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Effects of experimental modification of temperature and humidity on abundance of dermestid beetles in nests of blue tits

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Abstract

Many factors may affect the diversity and abundance of arthropods in their natural habitats including changes in temperature and humidity. Sometimes, large arthropods remain undetected in unsuspected habitats such as bird nests. Here, we explore the effects of an experiment modifying temperature and relative humidity inside the nest of a troglodyte bird species, the blue tit, *Cyanistes caeruleus* (L.) (Passeriformes: Paridae), on the abundance of dermestid beetles (Coleoptera: Dermestidae) inhabiting the nests. Ten taxa were identified, six at the species level and four—based on larval stages—at the genus level. Most of the dermestids found in the larval stage were nidicolous dermestids of the genus *Anthrenus*. Specimens of necrobiont dermestids (those that feed on carcasses in both the larval and adult stages) were found in lower numbers, and almost always in adult stages. The abundance of dermestid larvae found in blue tit nests where the temperature or the humidity were experimentally increased was significantly higher than in the control nests. In addition, adult necrobiont dermestids of genus *Dermestes* appeared more frequently in those nests where corpses of blue tit nestlings were found.

KEYWORDS

Anthrenus, Aves, Coleoptera, *Cyanistes caeruleus*, *Dermestes*, Dermestidae, Mediterranean region, nest fauna, nest microclimate, nest-boxes, passerine birds

INTRODUCTION

Nests of cavity-nesting bird species represent a particularly suitable habitat for the development of several arthropods (Masan & Kristofik, 1995; Merkl et al., 2004; Szabó et al., 2002). Nesting cavities provide a partially isolated space from the outside environment, offering conditions of relatively constant temperature and humidity. The microclimate-generated inside nest cavities is an important factor in the determination of the arthropod species inhabiting the nest (Hanzelka et al., 2023; McComb & Noble, 1981). For example, temperature and humidity are two closely correlated parameters, which have a direct effect on the development of ectoparasites in bird nests (Cantarero, López-Arrabé, Rodríguez-García, et al., 2013; Merino & Potti, 1996). It is known that the presence of fleas increases with relative humidity up to a certain level in passerine nests (Heeb et al., 2000). Furthermore, experimental increases in temperature in nests of blue tit, *Cyanistes caeruleus* (L.) (Passeriformes: Paridae), have significant detrimental effects on the development of parasitic blowfly pupae, *Protocalliphora azurea* (Fallén), and dermanyssid mites (Castaño-Vázquez et al., 2021). In general, temperature affects most aspects of the biology of insects including metabolic rates, the limits of physiological function, developmental times, and behaviour and population survival (Lee, 1991; Wilches et al., 2016).

Nesting sites for birds constitute micro-environments very likely to be colonized by arthropod fauna, mainly parasites, predators and commensals. Nest-dwelling parasites have been thoroughly studied due to their detrimental effects on birds (Cantarero, López-Arrabé, Redondo, et al., 2013; Loye & Zuk, 1991; Merino, 2010; Merino & Potti, 1995). However, the importance of other nest-dwelling arthropod fauna, which may represent a valuable component of biodiversity, is largely unknown (Burtt et al., 1991; Møller, 2008; Rózsa, 1992). In many cases, the lack of information about the diversity of species in bird nests and their interactions is the main impediment to understand the relevance of the ecological processes taking place there (Møller et al., 2013; Salido et al., 2021).

The composition of bird nests includes, among other materials such as moss, leaves and twigs, nest detritus and bird droppings. This unusual composition makes bird nests specialized habitats and, as a consequence, attracts nidicolous arthropods (i.e., invertebrates that colonize bird nests and complete all or part of their life cycle in these habitats). As nests are patchy habitats, nidicolous fauna specialized in exploiting these resources are prone to local extinction, as nests are not self-sustaining habitats (Beaver, 1977). Nidicolous fauna includes detritivorous species (feeding on decaying organic matter), necrophagous species (feeding on carcasses or carrion) and carnivorous species (preying on other invertebrates such as dipteran larvae or pupae) (Cosandey et al., 2021; Nordberg, 1936). Although there are a few studies describing this nidicolous fauna (Cosandey et al., 2021; Hanzelka et al., 2023; Hicks, 1953; Jurík & Šustek, 1978; Krištofík et al., 2009; Lynch et al., 2020; Woodroffe, 1953) information about the factors that determine the distribution and diversity of these species is extremely limited. Coleopteran species is one of the most frequent groups of nidicolous fauna in bird nests. These species keep the nest clean by feeding on carcasses and decomposing remains, and also keep nest-dwelling parasite populations under control (Cosandey et al., 2021).

A total of 1813 species of dermestids from 71 genera have been described (Háva, 2023), being one of the best studied nidicolous arthropods that play an important role in the decomposition of carrion and remains located in host nests. They are small beetles (ranging in size from 1 to 12 mm) considered xerophilic scavengers due to their ability to feed on animal matter with low water content (15%–10%). They are very cosmopolitan animals and may be found in hymenopteran and bird nests, carcasses or stored products and textiles. All the larvae of this group are necrophagous except for the subfamily Orphilinae, although they are not all equally voracious and do not feed on the same type of carcasses. Dermestids in the adult stage may be necrophagous (i.e., necrobionts) or antophagous (i.e., nidicolous; although adults feed on flowers) (Zhantiev, 2009). Some species, such as those from the Anthrenini tribe (Megatominae: Anthrenini) and the Attageninae subfamily are some of the few animals able to feed on keratin. All of these characteristics make dermestids an ideal group to exploit harsh terrestrial environments, including bird nests (Kiselyova & Mchugh, 2006; Motyka et al., 2022; Rebolledo et al., 1994).

Studies on this group of beetles focus on their phylogeny and taxonomy (Zeng et al., 2021; Zhou et al., 2022), on their role as important domestic and storage pests (Arthur et al., 2018; Athanassiou et al., 2019) and on their forensic importance (Magni et al., 2015; Martín-Vega et al., 2017). Studies carried out on captive-bred specimens of the genus *Dermestes* (Zanetti et al., 2016) have revealed that the life cycle of dermestids is highly variable. For example, depending on the species and factors such as temperature, food, and stress, larvae undergo between three and 30 instars (Esperk et al., 2007). However, to our knowledge, there are no previous studies on the diversity and drivers of the distribution of these beetles in bird nests.

In the current scenario of climate change, it is interesting to know how alterations in temperature and humidity affect the abundance of various arthropods (Jaworski & Hilszczański, 2013; Pureswaran et al., 2018; Robinet & Roques, 2010). Thus, the goal of this study was to determine which dermestid species inhabit blue tit nests and explore the factors that influence their local abundance. We do so by taking an experimental approach to artificially manipulate blue tit nest temperature and humidity.

