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DIPTERAN ASSEMBLAGES IN RED-FOOTED FALCON (*FALCO VESPERTINUS*) NEST BOXES

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The Red-footed Falcon (*Falco vespertinus*) is a strictly protected raptor species in Hungary (*ca* 600 pairs). It naturally breeds in rook, crow or magpie nests that are rebuilt every year, however, most of these nests disappeared by the end of the 20th century. In the early 2000's more than a 3,000 artificial nest boxes were installed in the country, increasing the number of breeding pairs considerably. This prompts the question whether breeding birds might face an increased number of nest-dwelling ectoparasites due to the annual re-use of nesting sites. The nest material was collected from 59 nest boxes (not cleaned for 3 years) in Northern Hungary after the breeding season in 2009 and from 17 nest boxes (cleaned in previous year) in 2010. Emerging dipteran imagoes were identified to species level. Altogether 45,487 individuals of 42 fly species (2010: 37, 2011: 14) were reared; 88.1% of that was *Carnus hemapterus*, a well-known blood-sucking parasite. The number of *C. hemapterus* was significantly higher in nests where the last breeding bird species was Common Kestrel than Red-footed Falcon. In freshly cleaned nest boxes one order of magnitude lower number of *C. hemapterus* specimens were found. Our results indicate the necessity of cleaning the nest boxes annually.

Key words: bird nest, *Carnus hemapterus*, nest box cleaning, parasites, saprophytic flies.

INTRODUCTION

In the 1940s about 2000–2500 pairs of Red-footed Falcons (*Falco vespertinus* Linnaeus, 1766) bred in Hungary predominantly using Rook (*Corvus frugilegus* Linnaeus, 1758) nests. However, due to poisoning of corvids and changes in land use including a decline of animal husbandry, approximately 90% of previously available rookeries either became demolished or moved to urban habitats (Seres & Liker 2015) that are unsuitable for Red-footed Falcons (Fehérvári *et al.* 2009). Consequently, by 2006 the estimated number of Red-footed Falcon pairs was reduced to less than 600. An international conservation program (LIFE05 NAT/H/000122) initiated in 2006 with the primary objective to halt this tendency succeeded in increasing the number of breeding pairs, primarily through provisioning over 3,500 nest boxes. Today, approximately two-thirds of Red-footed Falcon pairs breed in these man-made structures in Hungary (Palatitz *et al.* 2015). However, the breeding birds might face new challenges here as compared to their natural nesting sites.

Colonial species, such as the Red-footed Falcon may experience higher prevalence of ectoparasites than solitary breeders (Brown & Brown 2004, Rózsa *et al.* 1996) that constitutes one of the main costs of coloniality (Brown & Brown 1986). Furthermore, while the Rook nests are rebuilt every year (Horváth *et al.* 2015), food remains and faeces accumulate in the litter of artificial nest boxes through subsequent years. Consequently, the number of blood-sucking arthropods, such as certain dipteran flies developing, overwintering or breeding in the nest material may increase in the boxes from year to year, resulting in increased parasitism for the nesting birds (Møller *et al.* 1990). Furthermore, bird species other than Red-footed Falcon also use these artificial nest boxes and they can possibly increase the abundance and diversity of ectoparasitic insects living there.

The nest-dwelling dipteran larvae are either (i) parasites sucking the birds' blood or tissue fluids, (ii) or enter the nestlings' epidermis to cause myiasis, (iii) or saprophages feeding on the litter and other organic substrates, (iv) or predators of other nidicolous invertebrates. Imagoes of some dipterans are sucking avian blood, while adults of some other fly species use avian nests as overwintering shelters.

Blood-sucking and nest-dwelling dipteran flies can exert various effects on avian broods. They might decrease the chicks' condition (Hoi *et al.* 2010), increase nestling mortality (Richner *et al.* 1993), increase physiological stress (Martínez-Padilla *et al.* 2004, Tomás *et al.* 2008, Cantarero *et al.* 2013), or decrease their fitness indirectly by transmission of blood parasites (Richner *et al.* 1993, Martínez-De La Puente *et al.* 2013).

In this study we investigated the dipteran assemblages of 3 years old accumulated, and one year old fresh nest materials from nest boxes after the breeding season of Red-footed Falcons. We aimed to answer the following questions:

1) was the species richness and abundance of the dipteran larval assemblages in the 3-year-old nesting material affected by the (i) number of breeding bird species during the former 3 years; (ii) or the species of the last bird breeding in the box?

2) What is the composition of the Diptera community in the 3 years versus the 1 year old accumulated nest material?

