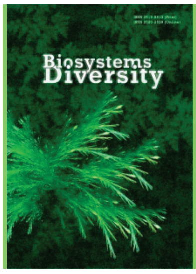

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Groupings of arthropods in nest boxes inhabited by *Phoenicurus phoenicurus* in pine forests of Northeastern Ukraine

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The common redstart *Phoenicurus phoenicurus* (Passeriformes, Muscicapidae) is one the most appealing insect-eating birds living in parks, gardens, and other cultured landscapes of Europe, Central and Western Asia, and Northern Africa. We analyzed the nests of *Ph. phoenicurus* after the chicks had flown away. Throughout the reproductive period, in the pine forests of Northeastern Ukraine, those nests contained 23 species of arthropods, belonging to 15 families, 9 orders. The analysis of the distribution of arthropods by ecological groups revealed a correlation between the number of arthropods and parameters of breeding success and air temperature in the national nature parks. To attract *Ph. phoenicurus* to the pine forests of the region, we used standard-sized artificial nests made of wooden sections. The results of the study demonstrated a high level of biodiversity of nidicolous arthropods in the nests of *Ph. phoenicurus* in the pine forests in 2019–2023. The largest share of nidicolous invertebrates among the ecological groups was comprised of "nourishment for chicks". A large portion of arthropods in the nest of *Ph. phoenicurus* was polyphages. The results provide a better understandanding of the dynamics of invertebrates' populations in artificial nests occupied by *Ph. phoenicurus*, their effect on the breeding successfulness of this species, and also other significant factors. This is important for designing effective strategies of preserving the populations of this species in the region of research. Further research is needed to specify the factors influencing the distribution of the bird and species composition of arthropods in its nests in other types of ecosystems within the bird's range.

Keywords: common redstart; arthropods; nestboxes; pine forest; ecological groups; consortial relations; fauna of nests.

Introduction

Due to anthropogenic modification of the environment, the number of natural places where tree-hole-nesting birds could move to is rapidly declining. Installing nest boxes all around the globe (Riggio et al., 2023; Thompson et al., 2023) can easily compensate for the low number of tree hollows, which is a limiting factor for cavity-nesting birds' populations, especially in forests. Birdhouses in pine forests of Northeastern Ukraine create favorable conditions for nesting of *Phoenicurus phoenicurus* (Linnaeus, 1758) (Yarys et al., 2021a, 2021b; Yarys, 2022). To construct their nests, birds use natural and anthropogenic materials, which over time turn to organic remains that become a food source and microenvironment for various arthropods (Jaworski et al., 2022; Błoszyk et al., 2024). In turn, insects are a food source for various forest inhabitants; they perform the roles of pollinators, omnivores, herbivores, carnivores, and destructors, thus supporting the ecological balance of the entire biodiversity (Brygadyrenko, 2014; Faly & Brygadyrenko, 2014; Chaplygina et al., 2015; Chebitko, 2019; Pokhylenko et al., 2019).

Factors limiting the composition and numbers of arthropods in artificial nests have been the subject of numerous studies (Hurtrez-Boussès et al., 1997; Chaplygina et al., 2018, 2019, 2020). In particular, studies revealed that numbers of arthropods in nests are subject to bird species (López-Rull & García, 2015; Fecchio et al., 2017), nest location (López-Rull & García, 2015), materials and architecture of the nests (Mainwaring et al., 2014; Boyes & Lewis, 2019), and microclimate in those artificial nests (Hanzelka et al., 2023), which together determine the diversity of arthropods in those nests (Callan et al., 2023). Since temperature and humidity are closely interrelated parameters, they directly affect the breeding of ectoparasites in birds' nests (Veiga, 2020; Sudyka et al., 2022). Experimental studies revealed that temperature rise in nests of *Cyanistes caeruleus* (Linnaeus, 1758) negatively affects the development of pupae of the parasitic flies *Protocalliphora azurea* (Fallen, 1817) and mites of the Dermanyssidae family (Castaño-Vázquez et al., 2021). Also, temperature has a crucial effect on various aspects of insects' biology, including metabolism, thresholds of physiological processes, development duration, behavior, and survival of populations (Buckley, 2022; Dunn et al., 2023).

According to Mainwaring et al. (2014), López-Rull & García (2015), the dominant arthropods in artificial bird nests are ectoparasites of chicks, which reduce their survival. Błoszyk et al. (2024) found that groupings of Uropodina in the examined nests in the National Park Tuchola Forest (Poland) consisted of two species of mites: *Leiodinychus orbicularis* (C. L. Koch, 1839) and *Chiropturopoda nidiphila* (Wiśniewski & Hirschmann, 1993). The first of them is a representative of the group of barn mites, which does not parasitize birds, but occurs in compost, decomposing leaves, upper soil layer, mosses, hay and straw, anthills, mole burrows, and bird nests. In the Mediterrainian-type region of the Central Chile, in all the collected bird nests, 43 taxonomic objects were identified belonging to 18 orders and 5 classes: Arachnida, Diplopoda, Entognatha, Insecta, and Malacostraca. In the northern region of Central Chile (the driest and warmest), bird nests were found to contain Hemiptera and Hymenoptera; by contrast, in the southern region (the wettest and coolest), species of Collembola, Dermaptera, and Diplopoda were found in the nests (Carvallo et al., 2020).

The most recent studies emphasize the importance of understanding the effects of various factors on the numbers and diversity of arthropods in bird nests, particularly those of *Ph. phoenicurus* that nest in bird houses. Analysis of interrelations between arthropods and *Ph. phoenicurus*, especially in the context of research of parasitic insects, allows us to identify important aspects that affect the success of egg incubation (Rizwan et al., 2023) and survival of chicks (Laska et al., 2023). Based on those data, measures can be developed to protect *Ph. phoenicurus* and reduce threats associated with the rising number of particular arthropods in artificial nests in pine forests of Ukraine. Furthermore, studies of nidicoles in nests of *Ph. phoenicurus* can be important for the understanding of how the global climate changes contribute to the loss of biodiversity, and can help analyze consequences of environmental changes for the studied bird populations in the future.

