan in May 2013 (Fig. 1). Several twigs were put in each box as nest material. In spring 2014, Ural owls bred in each box, with one or two chicks fledged by late May. All or half the organic contents (feathers, owl pellets, faeces and other detritus) were collected from each of three or four randomly chosen boxes on 7 June, 17 August, 18 October and 6 December 2014; as a result, the organic contents in five boxes were collected twice (Table 1). Feathers were present in only two boxes in June and August. The quantity of nest material collected at any one time ranged from 0.6 to 3.1 litres.

Sampling using artificial birds' nests

Artificial birds' nests were made according to Robinson & Nielsen (1993) using plastic mesh bags (16 × 20 cm in size; 3 × 3 mm in mesh size) stuffed with 10 g of dry duck down bound together with 5 g of beer yeast and some water. Four artificial nests were hung on tree branches (several hundred meters apart; 90 to 120 m a.s.l.) at 1.5 m above the ground in a secondary deciduous forest in the Toyota City Nature Sanctuary, Aichi Prefecture on 7 June, 17 August and 18 October 2014 (hereafter referred to as forest artificial nests; Fig. 1). To compare the species composition of the moths in the forest and that in the urban area, three artificial bird nests were set-up at the Toyota Yahagi River Institute in the urban area of Toyota City on 2 June, 18 August and 16 October 2014 (hereafter referred to as urban artificial nests; Fig. 1); this site is 400 m from the nearest green park. Two artificial nests were hung on the branches of trees at this site, while the third was hung under the eaves of a building. The nests were retrieved approximately two months later on 17 August, 18 October or 6 December 2014.

Rearing

Organic contents collected from each owl nest box on each occasion they were sampled were put in one to three plastic boxes (16 cm wide, 22 cm long, 8 cm deep) according to the amount. To ventilate the boxes, the centre of the lid of each box was cut away to form 4-cm square window, which was covered by a sheet of fine plastic mesh. Duck down from each artificial nest was also kept in a plastic box of the same type. These boxes were stored under semi-natural temperature and light-dark photoperiod conditions (adjusted to monthly average values in field) in an incubator for two to seven months according to the collection date; materials collected in June, August, October and December were kept