MATERIALS AND METHODS

Study area

The study area is located in a Pyrenean oak (*Quercus pyrenaica* Willd) deciduous forest in Valsaín (Segovia, central Spain; 40°53′ N, 4°01′ W, 1200 m a.s.l.). This geographical area is characterized by a sub-Mediterranean climate (warm temperate), with a hot and dry summer climate (mean July temperature: 18.3°C), whereas winter climatology is cool (mean January temperature: 1.2°C) (Pardos et al., 2017). The average temperature during the study period (13 April to 15 June 2021) was 14.3°C, and total precipitation was 99.6 mm (AEMET, 2021).

Blue tit is a small passerine bird species readily accepting nest-boxes to breed. Nest-boxes in our study area are made of pinewood and measure 17.5 cm high, 11.7 cm wide and 12.5 cm deep (about 2500 cm^3 inside). Blue tits build their nests mainly from moss. The boxes were hung from branches between 3 and 5 m high and were periodically checked to determine specific reproductive parameters of the birds such as laying date, clutch and brood size and hatching date (Merino et al., 2000). The height at which each nest-box was located was measured with a laser meter (Laser Distance Meter DT50; DTAPE, Guangdong, China) from the ground to the base of the nest box.

Experimental protocol

The nests used in this study were the same as previously used for a study on the effects of experimental alteration of temperature and humidity on nest-dwelling ectoparasites and their bird hosts (García-del Río et al., 2024). Thus, the experimental protocol and the results of the experimental manipulation have been described elsewhere (García-del Río et al., 2024). In brief, nest trios with a similar number of nestlings (± 1 nestling) and hatching date (± 1 day) were selected and assigned to different treatments: control nests (hereafter, CTR), nests that were artificially heated (H) and nests that were artificially humidified (HUM). A total of 48 nest-boxes (16 CTR, 16 H, and 16 HUM) were used. However, one HUM-nest was lost due to predation during the experiment. As a result, the overall sample size was reduced to 47 nests. On Day 3 of nestling age, each nest was supplied with a temperature/humidity sensor that was placed inside each box (Thermochron DS1923; 6 × 17 mm, temperature range: −20 to +85°C; resolution 0.0625°C; humidity range: 0%–100% with a resolution of 0.04%; Maxim IC, USA). The same day, H and HUM-nests were supplied with a heat mat (7 × 7 cm, 5 V/3.5 W; Thermo Flächenheizungs, Rohrbach, Germany) placed on the floor of the nest-box and separated from the nest material with a metal grid, connected through a cord to 9-V power banks. We also placed a heat mat on the HUM-nests to avoid the potential effect that increased humidity can have by decreasing temperature, because in previous studies, the experimental manipulation of temperature showed an inverse relationship with humidity (Castaño-Vázquez et al., 2018, 2021, 2022). In HUM treatments along with the heat mat, sponges moistened with water and moisture-preserving gel (Aquaplant Complet Gel—FLOWER, composed of water, microcellulose and monopotassium phosphate) were placed. A metal grid and a cord were also installed at CTR-nests, but heat mats and power banks were not installed. During the following days of nestling age, HUM-nests were periodically sprayed with water. On Day 17 of nestling age, batteries were removed and nest-box entrance orientation, which remained constant throughout the study period, was measured with a digital compass. Average temperature and relative humidity recorded between Days 4 and 16 of nestling age were calculated to test the effect of treatment on those variables. Lastly, once nestlings flew on Day 20 or 21 of nestling age, nests were collected in sealed plastic bags conveniently identified. For more details, see García-del Río et al. (2024).

Nests were stored in a freezer at −20°C for about 2 months and then transported to a cold chamber (4°C) in the facilities of the National Museum of Natural Sciences (Madrid, Spain) until inspection. The dead dermestids contained in the dry plant material of the nest were collected individually using entomological forceps by dismantling the nest gradually. Using a stereo microscope (SZX7; Olympus, Tokyo, Japan), we identified the specimens morphologically according to criteria from the specialized literature (Beal, 1959, 1998; Háva, 2004; Peacock, 1993) and subsequently confirmed by Jiří Háva (a dermestid taxonomic expert). The specimens were then classified according to their stage of development (larva or adult) and to their ecotrophic group (necrobionts or nidicolous) (Zhantiev, 2009).

Statistical analysis

The effect of experimental treatment on temperature and relative humidity inside nests was tested using a univariate ANOVA. Tukey's honestly significant difference post hoc tests with multiple comparisons based on the observed means were performed to look for significant differences between treatments (CTR, H and HUM). Before the analysis, the total relative humidity was transformed to the inverse of itself (1/relative humidity), to comply to normality assumptions in order to use parametric statistics. Temperature and relative humidity data consisted of daily averages of temperature and humidity for each nest (24 h). Averages from Days 4 to 16 post-hatching of each nest were calculated and used as values of temperature and total relative humidity (García-del Río et al., 2024). Orientation of nest-boxes was measured in sexagesimal degrees system. Orientation was simplified to a categorical variable with eight levels (N, NE, E, SE, S, SW, W and NW) to explore the orientation of the nest-boxes studied. In addition, the height of each of the 47 nest-boxes were also calculated.

Dermestids in blue tit nests followed a geometric distribution (a particular type of negative binomial distribution). Thus, we used generalized linear models (GzLM) with a negative binomial distribution and a logarithmic link function to analyse the dermestid abundance data. Dermestids were classified in four variables (necrobiont larvae, nidicolous larvae, necrobiont adults and nidicolous adults). However, the abundance of necrobiont larvae and nidicolous adults was insufficient to run the models with these variables. Therefore, we decided to run models with the following variables: nidicolous larvae, necrobiont adults, total larvae and total adults. Each of these four variables was used as dependent variable. Temperature, relative humidity and their interaction were introduced at each model as independent covariables as well as the height and orientation of the nest-box. In addition, the presence of dead nestlings and experimental treatment were included as factors. By including both experimental treatment and the average temperature and relative humidity variables for each nest in the same model, we explored whether the potential effect on dermestid abundance is due to the experimental treatment or to the gradient in temperature or relative humidity generated inside nest-boxes.

Each model was tested using an Omnibus test to assess the significance of the overall model by calculating whether the explained variance is significantly higher than the unexplained variance. The Omnibus test used to compare the current model against the null (in this case, intercept) was a likelihood-ratio χ^2 test. Only when this test was significant, the effect of significant independent variables was explored. In addition, Wald χ^2 test was used as a post hoc test to compare differences among factor categories with more than two levels. Pearson's post was used to compare differences among factor categories with two levels.