3) Is the hatching of *Carnus hemapterus* synchronised with the breeding periods of the different bird species using the same box?

MATERIAL AND METHODS

Study site and sampling

Field work was carried out in Borsodi-Mezőség, Mezőcsát (N47,769° E20,892°), Mezőnagymihály (N47,788°E 20,818°), at the protected area of the Bükk National Park Directorate in Northern Hungary in 2009 and 2010. Over 60–80 pairs of Red-footed Falcons bred in this area in nearly 200 artificial nest boxes each year, along with numerous Common Kestrels (*Falco tinnunculus* Linnaeus, 1758), Jackdaws (*Corvus monedula* Linnaeus, 1758) and Long-eared Owls (*Asio otus* (Linnaeus, 1758)). The investigated nest boxes were installed in the crown of Black locust (*Robinia pseudoacacia*) and poplar (*Populus* sp.) trees in 2006. The usual breeding bird sequence in a year is the following: Jackdaw, Long-eared Owl, Kestrel, Red-footed Falcon. Generally, Red-footed Falcons and the Kestrels start the breeding when the fledgling of Jackdaws left the nest boxes and, therefore, two consecutive species may occupy a given nest box in the same breeding season.

In 2009 we collected nest material from 59 nest boxes that were not cleaned for 3 years, while in 2010 we sampled the one-year old nest material from 17 nest boxes, cleaned in the year before. In the 2009 breeding season, the bird species breeding in the nest boxes were Long-eared Owl (n = 5), Jackdaw followed by Red-footed Falcon or Common Kestrel (n = 6), Red-footed Falcon (n = 16), Common Kestrel (n = 32); in 2010 all the nest boxes were occupied by Red-footed Falcon (n = 17). The nest materials were collected both years in October, when the nestlings already flew out, and stored in 10 × 30 cm linen sacks. As the identification of dipteran larvae is generally very difficult even at family level (Smith *et al.* 2000), we decided to rear the larvae to adults. We overwintered the nest substance in a cellar (to ensure stable temperature and similar overwintering probability). Translucent PET bottles were used in order to trap the hatching flies (Fig. 1). The hatching insects were collected in the next year from the end of April till August in every two weeks. All reared specimens were identified to species level.

Fig.1. Linen sack with translucent PET bottles were used to trap the hatching flies

Statistical analyses

We used generalized linear mixed effects models (GLMMs) to assess effects of number of breeding species over the 3 years, and the last breeding species on the species richness and abundance of all dipteran species and the abundance of *Carnus hemapterus*. Abundance of all dipterans and that of *C. hemapterus* were log10 transformed to reach normal residual distribution. We tested all predictor variables for multicollinearity by calculating the variance inflation factor (VIF) using vif function or Chi-squared test of independence for categorial variables. A maximum VIF value of 5 was taken as an indicator of multicollinearity (Rogerson 2001). The abundance of all dipterans was analysed at nest box level as collected, which were nested according to the colonies and those in settlements as random factors: settlement/colony. In addition, all pair-wise interactions were tested between the explanatory variables. Terms were removed sequentially in backward stepwise selection until only significant interactions and main effects ($P > 0.05$ from F test) remained in the minimal adequate model. All analyses were carried out in R, version 3.2.3 (R Core Team 2016) using the following packages: nlme (Pinheiro *et al.* 2017), stats (R Core Team 2016) and fmsb (Nakazawa 2015).

RESULTS

During the two-year study period 45,487 specimens of 42 dipteran species (2010: 37 species; 2011: 14 species) were reared from the 76 nests. According to the feeding habit of the larvae, 10 species (Muscidae, Sarcophagidae and Scenopinidae) were predatory, 32 species saprophagous, and only imagoes of 2 species proved to be blood-suckers. The overwhelming majority (88.1%) of individuals represented a single species, *Carnus hemapterus* (Table 1).

Table 1. Dipteran species reared, their larval feeding habit (LFH), total number of individuals (N) and occurrence ratio (OR) in the three-years old (2009) and one-year old (2010) nest box material. Abbreviation: SA = saprophagous, PR = predator.