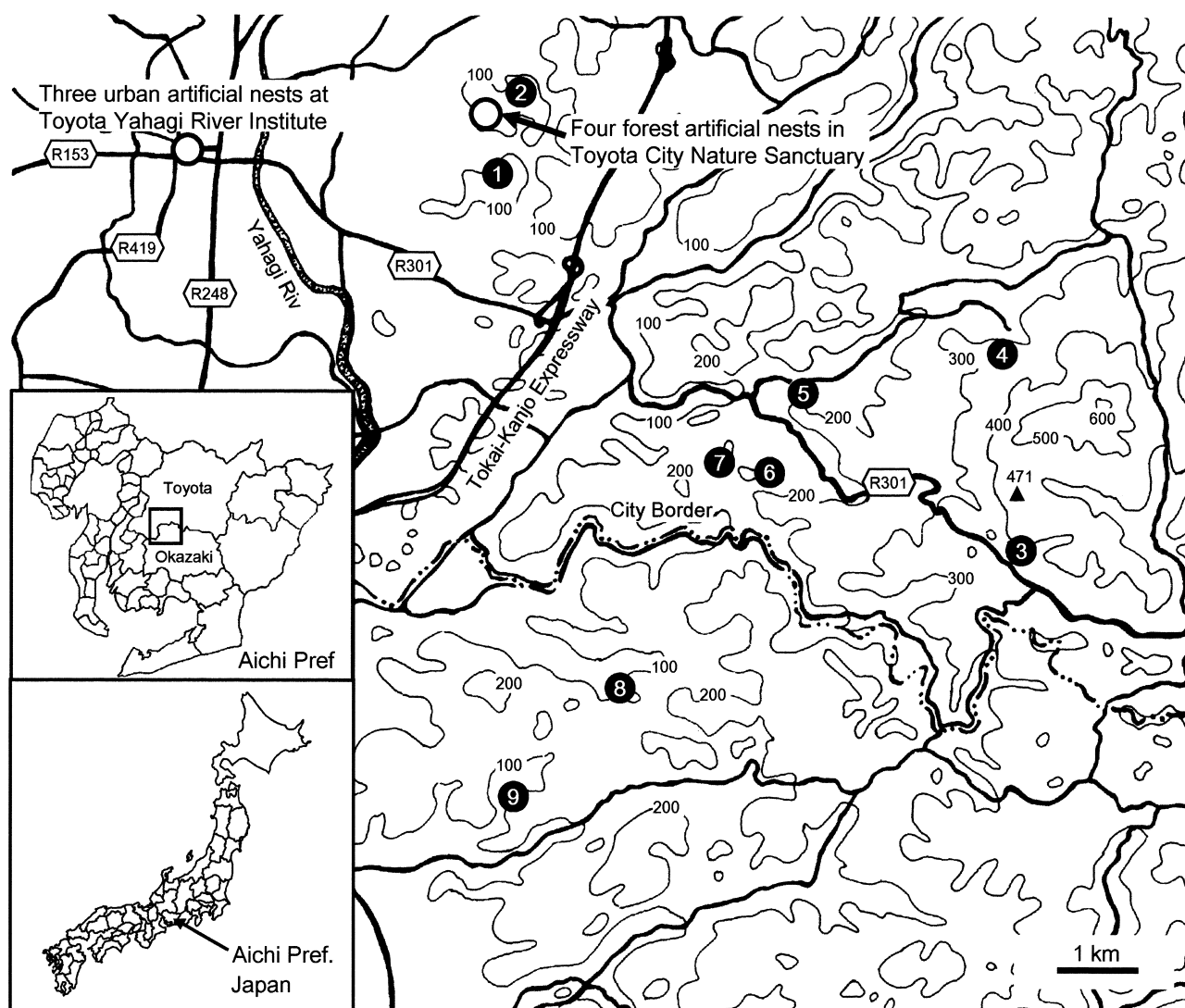


Fig. 1. Location of owl nest boxes (solid circles) and artificial bird nests (open circles). Four and three artificial nests (mesh bags stuffed with duck down) were located in a deciduous forest in the Toyota City Nature Sanctuary (forest artificial nests) and at the Toyota Yahagi River Institute in an urban area (urban artificial nests), respectively.

for two, two, seven and five months, respectively. Adult moths emerging during these periods were identified to species and the numbers were counted. The number of cocoons of *M. congestella* within which a dead or alive mature larva or a pupa existed was also counted. *Niditinea tugurialis* and *N. piercella* were distinguished by their genitalia according to Nasu & Sato (2016).

Niditinea piercella is sometimes treated as a junior synonym of *N. striolella* (Matsumura) (Karsholt & Razowski, 1996; Gaedike, 2000, 2019). However, the drawings of male and female genitalia identified as those of *N. pacifella* (which is a junior synonym of *N. striolella*) in Zagulyaev (1960) differ greatly from those of *N. piercella* in Pelham-Clinton (1985). According to these authors, *N. striolella* occurs in the Russian Far East and Japan, while *N. piercella* is found in Britain and continental Europe. Accordingly, Robinson (2009) recommends keeping the two species separate until material from across the continent can be compared. Recently, Sakai (2013) and Nasu & Sato (2016), based on the structure of the male and female genitalia of Japanese specimens of possible *N. striolella* and *N. piercella*, conclude that these two species are distinctly different. Therefore, this paper treats *N. piercella* and *N. striolella* as two species.

Table 1. Details of owl-nest contents and when collected. Contents of nests 1, 2, 4, 6 and 7 (bold-face) were collected twice on different dates. Half the contents of these nests was sampled the first time and the remaining contents the second time. Nest numbers correspond to those in Fig. 1.

Collection date	Nest No.	Nest content collected	
		Amount (l)	Proportion
7 June 2014	1	0.6	1/2
	2	1.6	1/2
	3	4.8	1
	4	1.8	1/2
17 August 2014	1	0.6	1
	5	2.7	1
	6	0.5	1/2
18 October 2014	7	2.5	1/2
	4	1.6	1
	7	2.5	1
6 December 2014	8	3.1	1
	2	1.6	1
	6	0.5	1
	9	3	1

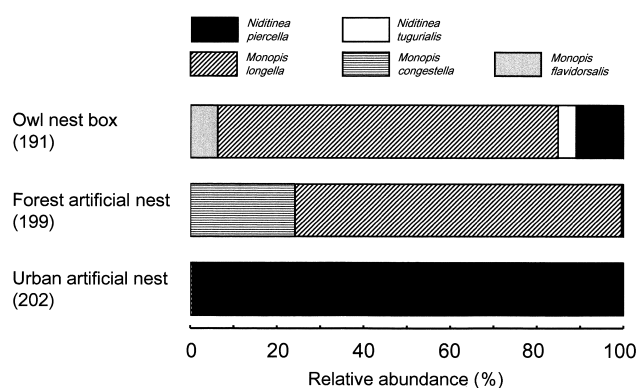


Fig. 2. Relative abundance of moths of Tineinae reared from the contents of owl nest boxes, forest artificial nests and urban artificial nests. Numbers in parentheses represent the total number of moths. Nine owl nest boxes were located in a forest covering a geographic region, while forest artificial nests and three urban artificial nests were located in a small forest and at an institute in an urban area, respectively (see Fig. 1).