All graphs and statistical analyses were performed with Microsoft Excel for Microsoft 365 MSO (v.2211 build 16.0.15831.20098) 64-bit, STATISTICA v.7.0 (StatSoft 1984–2004) and IBM-SPSS Statistics for Windows v.25.0 (IBM, Armonk, NY, USA).

RESULTS

Experimental treatment—Modification of microclimatic variables

As described elsewhere the treatment generated significant differences between the experimental groups (García-del Río et al., 2024). Artificially heated nests (H-nest) had a significant higher average temperature than control nests (1.86°C higher), whereas there were no significant differences in temperature between H- and HUM-nest or between HUM- and CTR-nests (García-del Río et al., 2024). Relative humidity was significantly higher in HUM-nest than in CTR- and H-nest (15.7% and 17.5%, respectively), whereas there were no significant differences in humidity between H- and CTR-nests (García-del Río et al., 2024).

Height and orientation

The nest-boxes studied showed seven levels of orientation (NE, E, SE, S, SW, W and NW). Surprisingly, no nest-boxes had N orientation. The most frequent orientation was SE and the mean (±SD) height of all nest-boxes was 3.85 ± 0.50 m (range: 2.89–5.36). The proportion of nest-boxes and the average height for each orientation are shown in Table 1.

Dermestid taxa and abundance

Dermestid larvae were found in 42 of 47 nests examined, whereas adult dermestids were found in 15 of 47 nests. More specifically, nidicolous adults were found in four nests and nidicolous larvae in 39 nests; necrobiont larvae were found in only four nests and necrobiont adults in 12 nests. Taxa considered as nidicolous were those of genera *Anthrenus*, *Attagenus* and *Trogoderma*, as well as the species *Trinodes hirtus* Fabricius. On the other hand, necrobiont taxa were composed of specimens of the genus *Dermestes*. Many of the larvae, given the impossibility of morphological identification to species, were identified at the genus level. The list of specimens found in the nests is shown in Table 2. Some of the specimens found are shown in Figure 1. For more information, see Table S1.

TABLE 1 Proportion of blue tit nest boxes oriented at the various directions and their estimated mean (±SD) height (m) during the study.

Orientation	Number (%)	Height (m)
NE	9 (19.14)	3.488 ± 0.155
E	1 (2.12)	3.730 ± 0.466
SE	16 (34.0)	4.032 ± 0.117
S	3 (6.40)	4.357 ± 0.269
SW	9 (19.14)	3.761 ± 0.155
W	2 (4.30)	4.155 ± 0.330
NW	7 (14.9)	3.769 ± 0.176
N	0	na

Distribution of dermestid larvae and adults

A total of 404 dermestid larvae (91.6%) and 37 adults (8.4%) were found in 42 of the 47 blue tit nests studied. Nestling blue tits were found dead in six of the 47 nests studied. Although all nestlings died in nests with altered temperature and humidity (H and HUM), the presence of dead nestlings does not differ between treatments (Pearson $\chi^2 = 3.561$, df = 2, $p = 0.17$) nor even comparing control nest versus nests with altered temperature and humidity (H and HUM nests vs. CTR nests: Pearson $\chi^2 = 3.550$, df = 1, $p = 0.060$). Adult necrobiont dermestids were found in four of those six nests, representing more than 78% of adult necrobionts dermestids found in this study (26 out of 33; i.e., 78.8%). There were no adult nidicolous or necrobiont larvae in those six nests; however, nidicolous larvae were found in five of the six nests where dead blue tit nestlings were found (Table S1). The abundance and percentage represented by each taxon according to their stage of development is shown in Table 2.

The experimental treatment was the only explanatory variable in the model performed for total dermestid larvae ($F_{2,38} = 4.83$, $p = 0.013$; Table 3). The abundance of total larvae was higher in H- and HUM-nests than in CTR-nests (Wald $\chi^2 = 11.54$ and 12.22, respectively, both df = 1, $p < 0.001$), whereas there were no differences between H- and HUM-nests (Wald $\chi^2 = 0.02$, df = 1, $p = 0.88$). Experimental treatment was also the only explanatory variable in the model

TABLE 2 Number of dermestid species found in blue tit nests (abundance) and the percentage of the total number of individuals for each stage (larval or adult). Specimens have been classified based on their ecotrophic group and their stage of development (larva or adult).

Stage	Genus/species	Ecotrophic group	Abundance	% (within stage)
Larval	*Anthrenus*	Nidicolous	392	97.02
	Attagenus	Nidicolous	4	0.99
	Dermestes	Necrobiont	5	1.24
	Trinodes hirtus Fabricius	Nidicolous	1	0.25
	Trogoderma	Nidicolous	2	0.5
	Total		404	100
Adult	*Anthrenus angustefasciatus* Ganglbauer	Nidicolous	3	8.1
	Anthrenus isabellinus Küster	Nidicolous	1	2.7
	Dermestes frischii Kugelann	Necrobiont	1	2.7
	Dermestes peruvianus Castelnau	Necrobiont	1	2.7
	Dermestes undulatus Brahm	Necrobiont	31	83.8
	Total		37	100

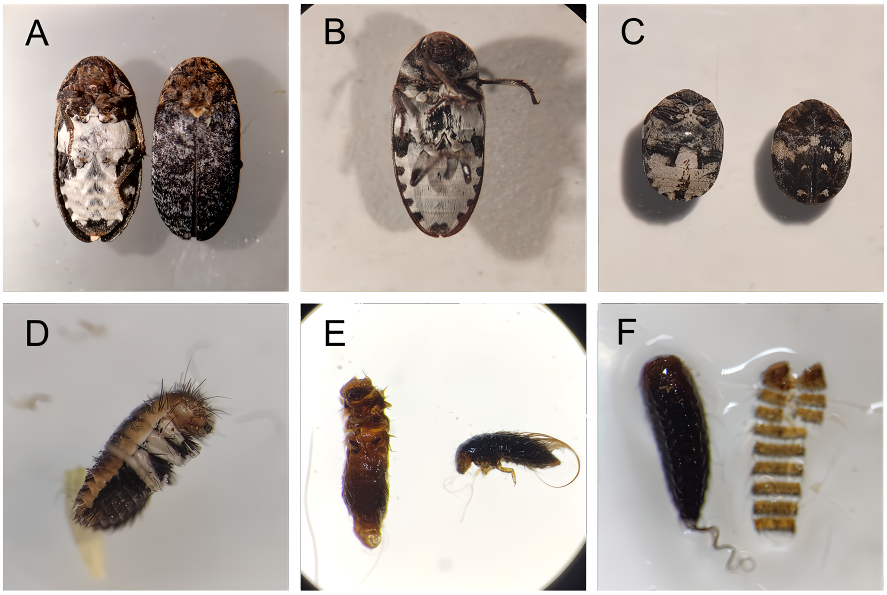

FIGURE 1 Some dermestids specimens found in blue tit nest: (A) *Dermestes undulatus*; (B) *Dermestes frischii*; (C) *Anthrenus angustefasciatus*; (D) *Anthrenus* sp. larva; (E) *Trogoderma* sp. (left) and *Trinodes hirtus* (right) larvae; (F) *Attagenus* sp. larva (left) and exuvia (right).