Materials and methods

The areas of the research are situated in the northeast Ukraine within the Dnipro Lowland and the Poltava Plain (Fig. 1a, 1b). By physical-geographic zoning, the territory belongs to the forest-steppe zone, east Ukrainian forests steppe land, and Kharkiv and Sumy slope-highland region. The typical soils are gray, dark-gray loess chernozems, and in some areas podzolized chernozems on loess-like loams. The climate is moderate, with a sufficient amount of precipitations. The balanced water regime of the ecosystesms of the Northeast Ukraine is supported by the Dnipro, Vorskla, and Siverskyi Donets.

The vegetation in the study areas was identified as follows. In the pine forest of the Hetmanskyi National Nature Park near the Klymentove village, the tree stand comprises *Pinus sylvestris* (L.); the second stratum is formed of *Quercus robur* L., *Tilia cordata* Mill., *Prunus padus* L., *Sambucus racemosa* L., *Robinia pseudoacacia* L., *Ulmus glabra* Huds., and *Betula pendula* Roth; the understory consisted of *Sorbus aucuparia* L., *Corylus avellana* (L.) H. Karst., and *Acer tataricum* L.; and the herbaceous-shrub stratum included *Pteridium aquilinum* (L.) Kuhn, *Polygonatum odoratum* (Mill.) Druce, *Milium effusum* L., *Convallaria majalis* L., *Peucedanum oreoselinum* (L.) Moench, *Stellaria holostea* (L.) M. T. Sharples & E. A. Tripp, *Carex pilosa* Scop., and *Poa angustifolia* L. In the Homilshanski Forests National Nature Park near the Zadonetske village, the tree stand and understory is dominated by *P. sylvestris*, the understory is composed of *P. padus*, *C. avellana*, *A. tataricum*, and *S. racemosa*, and the herbaceous stratum is comprised of *Festuca beckeri* (Hack.) Trautv., *Centaurea jacea* L., *Knautia arvensis* (L.) Coult., *Hypericum perforatum* L., *Anthericum ramosum* L., and *Euphorbia nicaeensis* All.

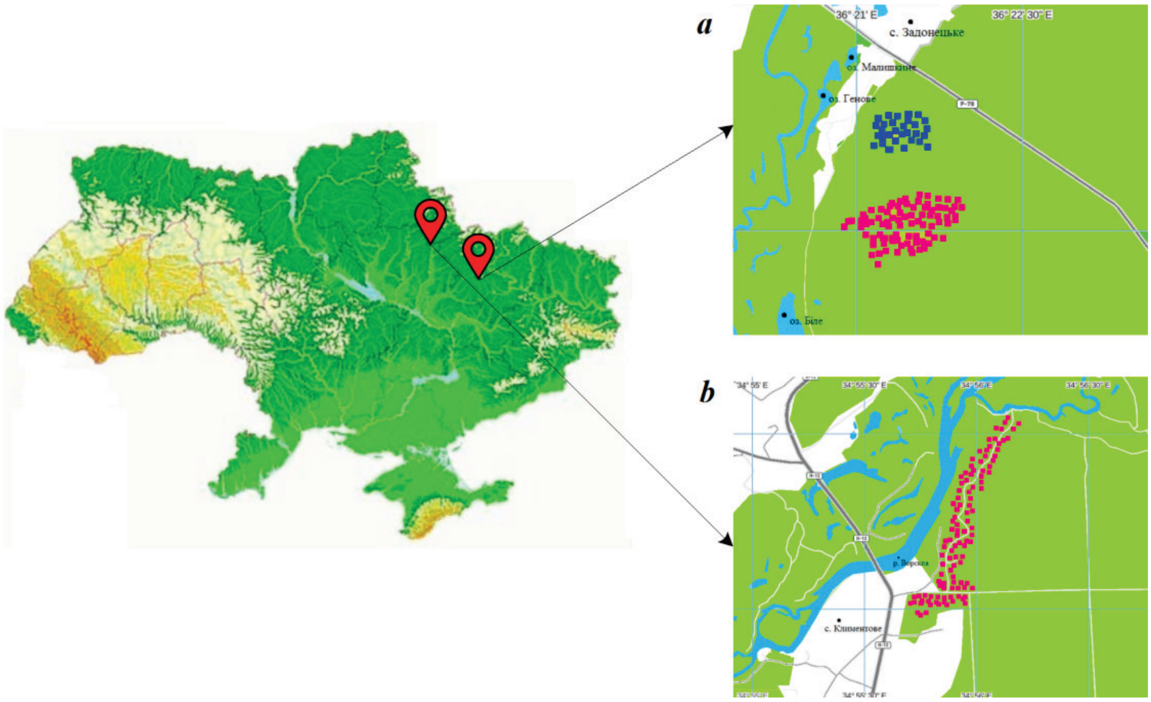

Fig. 1. Locations of the research areas of Ukraine: the territories of Homilshanski Forests (*a*) and Hetmanskyi (*b*) national nature parks

To attract cavity-nesting birds, particularly *Ph. phoenicurus*, to the pine forests, we used standard-sized nest boxes made of wooden sections, with the hollow diameter of 3 cm, placed at the height of 1–3 m. The front wall in such nest box is removable, which makes the boxes easy to inspect. With time, this allows an increase in the taxonomic diversity of various groups of mammals and birds, which use them facultatively, when the front wall is lost.

In 2014, a line of nest boxes was established (n = 100) in the pine forest of the Hetmanskyi Park (50°22'57" N 34°55'34" E) near Klymentove village in Sumy Oblast. Later, in 2017, an identical line of nest boxes was established in the pine forest of Homilshanski Forests Park (49°38'12" N 36°18'27" E) (n = 100) near Zadonetske village in Kharkiv Oblast. The research was carried out in 2019–2023 during the nesting period, from the first decade of April till the third decade of July, annually, making 3–5 inspections at each location. A total of 33 nests was described.