Statistical analysis

To determine whether there are differences in the niches of the different species of moths we carried out a non-metric multidimensional scaling (NMDS) and cluster analysis using arcsine-transformed proportions of individual species in owl nest boxes, forest artificial nests and urban artificial nests. Both statistical procedures were based on a Bray-Curtis dissimilarity matrix. Niche differences were visualized using a NMDS ordination plot in 2D space. Moth species with similar niches were grouped by cluster analysis using Ward's linkage method. These procedures were performed using IBM SPSS ver. 25 (IBM 2017).

RESULTS

A total of 592 individuals of five species of Tineinae, i.e., *M. longella*, *M. congestella*, *M. flavidorsalis*, *N. tugurialis* and *N. piercella*, were obtained from owl nest boxes and artificial nests (Fig. 2). The composition of species in the owl nest boxes, forest artificial nests and urban artificial nests differed. The dominant species in owl nest boxes was *M. longella* (78.5%), followed by *N. piercella* (11.0%). The dominant species in forest artificial nests was also *M. longella* (75.4%), followed by *M. congestella* (24.1%), which was not found in owl nest boxes. *Monopis flavidorsalis* was recorded only from owl nest boxes (6.3%). Most moths in urban artificial nests were *N. piercella* (99.5%) with the other species *M. longella* (0.5%). *Niditinea piercella* was also common in owl nest boxes (11.0%), but not in forest artificial nests. *Niditinea tugurialis* was found in both owl nest boxes (4.2%) and forest artificial nests (0.5%), but not in urban artificial nests.

The NMDS ordination plot in 2D space (Fig. 3A) had a stress value of 0.0091. This near-to-zero value indicates that the plot is a reliable representation (Clarke, 1993). The diagram appears to show that the five species of Tineinae are classified into three groups. *Monopis longella* and *M. congestella* belong to the same group, while *M. flavidorsalis* and *N. tugurialis* are classed together. *Niditinea piercella* forms a separate group. This classification was confirmed by cluster analysis (Fig. 3B). The dendrogram

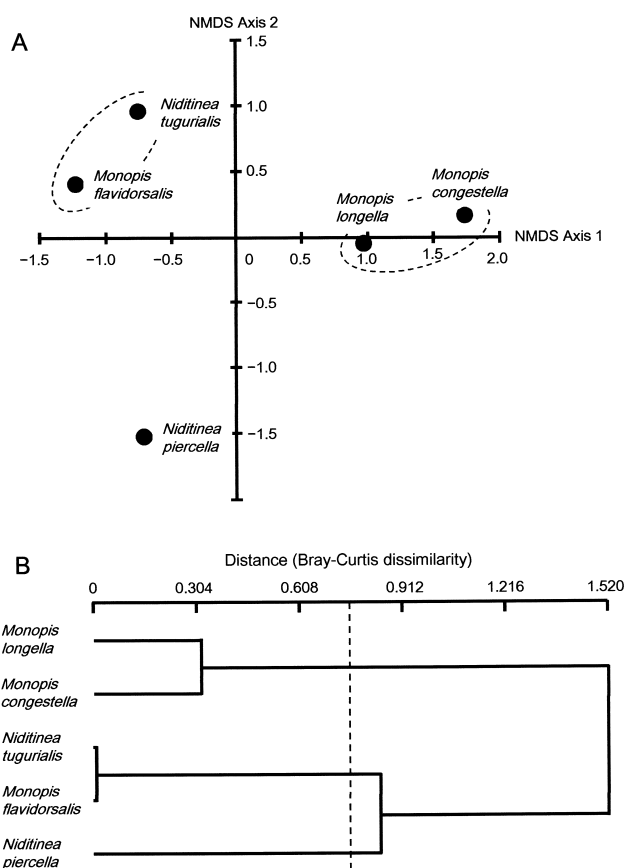


Fig. 3. NMDS ordination plot (A) and dendrogram obtained using cluster analysis (B) of the relative abundances of individual species in each nest (Fig. 2). The five species are classified into three groups: (1) *Monopis longella* and *M. congestella*, (2) *M. flavidorsalis* and *Niditinea tugurialis*, and (3) *N. piercella*. The vertical dotted line on panel B indicates the level of 50% dissimilarity.

and the NMDS diagram both put the five species into three groups.