TABLE 3 Tests of model effects (generalized linear model) for the dependent variable 'total dermestid larvae'. Experimental treatment and dead nestlings were considered as independent factorial variables; orientation and height of the nest-box, temperature, relative humidity, and their interaction were introduced at each model as independent covariables.

Independent variables	*F*	df	*p*
Experimental treatment	4.83	2,38	0.013
Dead nestlings	3.46	1,38	0.070
Orientation (degrees)	0.36	1,38	0.55
Height	0.005	1,38	0.95
Temperature	0.98	1,38	0.33
Relative humidity	0.49	1,38	0.50
Temperature × relative humidity	0.62	1,38	0.44

Note: Model Omnibus test: likelihood-ratio $\chi^2 = 19.65$, df = 8, $p = 0.012$.

for nidicolous larvae abundance ($F_{2,38} = 5.18$, $p = 0.010$; Table 4, Figure 2). The abundance of nidicolous larvae was higher in H- and HUM-nests than in CTR-nests (Wald $\chi^2 = 11.94$ and 12.72, respectively, both df = 1, $p < 0.001$) whereas there were no differences between H- and HUM-nests (Wald $\chi^2 = 0.03$, df = 1, $p = 0.87$).

Only the presence of dead blue tit nestlings had a significant effect on the abundance of total adult dermestids ($F_{1,38} = 7.49$, $p = 0.009$; Table 5) as well as on the abundance of adult necrobiont dermestids ($F_{1,38} = 11.83$, $p = 0.001$; Table 6). In both cases, the presence of adult dermestids was higher in nests with dead blue tit nestlings. This result is maintained even when an influential point (a nest with 17 specimens compared with a mean value of 4 for the rest of nests) is excluded from the analyses (*n* = 46) (Model Omnibus test: likelihood-ratio $\chi^2 = 17.61$, df = 8, $p = 0.024$; dead nestlings: $F_{1,37} = 11.16$, $p = 0.002$).

TABLE 4 Tests of model effects (generalized linear model) for the dependent variable 'nidicolous dermestid larvae'. Experimental treatment and dead nestlings were considered as independent factorial variables; orientation and height of the nest-box, temperature, relative humidity, and their interaction were introduced at each model as independent covariables.

Independent variables	*F*	df	*p*
Experimental treatment	5.18	2,38	0.010
Dead nestlings	3.42	1,38	0.072
Orientation (degrees)	0.45	1,38	0.50
Height	<0.001	1,38	0.99
Temperature	0.89	1,38	0.35
Relative humidity	0.41	1,38	0.52
Temperature × relative humidity	0.56	1,38	0.46

Note: Model Omnibus test: likelihood-ratio $\chi^2 = 20.38$, df = 8, $p = 0.009$.

TABLE 5 Tests of model effects (generalized linear model) for the dependent variable 'total adult dermestids'. Experimental treatment and dead nestlings were considered as independent factorial variables; orientation and height of the nest-box, temperature, relative humidity, and their interaction were introduced at each model as independent covariables.

Independent variables	*F*	df	*p*
Experimental treatment	0.73	2,38	0.49
Dead nestlings	7.49	1,38	0.009
Orientation (degrees)	0.12	1,38	0.73
Height	0.03	1,38	0.86
Temperature	0.13	1,38	0.71
Relative humidity	0.37	1,38	0.54
Temperature × relative humidity	0.30	1,38	0.59

Note: Model Omnibus test: likelihood-ratio $\chi^2 = 28.30$, df = 8, $p < 0.001$.

TABLE 6 Tests of model effects (generalized linear model) for the dependent variable 'adult necrobiont dermestids'. Experimental treatment and dead nestlings were considered as independent factorial variables; orientation and height of the nest-box, temperature, relative humidity and their interaction were introduced at each model as independent covariables.

Independent variables	*F*	df	*p*
Experimental treatment	1.32	2,38	0.28
Dead nestlings	11.83	1,38	0.001
Orientation (degrees)	0.17	1,38	0.68
Height	0.25	1,38	0.62
Temperature	1.10	1,38	0.30
Relative humidity	1.70	1,38	0.20
Temperature × relative humidity	1.42	1,38	0.24

Note: Model Omnibus test: likelihood-ratio $\chi^2 = 43.50$, df = 8, $p < 0.001$.

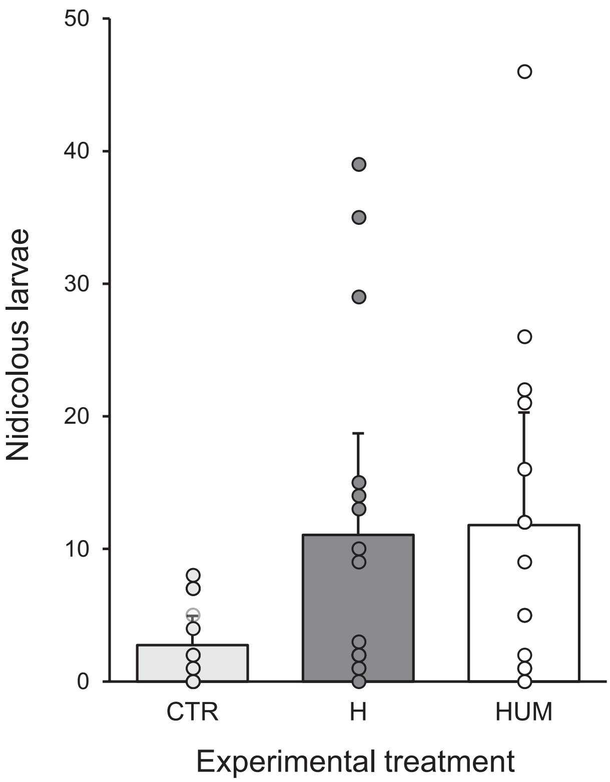

FIGURE 2 Mean (+SE) number of nidicolous dermestid larvae in each experimental treatment. The dots indicate individual larvae. CTR, control; H, heated; HUM, humidified.