To identify the fauna of nidicoles, we analyzed 11 nests of *Ph. phoenicurus* after chicks had flown away. When collecting samples from the nests from natural environment, they were treated with chloroform in a densely laced polyethylene bag with a label. The nests were dismantled manually, and while inspecting them, we used insect pins, pincettes, and magnifying glasses. The share of species was quantified according to the number of individuals in each sample. To assess the similarity between the nest groupings of arthropods in Homilshanski Forests near the Zadonetske village and Hetmanskyi near the Klymentove village, we used the tests of Kolmohorov-Smirnov (0.02) and Anderson-Darling (0.01). Both tests confirmed the statistically significant difference between the two totals of species in Hetmanskyi and Homilshanski Forests ($P < 0.05$).

Results

During the 2019–2023 reproductive periods of *Ph. phoenicurus*, in the pine forests of Northeast Ukraine, the nest boxes (Fig. 2) were found to contain 9 orders, 15 families, 23 species of nidicoles (Table 1).

The formation of a diverse species composition of nidicoles is associated with the period when the birds return to nesting sites after migration. According to our observations, arrival of *Ph. phoenicurus* to the monitored pine forests where the nest boxes were installed, took place in the second-third decade of April and the first decade of May (4/11-5/10) at the average temperature of +12 °C. Old males arrived at the nesting sites first, easily recognized by their distinct singing and bright colors. Females appeared days later. For over a week after the arrival, the males kept separate from females, but already in mid April the birds started to be seen in pairs. The first built nests in the nestboxes in Hetmanskyi and Homilshanski Forests were found in the first and second decades of May (5/01-5/10).

Table 1
Distribution of nidicoles in the nest boxes of according to various taxonomic and ecological groups in the pine forest of Northeast Ukraine during 2019–2023

Taxon name			Environmental groups						Territory	
Order	Family	Species	Obligate nidicoles	Facultative nidicoles	Diet for chicks	Biotopic affiliation	Day activity	Trophic group	NPP Homilshansky Forests	Hetmanskyi NNP
Coleoptera	Elateridae	*Athous haemorrhoidalis* (Fabricius, 1801)	–	–	+	f	dt	p	27	24
		Ampedus sanquinoletus (Schrank, 1789)	–	+	+	f	dt	p	0	4 (imago), 1 (larva)
		Ectinus aterrimus (Linnaeus, 1761)	–	–	+	f	dt	p	7	4
		Agriotes ustulatus (Schaller, 1783)	–	–	+	md	dt	p	2	4
		Hypoganus inunctus (Lacordaire, 1835)	–	–	+	f	dt	e	1	0
		Selatosomus latus (Fabricius, 1801)	–	–	+	pt	dt	ph	16	14
		Melanotus villosus Gmelin, 1789	–	–	+	f	dt	p	3	0
	Tenebrionidae	*Pseudocistela ceramboides* (Linnaeus, 1761)	–	–	+	f	rc	s	17	3
		Prionychus ater (Fabricius, 1775)	–	+	–	f	tn	s	8	0
	Dermestidae	*Dermestes murinus* Linnaeus, 1758	+	–	–	pt	dt	n	0	1
		Attagenus schaefferi (Herbst, 1792)	–	+	–	sn	dt	p	5	0
	Coccinellidae	*Calvia quatuordecimpunctata* (Linnaeus, 1758)	–	–	+	pt	dt	e	0	2
	Cerambycidae	*Stenurella melanura* (Linnaeus, 1758)	–	–	+	pt	tn	ph	9	2
	Scarabaeidae	*Phyllopertha horticola* (Linnaeus, 1758)	–	–	+	bs	tn	ph	7	0
Hemiptera	Pentatomidae	*Palomena prasina* (Linnaeus, 1761)	–	–	+	sn	dt	p	4	3
	Coreidae	*Coreus marginatus* (Linnaeus, 1758)	–	–	+	pt	dt	ph	0	2
		Nemocoris falleni Sahlberg, 1848	–	–	+	pt	dt	ph	0	1
Diptera	Calliphoridae	*Protocalliphora azurea* (Fallen, 1817)	+	–	–	sn	dt	n	5 (imago), 11 (pupae)	5
		Lucilia caesar (Linnaeus, 1758)	+	–	–	sn	dt	n	6 (imago), 4 (pupae)	0
Blattodea	Ectobiidae	*Ectobius lapponicus* (Linnaeus, 1758)	–	+	–	md	rc	ph	4	0
Lepidoptera	Noctuidae	Noctuidae spp.	–	–	+	pt	rc	ph	6	0
Hymenoptera	Vespidae	Eumeninae spp.	–	–	+	md	dt	ph	0	2
Mesostigmata	Laelapidae	*Androlaelaps casalis* (Berlese, 1887)	–	+	–	pt	rc	e	6	0
Isopoda	Armadillidiidae	*Armadillidium vulgare* Latreille, 1804	–	+	–	pt	tn	s	7	2
Julida	Julidae	*Rossiulus kessleri* (Lohmander, 1927)	–	+	–	f	tn	s	0	1

Note: "+" – occurrence of species in the ecological group; biotopic affiliation: pt – polytope, md – meadow, f – forest, sy – synanthropic, bs – on the bushes; day activity: rc – round-the-clock, tn – twilight and nocturnal, dt – daytime; trophic group: ph – phytophages, e – entomophages, p – polyphages, n – necrophages, s – saprophages.

Fig. 2. Reproductive biology of *Ph. phoenicurus* in pine forest: *a* – female (♀), *b* – nest inside a nestbox, *c* – clutch of 7 eggs, *d* – 6-day-old chicks

The first egg clutches of *Ph. phoenicurus* in Hetmaskyi were found on May 5, at the temperature of +18 °C; and in Homilshanski Forests on May 10, at the temperature of +17 °C (r = 0.94, P < 0.01, Fig. 3a, 3b). The incubation lasted on average 15–20 days. In the pine forests of northeastern Ukraine, mass hatching of the chicks occurred in the third decade of May and first-second decades of June (May 21 – June 30), at the temperature of +21.6 °C (r = 0.80, P < 0.01). The mass flight of fledglings was recorded in the second-third decades of June and the second decade of July (June 11-July 20), at the temperature of +20.5 ± 1.5 °C (r = 0.86, P < 0.01).