No adult moths emerged from the contents collected from owl nest boxes or urban artificial nests in December. *Monopis longella* adults were reared from owl nest contents collected in June, August and October (Fig. 4A), and from forest artificial nests in August, October and December (Fig. 4B), which indicates two peaks in occurrence. *Monopis congestella* and *M. flavidorsalis* were recorded in forest artificial nests in August, October and December, and in owl nest boxes in June, August and October. Larvae of *M. congestella* that were collected in December grew into final stage and used silk to construct a cocoon of down, but all of them subsequently died from unknown causes. In comparison to the species of *Monopis*, *N. piercella* and *N. tugurialis* were present for short periods from June to August and June to October, respectively.

DISCUSSION

We found five species of Tineinae (Tineidae) that feed on keratin/chitin in the organic contents of owl nest boxes and artificial nests (i.e., duck down stuffed in mesh bags) placed in a forest and urban areas. These moths were assigned to one of three groups, which include: (1) *M. longella* and *M.*

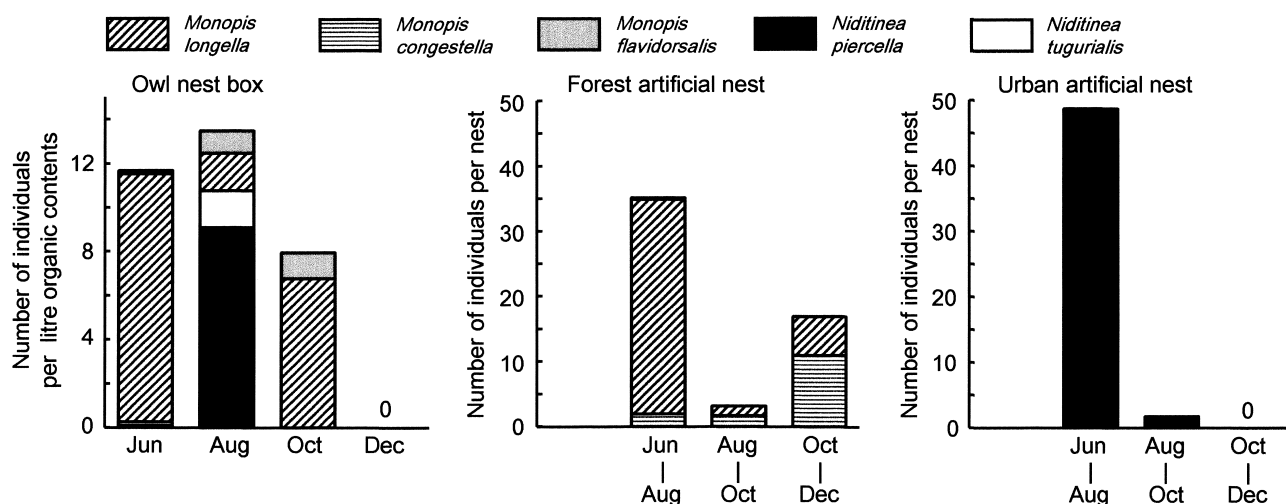


Fig. 4. Bimonthly composition of the species recorded in owl nest boxes, forest artificial nests and urban artificial nests. Abundances of moths are expressed in terms of the number of individuals per litre of the organic content of a nest or per artificial nest.

congestella, (2) *M. flavidorsalis* and *N. tigurialis*, and (3) *N. piercella* (Fig. 3). However, unlike *M. longella*, most *M. congestella* were found in forest artificial nests, which is not reflected in the above three-group classification.

Robinson (2004) suggests that the type of nest and food resource are important in determining niche separation in keratin/chitin feeding moths and defines four types of nests: damp concealed, dry concealed, damp exposed and dry exposed. Based on his definitions, owl nest boxes in the present study are classed as damp exposed, because the top is open and drainage is poor, so the organic contents in the box are wet. Hence, these nest boxes are unlike natural owl nests, which are usually dry and concealed in cavities in tree trunks. In contrast, mesh bags filled with down to imitate bird nests are classed as dry exposed, because the bags were hung in trees or in the eaves of a building, so the down remained dry although left outdoors for two months. Robinson (2004) describes the food sources of keratin/chitin feeding larvae as either compact or loose. The former includes carnivore droppings, raptor pellets and guano, while the latter mainly comprises hair, fur and feathers. In this study, the contents of owl nest boxes are classed as a compact resource, while those in the artificial bird nests are classed as a loose resource.