DISCUSSION

In this study, we explore the effects of an experimental manipulation of the microclimatic variables (temperature and relative humidity) inside blue tit nest boxes on dermestid abundances. Our experiment generated a group of nests with higher temperature than controls (H-nests), a group of nests with higher humidity than the other groups (HUM-nests) and a control group with lower temperature than H-nests and lower relative humidity than HUM-nests (García-del Río et al., 2024). Both, temperature and relative humidity are two important variables for the survival of any insect (Gilbert & Raworth, 1996; Lee, 1991) and dermestids are no exception. Wilches et al. (2016) reviewed the optimal conditions for the development of different species of nidicolous and necrobionts dermestids. In general, optimal temperature values for larval development ranged from 25 to 35°C. Temperature values below 25°C decelerate the development of dermestids and modify the number of larval stages as shown for several dermestids: *Trogoderma versicolor* Creutzer (Hadaway, 1956), *Trogoderma granarium* Everts (Burges, 1959) and *Anthrenus coloratus* Reitter (Ansari, 2021). However, other nidicolous species, such as *Anthrenus verbasci* L., show optimal development at temperatures around 20°C (Blake, 1958).

The alteration of temperature and relative humidity inside nest-boxes had significant effects on the abundance of dermestids. Dermestid larvae, specifically nidicolous larvae, were the dominant group found in nests representing almost 99% of all larvae found. CTR-nests, where temperature and humidity were not altered, had fewer larvae than the H- and HUM-nests where an increase in temperature and humidity, respectively, was achieved. These results could be due to the important role of temperature on larval development (Bjørge et al., 2018; Buckley, 2022), but also imply a role of the increased relative humidity with respect to control nests on the development of dermestid larvae. In this respect, considerable previous evidence did not support that humidity was important in larval development, whereas other variables such as temperature and food availability were (Beal, 1998; Coombs, 1978; Rebolledo et al., 1994; Wilches et al., 2016). Previous studies with nidicolous dermestid species have shown that, under controlled laboratory conditions of fluctuating temperature and relative humidity, increasing temperature reduces incubation time, increases egg viability and reduces larval and pupal development time (up to an average maximum temperature value of 35°C; Ali et al., 2011; Ayappa et al., 1957; Burges & Cammell, 1964; Odeyemi & Hassana, 1993).

On the other hand, the importance of humidity differs considerably between the species studied. Many studies did not find that variation in humidity conditions affected larval development (Armes, 1990; Ayappa et al., 1957; Burges & Cammell, 1964). However, *Trogoderma* larvae prefer to occupy drier areas when exposed to humidity gradients (Yinon & Shulov, 1967). In larvae of necrobiont species, such as *Dermestes maculatus* DeGeer, the development period and number of larval stages increased when moisture conditions of the substrate increased (Ezenwaji & Obayi, 2004). However, for nidicolous larval species, extremely low humidity conditions prevented larval development (Blake, 1958); increasing relative humidity conditions reduced development time and the number of larval stages under laboratory conditions (Ali et al., 2011; Odeyemi & Hassana, 1993). Relative humidity also showed positive effects when adults of these species were studied, as they lived longer under conditions of high relative humidity (Ali et al., 2011; Burges & Cammell, 1964).

In addition, H- and HUM-nests differ significantly in humidity but not in temperature or abundance of dermestid larvae. Thus, we can conclude that both increase in humidity and temperature have positive effects on dermestid larvae abundance in comparison with conditions in CTR-nests but higher humidity does not have an additional effect on dermestid abundance in comparison with the effect of higher temperature of H-nests.

Necrobiont dermestids of the genus *Dermestes* was the largest group of adult Dermestidae in blue tit nests. Their distribution in nests was closely associated with the presence of nestling carcasses, being more frequent in those nests where a nestling died. Although the experimental alteration of temperature and humidity could affect the death of nestlings in the nests, the majority of dead nestlings had died later in the bird breeding period (nestlings of >10 days old) probably due to partial parental nest desertion. Even when we analysed the abundance of adult dermestids excluding an influential point, we found that the presence of dead nestlings remained a positive effect on adult dermestids. Anyway, the low numbers of adult dermestids detected in bird nests could be due to dispersal following their development.

Regarding the height and orientation of the nest boxes, these variables were shown to have no significant effect on dermestids abundance. Nest-boxes in our study area show a large range of different orientations without an apparent preference by the dermestids. The potential effect of cavity orientation on the environmental conditions inside the nest-boxes seems to be irrelevant for the colonization and later development of dermestids in the nests. Nest-boxes in our study are located at an average height of around 4 m but with relatively low variation among them and did not affect the presence of dermestids.

In this study, we have also revealed the dermestids diversity living inside nests of blue tits in a mountainous population in central Spain. Blue tit nests appear to be an important habitat for larvae of nidicolous dermestids, although it is necessary to know more on their presence in other bird nest species. In addition, they are also an occasional habitat for adult necrobiont dermestids. In this study, we noted dermestid species frequently found in bird nests. Two species of the subgenus *Anthrenus* sensu stricto were identified, *Anthrenus isabellinus* Küster and *Anthrenus angustefasciatus* Ganglbauer, which are usually found in bird nests (Foster & Holloway, 2015). Species of this subgenus are known to spend the winter diapause during the adult stage, awakening from lethargy in early spring when adults mate and reproduce. Females lay their eggs in bird nests and die soon after (Peacock, 1993; Zhantiev, 2009). Thus, we may expect that the *Anthrenus* larvae found, most of which certainly belong to *A. isabellinus* and *A. angustefasciatus*, hatched in blue tit nests from clutches laid at the beginning of the season by adult dermestids that subsequently died. That is, the four adult *Anthrenus* specimens collected could be adults that died in the nests shortly after laying their eggs. Species of the genera *Attagenus* and *Trogoderma* are also very common in bird nests (Zhantiev, 2009), and there are reports of *Attagenus* species feeding on *Protocalliphora* sp. blowfly pupae (Mason, 1936), a dipteran whose larvae are common hematophagous parasites of blue tit nestlings in our study area (Tomás et al., 2007). It was surprising to find *T. hirtus* in bird nests, because it is a species with a high level of specialization on inhabiting spider nests (Háva & Nardi, 2004). It is also known that *Dermestes undulatus* Brahm visits bird nests during the day in search of carcasses of small birds to feed on them (Veer et al., 1996; Zhantiev, 2009). The low occurrence of *Dermestes frischii* Kugelann in blue tit nests could be due to their preference for large carcasses (Martín-Vega et al., 2017). Finally, *Dermestes peruvianus* Castelnau is a species rarely recorded in bird nests, and only a few records mention its presence in these habitats (Ramachandran et al., 1997).