The topical relations (the concept invented by V. N. Beklemyshev in 1951 to indicate forms of relationships between populations in a biocoenosis when individuals of a population of one species affect and alter the physical-chemical conditions of existence of other species) between *Ph. phoenicurus* and various plants manifested not only in inhabitation of certain types of plant groups, but also in using them for song posts, food substrate, sites for nesting, sleep, and shelter during unfavorable conditions. Moreover, *B. pendula*, *P. sylvestris*, *T. cordata*, *P. avium*, and others that belong to consortia of *Ph. phoenicurus* create an environment for construction of this type of nests in birdhouses. The nests proper have intricate constructions, taking the form of dense cups with thick side walls and a deep, rounded basin. Inside, the nest is covered by thin dry Poaceae grass (50%). The lining comprised the last-year's leaves (6%), bast (10%), twigs of *P. sylvestris* (8%), *Sphagnum* sp. (3%), hair of mammals, particularly *Equus* sp. (4%), maple and ash keys (4%), feathers (6%) of the studied species, and less often there occurred feathers of *Parus major* Linnaeus, 1758, *Ficedula albicollis* (Temminck, 1815), and *Dendrocopos major* (Linnaeus, 1758). Sometimes, the nests contained materials of anthropogenic origin, such as pieces of threads, ropes, and bags (5%) (Yarys et al., 2021). The structural peculiarities of the nests such as their forms and composition of lining create specific microenvironment that promotes the formation of a distinctive composition of groups of nidicoles (Fig. 4).

The analysis of the content of nest boxes in the conditions of Northeast Ukraine revealed that the greatest share of ecological groups was occupied by "nourishment for chicks", equaling 12 taxa (70.6%) in Hetmanskyi and 11 taxa in Homilshanski Forests (61.1%); a much lower number was found for obligate nidicoles of the nests, equaling 2 (11.8%)

in Hetmanskyi and 2 (11.1%) in Homilskanski Forests. The data we obtained demonstrate that a large number of nest nidicoles that inhabit open spaces and forests – having a broad ecological plasticity – infiltrate residential landscapes (in Hetmanskyi, near Klymentove village, Fig. 5).

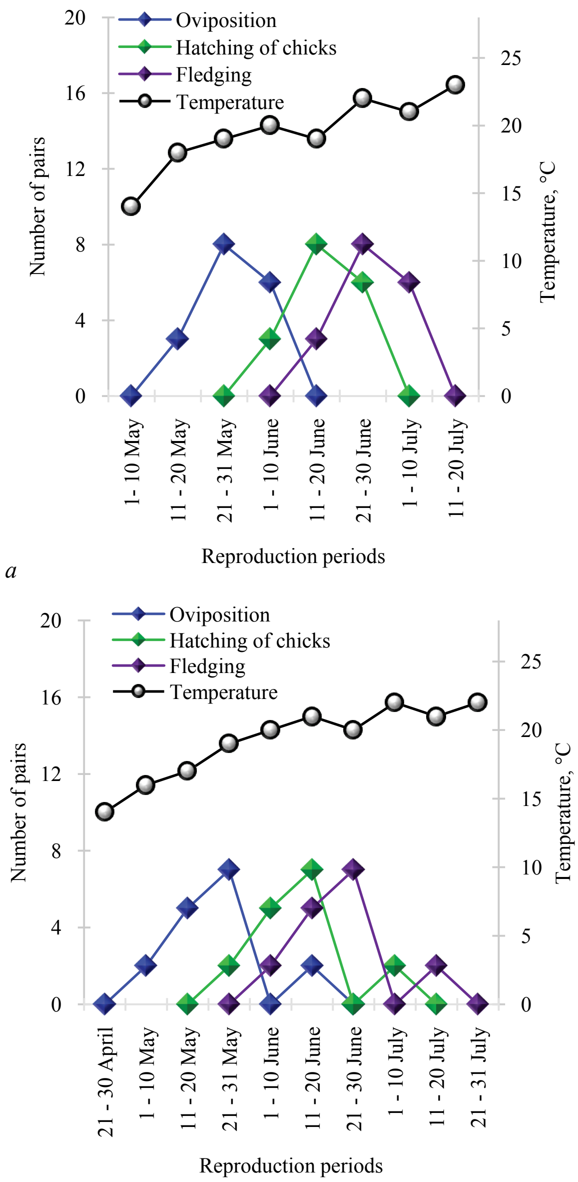

Fig. 3. Correlation between the duration of *Ph. phoenicurus* reproductive period and air temperature: *a* – in the Hetmanskyi pine forest, *b* – in the Homilshanski Forests pine forest

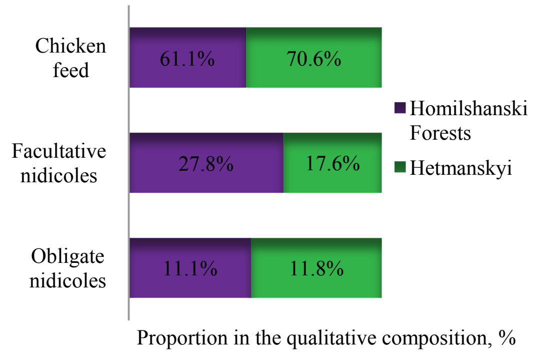

Fig. 4. Proportion of nidicoles in the nest boxes inhabited by *Ph. phoenicurus* according to ecological groups of nidicoles in the pine forests of Northeastern Ukraine in 2019–2023