Based on Robinson's (2004) definitions together with habitats (forest and urban) three groups of Tineinae moths may be characterized as follows: (1) *M. longella* and *M. congestella* inhabiting forests, (2) *M. flavidorsalis* and *N. tigurialis* exploiting damp exposed nests containing compact sources of food in forest, and (3) *N. piercella* mainly using dry exposed nests containing loose resources in urban areas. There may be doubts about the differences in niches of these moths, because the forest and urban artificial nests were in one forest and one urban area, respectively, whereas the owl nest boxes were spread across a geographical region (Fig. 1). Nevertheless, the urban site is regarded as typical because it is 400 m from the nearest green park and little affected by semi-natural environments. Furthermore, the forest where the owl nest boxes

were deployed is located in a wide stretch of hills covered by secondary deciduous forest dominated by oak, *Quercus serrata*. Hence, even if artificial nests had been set at other sites in the hills as the owl nest boxes were, some species might have been added, but the dominant species might have been little changed. In fact, *N. striolella* is the only Tineinae species recorded from owl nests in Japan, but was not recorded in the present study; in addition, this species is recorded only infrequently (Nasu et al., 2012b). Consequently, the differences in the niches of the five species of Tineinae seem acceptable, albeit insufficiently supported. Therefore, we compare the nature of the niches of these moths reported here with that reported in other studies.

In Japan, Nasu et al. (2007a, 2008b, 2012a, c) report that many more *M. longella* than *M. congestella* emerge from the organic contents of Ural owl nests (and concealed and open nest boxes) and of the nest boxes of the varied tit (*Sittiparus varius* Temminck & Schlegel). More *M. longella* than *M. congestella* are usually recorded from nest boxes of the Japanese tit (*Parus minor* Temminck & Schlegel, mis-described as *P. major* L.) and nests of Styan's grasshopper-warbler (*Locustella pleskei* Taczanowski) (Nasu et al., 2007b, 2012c). *Sittiparus varius* and *P. minor* nest boxes are dry and concealed, whereas those of *L. pleskei* are dry and exposed. These passerines are insectivorous and their nests contain faeces, fur and feathers. All these nests were located in secondary forests. In Korea, Lee et al. (2016) reared as many *M. congestella* as *M. longella* from the contents of mesh bags containing feathers, pellets and faeces of a raptor in a forest. In addition, Nasu et al. (2007b, 2012b; Y. Nasu & S. Murahama, unpubl. data) reared *M. longella*, but not *M. congestella*, from pellets of the common buzzard (*Buteo buteo* (L.)), sparrowhawk (*Accipiter nisus* (L.)) and common kestrel (*Falco tinnunculus* L.) lying on the ground, which indicates that *M. longella* prefers more compact sources of keratin/chitin than *M. congestella*. Combining these and our results, we conclude that (1) both *M. longella* and *M. congestella* are forest inhabitants, (2) *M. longella* has a larger niche breadth,

exploiting damp and dry concealed nests and dry exposed nests and consuming both compact and loose sources of food and (3) *M. congestella* has a smaller niche breadth, exploiting dry concealed and exposed nests and loose sources of food. However, this conclusion is partly inconsistent with Robinson's (2004) classification as he considers *M. longella* to be a damp-exposed nest exploiter. This inconsistency is possibly due to small sample size.

Monopis flavidorsalis and *N. tugurialis* [= *baryspilas*] are recorded from the pellets of common buzzards and sparrow hawk lying on the ground (Nasu et al., 2007b, 2012b). Taking our results into consideration, these two species are likely to prefer compact sources of food regardless of nest type. In addition, *N. tugurialis* is not only recorded from Ural owl nests (Nasu et al., 2007a, b, 2012a) but also the dry concealed nests of brown hawk-owl (*Ninox scutulata* (Raffles)) (Nasu et al., 2012a), Japanese tit nest boxes (Nasu et al., 2008b; Nasu & Saito 2008), varied tit nest boxes (Nasu et al., 2008b), damp exposed nests of the Oriental stork (*Ciconia boyciana* Swinhoe) (Nasu et al., 2010) and dry concealed nest boxes of the Oriental dollar bird (*Eurystomus orientalis* L.) (Nasu et al., 2012c). Moreover, adults and larvae of *N. tugurialis* are recorded from guano of the greater horseshoe bat (*Rhinolophus ferrumequinum* (Schreber)) (Nasu et al., 2016). These records might indicate that this species uses a variety of types of nest. However, specimens identified as *N. tugurialis* in studies before 2012 probably include *N. piercella*, because prior to that date genitalia were not used to distinguish between these morphologically very similar species (Nasu & Sato, 2016). This prevents a more rigorous assessment of the types of nests *N. tugurialis* tends to exploit. According to Robinson (2004), *N. tugurialis* exploits both damp-exposed and dry-exposed nests. If so, the niches of *N. tugurialis* and *M. flavidorsalis* might be different.