In conclusion, nest-dwelling dermestid larvae were positively affected by increases in temperature and in relative humidity, whereas the abundance of adult dermestids was associated with the presence of dead blue tit nestlings. The optimum developmental range for the larval species of *A. isabellinus* or *A. angustefasciatus* are unknown, as opposed to other species such as *A. verbasci*, which has been the model for in vitro studies of these nidicolous species for a long time (Blake, 1958, 1959; Nisimura & Numata, 2003). Based on those studies and our results, we may conclude that the larvae of nidicolous dermestids benefit from those nests where the average temperature throughout the breeding season is higher than the average temperature in their environment (i.e., that inside CTR-nests). Also, increased relative humidity inside nests in respect to unmanipulated nests (CTR-nests) had a positive effect on the abundance of dermestid larvae. Thus, the role of humidity on this group of beetles should be explored in depth in future studies. In addition, the study of the diversity and abundance of dermestids in nests from different bird species and populations will allow to obtain a better understanding of these specialized habitats for dermestid species. Nest-boxes are probably an important substitute for natural cavities providing a good habitat for dermestid species, covering all the trophic requirements they need. Therefore, small microclimatic changes inside nest-boxes are decisive for dermestids distribution and abundance (Pincebourde & Woods, 2020).

AUTHOR CONTRIBUTIONS

Javier García-Velasco: Conceptualization (equal); data curation (lead); formal analysis (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Jiří Háva:** Data curation (equal); validation (equal); writing – review and editing (equal). **Marina García-del Río:** Conceptualization (equal); methodology (equal); writing – review and editing (equal). **Alejandro Cantarero:** Methodology (equal); writing – review and editing (equal). **Francisco Castaño-Vázquez:** Methodology (equal); writing – review and editing (equal). **Yago Merino:** Methodology (equal); writing – review and editing (equal). **Jesús Selfa:** Project administration (supporting); writing – original draft (supporting); writing – review and editing (equal). **Santiago Merino:** Conceptualization (equal); funding acquisition (lead); methodology (equal); project administration (equal); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data presented in this study are available on request from the corresponding author.

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REFERENCES

AEMET. (2021) OpenData—Agencia Estatal de Meteorología. Gobierno de España. Available from: www.aemet.es/es/datos_abiertos/AEMET_OpenData [Accessed 5th September 2021].

Ali, M.F., Mashaly, A.M.A., Mohammed, A.A. & Mohammed, A.E.M.M. (2011) Effect of temperature and humidity on the biology of *Attagenus fasciatus* (Thunberg) (Coleoptera: Dermestidae). *Journal of Stored Products Research*, *47*(1), 25–31.

Ansari, M.F. (2021) Biology of *Anthrenus coloratus* Reitter (Dermestidae: Coleoptera) on four different food stuffs of animal origin under laboratory conditions. *Journal of Entomology and Zoology Studies*, *9*(3), 228–230.

Armes, N.J. (1990) The biology of *Anthrenus sarnicus* Mroczkowski (Coleoptera: Dermestidae): I. Egg and larval development. *Journal of Stored Products Research*, *26*(1), 11–22.

Arthur, F.H., Ghimire, M.N., Myers, S.W. & Phillips, T.W. (2018) Evaluation of pyrethroid insecticides and insect growth regulators applied to different surfaces for control of *Trogoderma granarium* (Coleoptera: Dermestidae) the khapra beetle. *Journal of Economic Entomology*, *111*(2), 612–619.

Athanassiou, C.G., Phillips, T.W. & Wakil, W. (2019) Biology and control of the khapra beetle, *Trogoderma granarium*, a major quarantine threat to global food security. *Annual Review of Entomology*, *64*, 131–148.

Ayappa, P.K., Cheema, P.S. & Perti, S.L. (1957) A life-history study of *Anthrenus flavipes* Lec.(Col., Dermestidae). *Bulletin of Entomological Research*, *48*(1), 185–198.

Beal, R.S., Jr. (1959) A key to the Nearctic genera of Dermestidae. *The Coleopterists' Bulletin*, *13*(4), 99–101.

Beal, R.S., Jr. (1998) Taxonomy and biology of Nearctic species of *Anthrenus* (Coleoptera: Dermestidae). *Transactions of the American Entomological Society*, *124*(3–4), 271–332.

Beaver, R.A. (1977) Non-equilibrium 'island' communities: Diptera breeding in dead snails. *Journal of Animal Ecology*, *46*, 783–798.

Bjørge, J.D., Overgaard, J., Malte, H., Gianotten, N. & Heckmann, L.H. (2018) Role of temperature on growth and metabolic rate in the tenebrionid beetles *Alphitobius diaperinus* and *Tenebrio molitor*. *Journal of Insect Physiology*, *107*, 89–96.

Blake, G.M. (1958) Diapause and the regulation of development in *Anthrenus verbasci* (L.) (Col., Dermestidae). *Bulletin of Entomological Research*, *49*(4), 751–775.

Blake, G.M. (1959) Control of diapause by an 'internal clock' in *Anthrenus verbasci* (L.) (Col., Dermestidae). *Nature*, *183*(4654), 126–127.

Buckley, L.B. (2022) Temperature-sensitive development shapes insect phenological responses to climate change. *Current Opinion in Insect Science*, *52*, 100897.

Burges, H.D. (1959) Studies on the dermestid beetle *Trogoderma granarium* Everts: ecology in malt stores. *Annals of Applied Biology*, *47*(3), 445–462.

Burges, H.D. & Cammell, M.E. (1964) Effect of temperature and humidity on *Trogoderma anthrenoides* (Sharp) (Coleoptera, Dermestidae) and comparisons with related species. *Bulletin of Entomological Research*, *55*(2), 313–325.

Burtt, E.H., Jr., Chow, W. & Babbitt, G.A. (1991) Occurrence and demography of mites of tree swallow, house wren, and eastern bluebird nests. In: Loye, J.E. & Zuk, M. (Eds.) *Bird-parasite interactions*. Oxford: Oxford University Press, pp. 104–122.

Cantarero, A., López-Arrabé, J., Redondo, A.J. & Moreno, J. (2013) Behavioural responses to ectoparasites in pied flycatchers *Ficedula hypoleuca*: an experimental study. *Journal of Avian Biology*, *44*(6), 591–599.

Cantarero, A., López-Arrabé, J., Rodríguez-García, V., González-Braojos, S., Ruiz-De-Castañeda, R., Redondo, A.J. et al. (2013) Factors affecting the presence and abundance of generalist ectoparasites in nests of three sympatric hole-nesting bird species. *Acta Ornithologica*, *48*(1), 39–54.