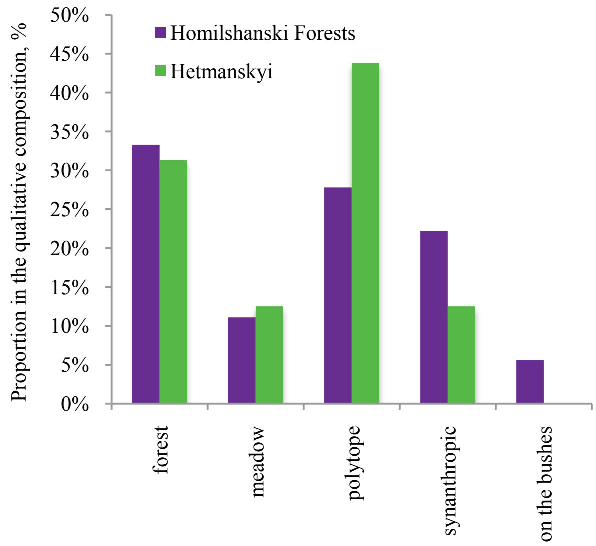

Fig. 5. Ratio of nidicoles in the artificial nests of *Ph. phoenicurus* according to biotope confinement in the pine forests of Northeastern Ukraine in 2019–2023

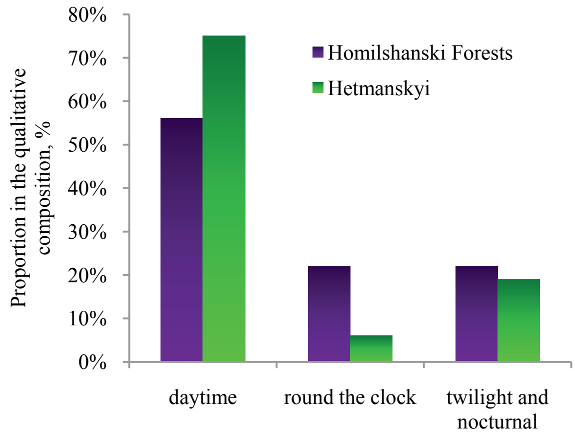

Fig. 6. Ratio of nidicoles in the nest of *Ph. phoenicurus* according to daily activity in the pine forests

The analysis of the ratio of representatives of various biotope groups revealed significant differences in the species composition between the parks. In Hetmansky, polytopic species of insects dominated, accounting for 44% of the general amount of representatives found. By contrast, in Homilshanski Forests, polytopic species accounted for a lower share, accounting for 28%. Also, in this territory, a large share of forest species of insects was seen, amounting to 33%, compared to 31% in Hetmanskyi. The meadow insects made up a lower share: 11% in Homilshanski Forests, compared to 13% in Hetmanskyi. Synanthropic species accounted for 22% in Homilshanski Forests and 13% in Hetmanskyi.

The daily activity indicated the hours when the nidicoles in the nests of *Ph. phoenicurus* actively search for food. This helps us to understand their strategy of feeding, choosing a place for hunting, and using the resources of the natural environment (Fig. 6).

In Hetmanskyi Forest, the share of daytime nidicoles accounted for 75%, whereas in Homilshanski Forests it equaled 56%. In the latter, the percentage of species that are active during the day equaled 22%, and that of twighlight-nocturnal species was 22%. At the same time, in Hetmanskyi, the lowest percentage of species was comprised of the categories round-the-clock (6%) and twighlight-nocturnal (19%) arthropods.

The greatest share of nidicoles found in the nests of *Ph. phoenicurus* in Homilshanski Forests comprised polyphages (33%), such as *Athous haemorrhoidalis*, *Ectinus atterimus*, *Agriotes ustulatus*, *Melanotus villosus*, *Attagenus schaefferi*, and *Palomena prasina*, phytophages (28%) and saprophages in the nest lining (17%), such as *Pseudocistela ceramboides*, *Prionychus ater*, and *Armadillidium vulgare*; the nests also contained entomophages (11%), namely *Androlaelaps casalis*, and necrophages (11%), such as *Protocalliphora azurea*, *Lucilia caesar* (Fig. 7).

In Hetmanskyi, polyphages accounted for 31% (including species such as *Athous haemorrhoidalis*, *Ampedus sanguinolentus*, *Ectinus atterimus*, *Agriotes ustulatus*, *Palomena prasina*), whereas phytophages comprised 31% as well (including *Selatosomus latus*, *Stenurella melanura*, *Coreus marginatus*, *Nemocoris fallen*, Eumeninae sp.). This is comparatively larger than the shares of those categories in Homilshanski Forests. By numbers, the subdominants were saprophages (19%), such as *Pseudocistela ceramboides*, *Armadillidium vulgare*, and *Rossiulus kessleri*.

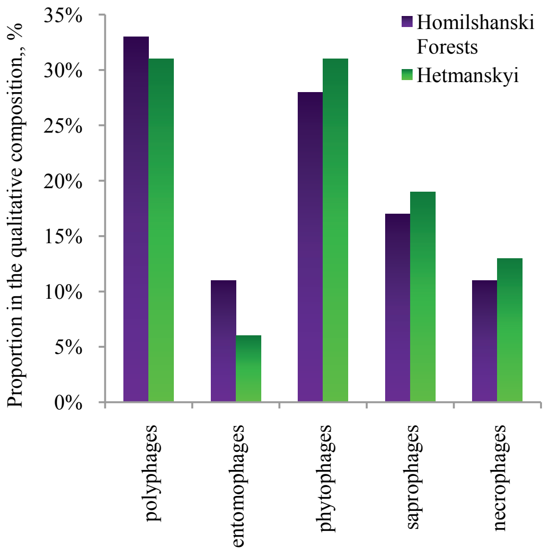

Fig. 7. Ratio of nidicoles in the nests of *Ph. phoenicurus* according to trophic specialization

The lowest number of all the trophic groups was observed for entomophages (6%), *Calvia quatuordecimpunctata* in Hetmanskyi.