Our results show that *N. piercella* has a very different niche from the remaining four species, depending primarily on dry exposed nests containing loose sources of food in urban areas. Nevertheless, it is puzzling that no *N. piercella* adults emerged from forest artificial nests despite the fact that this species inhabits forests and exploits owl nest boxes (Fig. 2). This might be due to the artificial nests only sampling a small area of forest. Contrary to our results, Robinson (2004, 2009) considers *N. piercella* to be an exploiter of concealed-nests based on his and other studies (Jalava, 1980; Pelham-Clinton, 1985; Robinson & Nielsen, 1993; Robinson, 2004). Results of recent studies of tawny owl (*Strix aluco* L.) nests in Poland (Jaworski et al., 2012) and concealed nests of passerines in mid-Wales, UK (Boyes & Lewis, 2019) support his proposal. However, specimens identified as *N. striolella* are probably *N. piercella* as mentioned above. In Japan, *N. striolella* is neither frequent nor dominant in owl nests (Nasu et al., 2012a), but is recorded occasionally in Oriental dollar bird nests (Nasu et al., 2012c). Another problem is that *N. piercella* was once confused with *N. tugurialis* in Japan as mentioned above (Nasu & Sato, 2016). To properly define

the niche of *N. piercella* we must collect further data and identify specimens more carefully.

Based on larval occurrence over more than three months, the five species of Tineinae in the present study are likely to be multivoltine. For *M. longella*, the two peaks in the year in larval occurrence (Fig. 4) probably indicate two generations. *Monopis longella* and *M. congestella* are believed to overwinter in the larval stage, because the larvae recorded in owl nest boxes and artificial bird nests in October and/or December developed into mature larvae or adults by May of the next year under semi-natural conditions. Overwintering of *M. longella*, *M. congestella* and *M. flavidorsalis* in the larval stage is reported by Nasu et al. (2007b, 2012b). Nevertheless, no adults emerged from organic contents collected from owl nest boxes in December (Fig. 4). One possible reason is that keratin/chitin resources had been mostly consumed or decomposed by that time. If so, the result might indicate that there is intense competition for food among larvae in owl nests. Although we did not record the overwintering stage of *N. piercella* and *N. tugurialis*, other studies report overwintering in the larval stage (Nasu et al., 2012c; Sakai, 2013).

Monopis congestella is known to be larviparous (Robinson, 1988, 2004; Nasu et al., 2008a). Females of *M. congestella* lay fully-developed first instar larvae, instead of laying eggs. Although larviparity is rare in Lepidoptera (Hinton, 1981; Heppner, 2009), it often occurs in *Monopis*; 12 of 90 species of *Monopis* are larviparous (Xiao & Li, 2006). Robinson (2004) presents two hypotheses for the evolution of larviparity in *Monopis*: (1) high mortality of eggs and newly-hatched larvae in bird nests due to predation by mites, and (2) females have difficulty finding more than one oviposition site or bird's nest. However, these hypotheses do not explain why the majority of *Monopis* species are oviparous. In *M. congestella*, the evolution of larviparity might be related to the main food source being feathers. The quantity of feathers in bird nests is usually small, so larvae that can pre-empt an eventual shortage of food have an advantage. To corroborate this hypothesis, we need to compare the feeding habits of larviparous and oviparous *Monopis*.

In conclusion, this study indicates that Tineinae moths associated with bird nests differ in their niches in terms of type of nest (concealed or exposed), source of keratin/chitin (raptor pellets or feathers) and habitat (forest or urban area). However, some problems remain unresolved. First, we cannot explain why *N. piercella* did not exploit the exposed nests in a forest where it lives even though it exploits such nests. Second, the degree to which Tineinae larvae compete for sources of keratin/chitin in owl nests is unclear. Third, the factors contributing to the evolution of larviparity in *Monopis* are unclear. We will address these problems in the near future.

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