Castaño-Vázquez, F., Martínez, J., Merino, S. & Lozano, A.M. (2018) Experimental manipulation of temperature reduce ectoparasites in nests of blue tits *Cyanistes caeruleus*. *Journal of Avian Biology*, *49*(8), e01695.

Castaño-Vázquez, F., Merino, S., Valera, F. & Veiga, J. (2022) Experimental manipulation of humidity in a cavity-nesting bird influences ectoparasites' abundance. *Parasitology*, *149*(4), 436–443.

Castaño-Vázquez, F., Schumm, Y.R., Bentele, A., Quillfeldt, P. & Merino, S. (2021) Experimental manipulation of cavity temperature produces differential effects on parasite abundances in blue tit nests at two different latitudes. *International Journal for Parasitology: Parasites and Wildlife*, *14*, 287–297.

Coombs, C.W. (1978) The effect of temperature and relative humidity upon the development and fecundity of *Dermestes lardarius* L. (Coleoptera, Dermestidae). *Journal of Stored Products Research*, *14*(2–3), 111–119.

Cosandey, V., Séchaud, R., Béziers, P., Chittaro, Y., Sanchez, A. & Roulin, A. (2021) Nidicolous beetle species richness is driven by Barn Owl's nests occupancy and landscape structure. *Journal of Ornithology*, *162*(3), 857–864.

Esperk, T., Tammaru, T. & Nylin, S. (2007) Intraspecific variability in number of larval instars in insects. *Journal of Economic Entomology*, *100*(3), 627–645.

Ezenwaji, H.M. & Obayi, N.S. (2004) The effect of fish moisture content on oviposition, fecundity and development of the hide beetle, *Dermestes maculatus* DeGeer (Coleoptera: Dermestidae). *Animal Research International*, *1*(1), 47–51.

Foster, C. & Holloway, G. (2015) *Anthrenus (anthrenus) augustefasciatus* (Coleoptera: Dermstidae), a species new to Britain. *British Journal of Entomology and Natural History*, *28*, 47–51.

García-del Río, M., Cantarero, A., Castaño-Vázquez, F., Merino, Y., García-Velasco, J. & Merino, S. (2024) Experimental manipulation of nest temperature and relative humidity reduces ectoparasites and affects body condition of blue tits *Cyanistes caeruleus*. *Ibis*. Available from: https://doi.org/10.1111/ibi.13346

Gilbert, N. & Raworth, D.A. (1996) Insects and temperature—a general theory. *The Canadian Entomologist*, *128*(1), 1–13.

Hadaway, A.B. (1956) The biology of the dermestid beetles, *Trogoderma granarium* Everts and *Trogoderma versicolor* (Creutz.). *Bulletin of Entomological Research*, *46*(4), 781–796.

Hanzelka, J., Baroni, D., Martikainen, P., Eeva, T. & Laaksonen, T. (2023) Cavity-breeding birds create specific microhabitats for diverse arthropod communities in boreal forests. *Biodiversity and Conservation*, *32*, 1–30.

Háva, J. (2004) World keys to the genera and subgenera of Dermestidae (Coleoptera), with descriptions, nomenclature and distributional records. *Acta Musei Nationalis Pragae, Series B, Natural History*, *60*(3–4), 149–164.

Háva, J. (2023) Online World catalogue of Dermestidae (Coleoptera). Available from: http://dermestidae.wz.cz/world-dermestidae/ [Accessed 18th January 2024].

Háva, J. & Nardi, G. (2004) Preliminary data on the Nosodendridae and Dermestidae (Coleoptera). Invertebrati di una foresta della Pianura Padana, Bosco della Fontana, Secondo contributo. *Conservazione Habitat Invertebrati*, *3*, 117–123.

Heeb, P., Kölliker, M. & Richner, H. (2000) Bird–ectoparasite interactions, nest humidity, and ectoparasite community structure. *Ecology*, *81*(4), 958–968.

Hicks, E.A. (1953) Observations on the insect fauna of birds' nests. *Journal of the Kansas Entomological Society*, *26*(1), 11–18.

Jaworski, T. & Hilszczański, J. (2013) The effect of temperature and humidity changes on insects development their impact on forest ecosystems in the context of expected climate change. *Forest Research Papers*, *74*(4), 345–355.

Jurík, M. & Šustek, Z. (1978) The Coleoptera of *Passer domesticus* in Czechoslovakia. *Vestnik Ceskoslovenske Spolecnosti Zoologicke*, *42*, 255–272.

Kiselyova, T. & Mchugh, J.V. (2006) A phylogenetic study of Dermestidae (Coleoptera) based on larval morphology. *Systematic Entomology*, *31*(3), 469–507.

Krištofík, J., Mašán, P., Šustek, Z. & Karaska, D. (2009) Arthropods in the nests of lesser spotted eagle (*Aquila pomarina*). *Biologia*, *64*(5), 974–980.

Lee, R.E. (1991) Principles of insect low temperature tolerance. In: Lee, R.E. & Denlinger, D.L. (Eds.) *Insects at low temperature*. Boston, MA: Springer, pp. 17–46.

Loye, J.E. & Zuk, M. (1991) *Bird-parasite interactions: ecology, evolution and behaviour*. Ornithology series, 2. London, UK: Oxford University Press.

Lynch, W.L., Philips, T.K. & Klompen, H. (2020) Arthropod fauna associated with black vulture and Turkey vulture nests (Accipitriformes: Cathartidae) in south-Central Kentucky, USA. *Biologia*, *75*(8), 1135–1142.

Magni, P.A., Voss, S.C., Testi, R., Borrini, M. & Dadour, I.R. (2015) A biological and procedural review of forensically significant *Dermestes* species (Coleoptera: Dermestidae). *Journal of Medical Entomology*, *52*(5), 755–769.

Martín-Vega, D., Díaz-Aranda, L.M., Baz, A. & Cifrián, B. (2017) Effect of temperature on the survival and development of three forensically relevant *Dermestes* species (Coleoptera: Dermestidae). *Journal of Medical Entomology*, *54*(5), 1140–1150.

Masan, P. & Kristofik, J. (1995) Mesostigmatid mites (Acarina, Mesostigmata) in the nests of penduline tit (*Remiz pendulinus*). *Biologia*, *50*(5), 481–485.

Mason, E.A. (1936) Parasitism of Bird's nests by *Protocalliphora* at Groton, Massachusetts. *Bird-Banding*, *7*(3), 112–121.

McComb, W.C. & Noble, R.E. (1981) Microclimates of nest boxes and natural cavities in bottomland hardwoods. *The Journal of Wildlife Management*, *45*(1), 284–289.