The analysis of biodiversity indices revealed high values of the Margalef index and Chao-1. Comparison of other biodiversity indices suggested somewhat difference between the parks (Table 2). In Hetmanskyi, the biodiversity indices of nidicoles in the nests of *Ph. phoenicurus* were the highest: the Menhinick index = 1.86, the Margalef index = 3.49, and the Shannon index = 2.36. The Berger-Parker index was almost the same for the both territories. Inhabitants of the nests of *Ph. phoenicurus* in nestboxes in Homilshanski Forests were more diverse and even, as reflected in the higher values of the Shannon, Brillouin, and Menhinick indices, compared to the nest boxes in Hetmanskyi.

Table 2
Biodiversity of the groups of arthropods in the nests of *Ph. phoenicurus* in nestboxes in the pine forests of Northeastern Ukraine

Parameters	Homilshanski Forests NPP	Hetmanskyi NNP
Dominance index	0.08	0.15
Simpson index	0.92	0.85
Shannon index	2.70	2.36
Buzas and Gibson's evenness	0.82	0.66
Brillouin's index	2.42	1.98
Menhinick index	1.52	1.86
Margalef index	3.44	3.49
Equitability index	0.93	0.85
Fisher's alpha index	5.49	6.28
Berger-Parker dominance index	0.19	0.32
Index Chao-1	18.50	16.49

In our study, we used the Pearson correlation matrix so as to simultaneously analyze the interrelations among several variables (year, number of arthropods, success of reproduction, and mean monthly temperature of the spring-summer period) in the two national parks of Ukraine.

According to the results, in the Homilshanski Forests pine forest, we found a stongly negative correlation between the number of arthropods and years of the study (–1.00), i.e. with each following year of the research, the number of arthropods in nests of *Ph. phoenicurus* in the birdhouses decreased. This may have been caused by the following factors. Moderate positive correlation between the parameter of breeding success and years of the research (0.81) showed that with each consequtive year, the breeding success of *Ph. phoenicurus* improved (–0.83). Increase in the number of arthropods in nest boxes can affect how successfully *Ph. phoenicurus* breeds (Fig. 8).

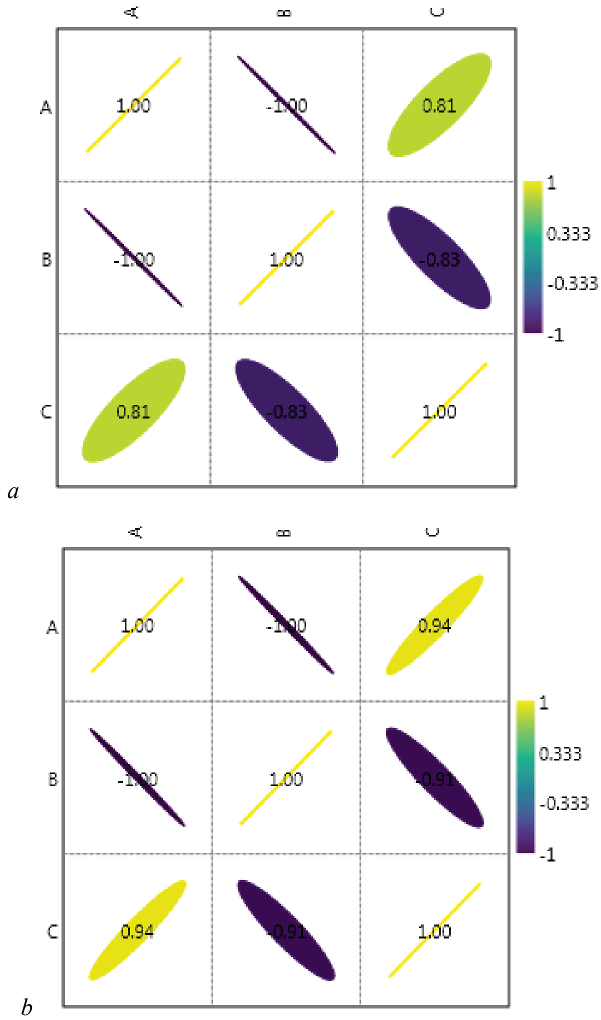

Fig. 8. Matrix of dispersion and the Pearson correlation coefficient for the interactions among three variables: A – year, B – number of arthropods, C – breeding success in pine forest; *a* – Homilshanski Forests, *b* – Hetmanskyi

In the Hetmanskyi pine forest, we saw a strong negative correlation between the number of arthropods and years of the research (–1.00), and also between the number of arthropods and the birds' breeding success (–0.91). A high positive correlation was seen between years of the study and the breeding successfulness (0.94).

Clearly, in both forest ecosystems, with each year of the research, the number of arthropods and the parameter of breeding success changed. An increase in the number of arthropods can have a substantial effect on how successfully the considered species breeds. The observed changes in the number of arthropods and breeding success underline the importance of regularly monitoring the condition of forest ecosystems for an extended period of time. This helps timely detection of changes and implementation of effective protective measures.

The analysis of correlation matrixes for Homilshanski Forests and Hetmanskyi indicated significant differences in the interrelations among years, number of arthropods, and mean monthly temperature of the spring-summer period (Fig. 9). In both cases, we saw a strong negative correlation between year and number of arthropods (–1.00). At the same time, the correlation between year and mean monthly temperature in Hetmanskyi Forest was 0.65 (moderate positive), while in Homilshanski Forests it was strongly negative (–0.87). Moreover, the correlation between the number of arthropods and mean monthly temperature varied from moderately negative (–0.59) in Hetmanskyi to strongly positive in Homilshanski Forests (0.85). This suggests a significant effect of the local environmental conditions on the interrelations between the studied variables, highlighting the importance of a contextual approach to analysis of ecological data.

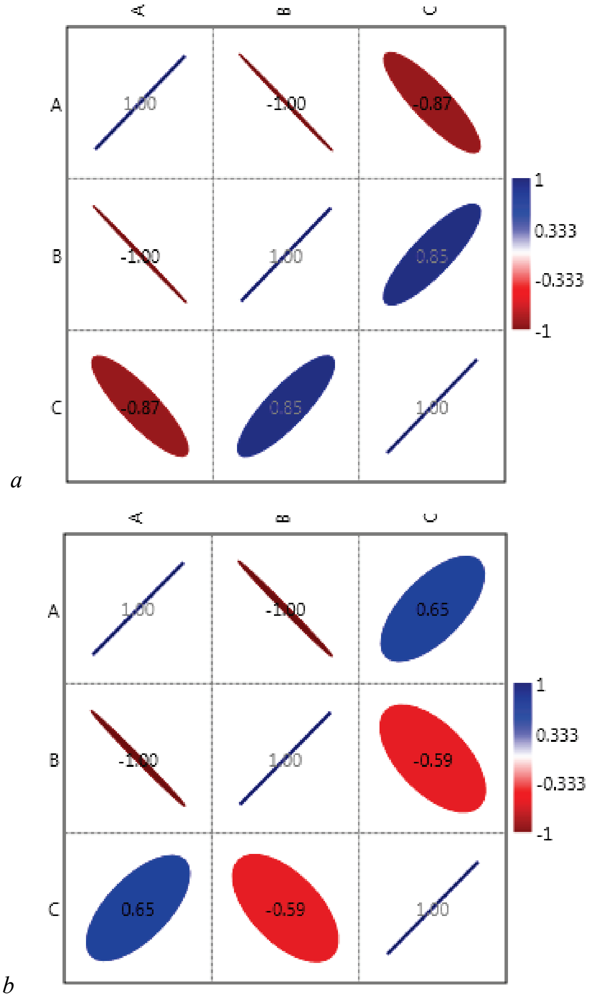

Fig. 9. Matrix of the Pearson correlation coefficients for three variables: A – year, B – number of arthropods, C – mean monthly temperature of the spring-summer period (01.05–20.07) in pine forest; *a* – Homilshanski Forests, *b* – Hetmanskyi Forest

Discussion

The results of our study of periods of oviposition, incubation, hatching, and fledging of *Ph. phoenicurus* allowed for an in-detail assessment of the effects of temperature conditions on the reproductive period of this bird. Delay in arrival of the females, compared to males, is a typical phenomenon for many birds, but we assume that in our case this allowed older *Ph. phoenicurus* males to occupy better territories for nesting. Since the first eggs in Hetmansky Forest were recorded on May 5 at the temperature of +18 °C, and in Homilshanski Forests on May 10 at the temperature of +17 °C, oviposition periods might depend on the temperature and geographic location. The incubation on average lasted 15–20 days, and mass hatching of chicks in the pine forests of northeast Ukraine took place in the third decade of May and the first-second decades of June at the temperature of +21.6 °C, which was confirmed by the high correlation coefficient ($r = 0.80$) and statistically significant level ($P < 0.01$). Mass fledging was seen in the second-third decades of June and the second decade of July at the temperature of +20.5 ± 1.5 °C ($r = 0.86$, $P < 0.01$), indicating significant correlation between temperature conditions and time of the birds' activity, and emphasizing the effect of seasonal changes on the phenological events in their life cycle. After flying from nests, the young birds still keep close to their parents for two weeks, which is essential for their adaptation and learning. This period provides young birds with the necessary protection from predators and promotes the learning of critically important survival skills from adults, which increases their chances of survival and further success in the wild (Mock, 2022). Understanding of those processes is important for assessing ecological and behavioral adaptations in the context of the climate changes (Åkesson et al., 2015).

Analysis of materials used in nest building, including anthropogenic components, is essential for understanding of the adaptive strategies of *Ph. phoenicurus* and impact of anthropogenic changes on ecological systems. Nests of the considered species are characterized by elaborate construction with thick side walls and rounded deepened basin, exemplifying a complex architecture. Use of an array of natural materials such as dry herbs, leaves, mosses, and feathers, together with the found anthropogenic materials (threads, string, bags) reflects the adaptive strategies of the species in response to environmental changes caused by human activity. This phenomenon demonstrates the ability of the species to effectively utilize new resources, which can positively affect their reproductive success due to easier access to materials and opportunity to create more protected or comfortable nests (Zawadzki et al., 2019; Jagiello et al., 2023). However, anthropogenic materials can also have negative impacts such as toxicity, threatening the health of birds and their brood, and can also potentially distort the ecological balance.

Direct topical relations of *Ph. phoenicurus* with various plants are multifaceted and multi-functional. Those connections are not limited to inhabitation of certain types of plant groups. They also encompass various aspects of bird's life such as using plants for song posts that are important for communication between individuals, and also as food substrate for nourishment. Furthermore, those plants serve as surroundings their nests, providing protection during breeding.

The data analysis we presented also demonstrates the diversity and ecological significance of species that inhabit nests of *Ph. phoenicurus* in birdboxes in different natural conditions. The collected data show that arthropods of nests of *Ph. phoenicurus* not only use the nest lining as a food source and place for breeding, but also actively affect the ecosystem, participating in the process of destruction of organic materials, and also parasitize the chicks. Moreover, presence of entomophages and other species that control populations of invasive pests indicates the important role of nest boxes as microsystems that support the balance between species and prevent excessive breeding of parasites and possible pathogens (Yarys et al., 2021a, 2021b).

In particular, among the studied arthropods, special attention should be paid to the representatives of Hemiptera, the Pentatomidae family – *Palomena prasina*, and the family Coreidae – *Coreus marginatus* and *Nemocoris falleni*, which end up in nests with brought-in nourishment for chicks or randomly, using plant detritus of the nests as: 1) food source; 2) place for winter diapauses. Of Diptera, we should note the Calliphoridae family, namely *Lucilia caesar*, which develops on chick corpses; the species *Protocalliphora azurea*, an ectoparasite that lives in the lining of nests of Passeriformes. Its larvae feed on blood of chicks, sucking them only for the period of nourishment, causing larval myiasis.

The Isopoda order was represented by only one species – *Armadillidium vulgare*. They feed mostly on plant decay (material for the nests), which was present in the nest boxes in large amounts. Of the Diplopoda class, we found the species *Rossiulus kessleri* – euribiont that is common in forests, southern oak forests, windbreaks in moderate latitudes, which consumes foliage (Pokhylenko et al., 2019; Kozak et al., 2020).