Merino, S. (2010) Immunocompetence and parasitism in nestlings from wild populations. *The Open Ornithology Journal*, *3*, 27–32.

Merino, S., Moreno, J., Sanz, J.J. & Arriero, E. (2000) Are avian blood parasites pathogenic in the wild? A medication experiment in blue tits (*Parus caeruleus*). *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *267*(1461), 2507–2510.

Merino, S. & Potti, J. (1995) Mites and blowflies decrease growth and survival in nestling pied flycatchers. *Oikos*, *73*, 95–103.

Merino, S. & Potti, J. (1996) Weather dependent effects of ectoparasites on their bird host. *Ecography*, *19*, 107–113.

Merkl, O., Bagyura, J. & Rózsa, L. (2004) Insects inhabiting Saker (*Falco cherrug*) nests in Hungary. *Ornis Hungarica*, *14*, 1–2.

Møller, A.P. (2008) Interactions between interactions: predator–prey, parasite–host, and mutualistic interactions. *Annals of the New York Academy of Sciences*, *1133*(1), 180–186.

Møller, A.P., Merino, S., Soler, J.J., Antonov, A., Badás, E.P., Calero-Torralbo, M.A. et al. (2013) Assessing the effects of climate on host-parasite interactions: a comparative study of European birds and their parasites. *PLoS One*, *8*(12), e82886.

Motyka, M., Kusy, D., Háva, J., Jahodářová, E., Bílková, R., Vogler, A.P. et al. (2022) Mitogenomic data elucidate the phylogeny and evolution of life strategies in Dermestidae (Coleoptera). *Systematic Entomology*, *47*(1), 82–93.

Nisimura, T. & Numata, H. (2003) Circannual control of the life cycle in the varied carpet beetle *Anthrenus verbasci*. *Functional Ecology*, *17*, 489–495.

Nordberg, S. (1936) Biologisch-okologische Untersuchungen uber die Vogel-nidicolen. *Acta Zoologica Fennica*, *21*, 1–168.

Odeyemi, O.O. & Hassana, T. (1993) Influence of temperature, humidity and photoperiod on oviposition and larval development in *Trogoderma granarium* Everts (Coleoptera: Dermestidae). *Applied Entomology and Zoology*, *28*(3), 275–281.

Pardos, M., Pérez, S., Calama, R., Alonso, R. & Lexer, M.J. (2017) Ecosystem service provision, management systems and climate change in Valsaín forest, central Spain. *Regional Environmental Change*, *17*, 17–32.

Peacock, E.R. (1993) *Adults and larvae of hide, larder, and carpet beetles and their relatives (Coleoptera: Dermestidae) and of Derodontid beetle (Coleoptera: Derodontidae)*. London, UK: Royal Entomological Society of London.

Pincebourde, S. & Woods, H.A. (2020) There is plenty of room at the bottom: microclimates drive insect vulnerability to climate change. *Current Opinion in Insect Science*, *41*, 63–70.

Pureswaran, D.S., Roques, A. & Battisti, A. (2018) Forest insects and climate change. *Current Forestry Reports*, *4*, 35–50.

Ramachandran, S., Hern, J., Almeyda, J., Main, J. & Patel, K.S. (1997) Contact dermatitis with cervical lymphadenopathy following exposure to the hide beetle, *Dermestes peruvianus*. *British Journal of Dermatology*, *136*(6), 943–945.

Rebolledo, R., Arroyo, M. & Del Estal, P. (1994) Ciclo vital y estacional de *Anthrenus verbasci* (L.) (Coleóptera: Dermestidae) en Madrid, sobre garbanzo un hospedero no habitual. *Boletín de sanidad vegetal. Plagas*, *20*(4), 881–888.

Robinet, C. & Roques, A. (2010) Direct impacts of recent climate warming on insect populations. *Integrative Zoology*, *5*(2), 132–142.

Rózsa, L. (1992) Points in question. Endangered parasite species. *International Journal for Parasitology*, *22*(3), 265–266.

Salido, A., Veiga, J., Reyes-López, J.L., Nieves-Aldrey, J.L. & Valera, F. (2021) Insect predation reduces the abundance of a nidicolous ectoparasite. *Ecological Entomology*, *46*(4), 988–998.

Szabó, K., Szalmás, A., Liker, A. & Barta, Z. (2002) Effects of haematophagous mites on nestling house sparrows (*Passer domesticus*). *Acta Parasitologica*, *47*(4), 318–322.

Tomás, G., Merino, S., Moreno, J., Morales, J. & Martínez-De La Puente, J. (2007) Impact of blood parasites on immunoglobulin level and parental effort: a medication field experiment on a wild passerine. *Functional Ecology*, *21*, 125–133.

Veer, V., Negi, B.K. & Rao, K.M. (1996) Dermestid beetles and some other insect pests associated with stored silkworm cocoons in India, including a world list of dermestid species found attacking this commodity. *Journal of Stored Products Research*, *32*(1), 69–89.

Wilches, D.M., Laird, R.A., Floate, K.D. & Fields, P.G. (2016) A review of diapause and tolerance to extreme temperatures in dermestids (Coleoptera). *Journal of Stored Products Research*, *68*, 50–62.

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*(4), 739–772.

Yinon, U. & Shulov, A. (1967) The humidity responses of *Trogoderma granarium* Everts (Col., Dermestidae). *Bulletin of Entomological Research*, *57*(3), 451–458.

Zanetti, N.I., Visciarelli, E.C. & Centeno, N.D. (2016) The effect of temperature and laboratory rearing conditions on the development of *Dermestes maculatus* (Coleoptera: Dermestidae). *Journal of Forensic Sciences*, *61*(2), 375–381.

Zeng, L., Pang, Y., Feng, S., Wang, Y., Stejskal, V., Aulicky, R. et al. (2021) Comparative mitochondrial genomics of five Dermestid beetles (Coleoptera: Dermestidae) and its implications for phylogeny. *Genomics*, *113*(1), 927–934.

Zhantiev, R.D. (2009) Ecology and classification of dermestid beetles (Coleoptera, Dermestidae) of the Palaearctic fauna. *Entomological Review*, *89*(2), 157–174.

Zhou, Y.L., Nicholls, J.A., Liu, Z.H., Hartley, D., Szito, A., Ślipiński, A. et al. (2022) Molecular phylogeny of Dermestidae (Coleoptera) reveals the polyphyletic nature of *Trogoderma* Latreille and the taxonomic placement of the Khapra Beetle *Trogoderma granarium* Everts. *Insect Systematics and Diversity*, *6*(6), 2.

SUPPORTING INFORMATION

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

Table S1. Data from the 47 nests used during the study period.

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