The Blattodea order was represented by *Ectobius lapponicus*, a nidicole that lives in forest litter and on corpses, winters in the ootheca stage in the litter; and also occurs in the diet of chicks of *Ph. phoenicurus*.

The species *Androlaelaps casalis* of the Laelapidae family is a typical entomophage often found in nests of various birds, including *Ph. phoenicurus* (Błoszyk et al., 2016; Garrido-Bautista et al., 2023). Considering the data of Alves et al. (2023), *A. casalis* feeds on juvenile stages of the mite *Dermanyssus gallinae*, hemophages and Tyroglyphoidea, and also dried blood and eggs of birds. In case of food shortage, *A. casalis* can become cannibalistic, attacking larvae and protonymphs (Czenze & Broders, 2011). In nests of *Ph. phoenicurus*, this mite can use various food sources that are available in the environment, including dead insects, carrion, possibly their own larvae, or other resources in nests. This type of interaction can be beneficial to *Ph. phoenicurus* during the reproduction period, because it promotes population control of insects that are harmful to it, which can parasitize birds or their chicks or be carriers of pathogens, causing infectious diseases, or can impose great harm on eggs and chicks, for example, by damaging, or eating, which can lead to loss of the brood and decline in bird populations.

The Coleoptera order is considered the richest in families and species that are saprophages that inhabit the century-old trees with hollows. Most of them were found in the diet of chicks and nest lining. The Elateridae family was represented by 5 species that are food in the diet of chicks. Those were *Athous haemorrhoidalis*, which is known for its beneficial qualities such as destroying larvae of hymenopteran and lepidopteran pests (Loskotova & Horak, 2016); *Ampedus sanguinolentus*, a cosmopolitan species, whose larvae develop in decaying trunks in river meadows and forests (Zaharia, 2006); *Ectinus aterrimus*, mostly a forest species that often occurs in decaying stumps, soil microbiota (Krzysztof, 2006); *Agriotes ustulatus*, a pest of the Poaceae family, which was reported to feed on plants of the Apiaceae family (*Heracleum mantegazzianum* Sommier & Levier, *H. sphondylium* L., *Anthriscus sylvestris* (L.) Hoffm.) in the study by Foster et al. (2019).

The Tenebrionidae family includes *Pseudocistela ceramboides* that is present in the diet of chicks, and the larval stage can be found in cavitated trunks of *Q. robur* (Milberg et al., 2016). *Prionychus ater* is a typical saproxylobiont, whose larvae (Lezhenina & Vasilieva, 2018) live under the bark and in rotten wood of *Q. robur*, and rarely other broad-leaved trees. Of the families Dermestidae, Coccinellidae, Cerambycidae, Rutelidae, we found one representative of each, namely *Dermestes murinus*, a nidicole (Fiera, 2013; Matuszewski et al., 2016); *Calvia quatuordecimpunctata*, a rare entomophage, possibly present in the diet of chicks; *Stenurella melanura*, a consumer of foliage from various trees, and a valuable component of the diet of *Ph. phoenicurus*; and *Phyllopertha horticola*, whose living environment is pastures with diversity of flowers and high share of weeds.

Our analysis of nidicoles in the nests of *Ph. phoenicurus* revealed that the greatest share was made up of arthropods that the birds use as nourishment for chicks. Of the arthropods found in the nest boxes of *Ph. phoenicurus*, *Athous haemorrhoidalis* numerically prevailed. The subdominant species in Hetmanskyi was *Selatosomus latus*; and in Homilshanskyi Forest it was *Pseudocistela ceramboides*.

The ratio between the biotope groups of nidicoles demonstrated significant differences between the parks, suggesting different ecological conditions. For example, prevalence of polytopic species in Hetmanskyi and larger share of forest species in Homilshanski Forests could be attributed to different characteristics of the environment, such as types of vegetation and level of anthropogenic impact.

The greater share of daytime species in Hetmanskyi indicates that those species have more opportunities for active feeding during the day. At the same time, the differences in the activity periods in Homilshanski Forest can point to different survival strategies depending on the ecological conditions and available resources.

The complexes of arthropods in the nests of *Ph. phoenicurus* in Homilshanski and Hetmanskyi Forests significantly varied in the trophic structure. In Homilshanski Forest, the greatest share was comprised of polyphages (33%), which have a broad food range. Phytophages accounted for 28%, and saprophages for 17%, which emphasizes the variety of sources of food for the chicks. At the same time, in Hetmanskyi Forest, polyphages made up 31%, while phytophages also accounted for 31%. The subdominant nidicoles in Hetmanskyi Forest were saprophages (19%), which could suggest specific ecological conditions in the area.

Conclusions

We found a high level of biodiversity of nidicoles in the nests of *Ph. phoenicurus* in the pine forests of northeast Ukraine in 2019–2023. Among the nidicoles, the greatest share was those for the nourishment of chicks. A significant portion of the arthropods in the nests of *Ph. phoenicurus* were polyphages. In Hetmanskyi, the indices of nidicole diversity in the nests of *Ph. phoenicurus* were the highest.

Employment of the Pearson correlation matrix revealed significant correlations among the year, number of arthropods, breeding success, and mean monthly temperature of the spring-summer period. In Homilshanski Forests, we observed a strong negative correlation (–1.00) between the years and significant number of arthropods, which could be related to the climate changes, loss of living locations, or anthropogenic activities. This underscores the necessity of monitoring for timely detection of changes and development of effective measures to preserve the ecosystems.

The obtained results allow a better understanding of the dynamics of populations of arthropods and reproduction of *Ph. phoenicurus* in the context of conditions that are important for preservation of biodiversity in the studied region, and also highlight the need of further research of the factors impacting the distribution and species composition of groups of arthropods in nests of *Ph. phoenicurus*.

The authors declare no conflict of interests.

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