Family	Species	LFH	2009		2010	
			N	OR (%)	N	OR (%)
Anthomyiidae	*Anthomyia procellaris* Rondani, 1866	SA	10	10.2	21	29.4
Carnidae	*Carnus hemapterus* Nitzsch, 1818	SA	39795	96.6	283	76.5
	Hemeromyia anthracina Collin, 1949	SA	586	64.4	14	17.6
	Hemeromyia longirostris Carles-Tolra, 1992	SA	8	8.5	0	0
	Meoneura neottiophila Collin, 1930	SA	0	0	8	23.5
	Meoneura prima (Becker, 1903)	SA	43	18.6	0	0
Cecidomyidae		SA	134	18.6	0	0
Drosophilidae	*Drosophila bifasciata* Pomini, 1940	SA	1	1.7	0	0
	Drosophila busckii Coquillett, 1901	SA	2	1.7	0	0
Fanniidae	*Fannia canicularis* (Linnaeus, 1761)	SA	24	20.3	0	0
	Fannia lineata (Stein, 1895)	SA	3	1.7	0	0
	Fannia manicata (Meigen, 1826)	SA	2	1.7	0	0

Family	Species	LFH	2009		2010	
			N	OR (%)	N	OR (%)
Fanniidae	*Fannia scalaris* (Fabricius, 1794)	SA	2	1.7	0	0
	Fannia sp. 1	SA	1	1.7	0	0
	Fannia sp. 2	SA	1	1.7	0	0
Heleomy-zidae	*Chiropteromyza broersei* (de Meijere, 1946)	SA	12	3.4	25	5.9
	Tephrochlamys laeta (Meigen, 1830)	SA	1	1.7	0	0
	Tephrochlamys rufiventris (Meigen, 1830)	SA	21	20.3	0	0
	Tephrochlamys tarsalis (Zetterstedt, 1847)	SA	1338	50.8	1378	94.1
Hippo-boscidae	*Ornithoica turdi* (Olivier in Latreille, 1811)	SA	1	1.7	0	0
Milichii-dae	*Leptometopa latipes* (Meigen, 1830)	SA	1451	71.2	118	82.4
	Madiza glabra Fallén, 1820	SA	11	3.4	0	0
Muscidae	*Hydrotaea armipes* (Fallén, 1825)	PR	13	6.8	0	0
	Hydrotaea hennigi Pont, 1985	PR	0	0	1	5.9
	Hydrotaea sp.	PR	0	0	1	5.9
	Muscidae sp. 1	PR	1	1.7	0	0
	Muscidae sp. 2	PR	8	1.7	0	0
	Muscina stabulans (Fallén, 1817)	PR	0	0	8	23.5
	Potamia littoralis Robineau-Desvoidy, 1830	PR	5	5.1	0	0
Psycho-didae	*Psychoda minuta* Banks, 1894	SA	0	0	59	35.3
Sarco-phagidae	*Sarcophaga argyrostoma* (Robineau-Des-voidy, 1830)	PR	11	5.1	0	0
	Sarcophagidae sp.	PR	1	1.7	0	0
Scenopi-nidae	*Scenopinus fenestralis* (Linnaeus, 1758)	PR	30	27.1	0	0
Sciaridae	*Bradysia* sp.	SA	1	1.7	0	0
	Sciaridae sp.	SA	1	1.7	0	0
Sphaero-ceridae	*Apteromyia claviventris* (Strobl, 1909)	SA	0	0	4	17.6
	Coproica hirtula (Rondani, 1880)	SA	11	10.2	0	0
	Ischiolepta pusilla (Fallén, 1820)	SA	4	6.8	0	0
	Spelobia sp.	SA	1	1.7	0	0
	Spelobia luteilabris (Rondani, 1880)	SA	0	0	11	17.6
	Spelobia pseudosetaria (Duda, 1918)	SA	15	15.3	6	17.6
	Telomerina flavipes (Meigen, 1830)	SA	1	1.7	0	0
	Total		43550		1937	

In boxes with nest material accumulated through three years, only the species identity of the last breeding bird had a significant effect on the number of *C. hemapterus* (df = 52, F = 4.187, p = 0.046). It was significantly higher when Common Kestrels bred in the same box in the former year, as compared to Red-footed Falcons (t = 2.1, df = 48.572, p = 0.041).

The average number of *C. hemapterus* in 2009 (3-year old nest material) was 674.5 ind./nest, while in 2010 (one year old nest material) it was 16.6 ind./nest. The hatching time curve of *C. hemapterus* was bimodal from the 2009 nest material from those nests, where both Jackdaws (early peak in May) and Kestrels or Red-Footed Falcons (a second peak in July) bred. Contrarily, this curve was unimodal from nest boxes with only one late breeding bird species in the last year, with its maximum in the second part of the summer (Fig. 2).

DISCUSSION

The breeding population of the Red-footed Falcon has been successfully increased in Hungary by using artificial nest boxes during the last ten years

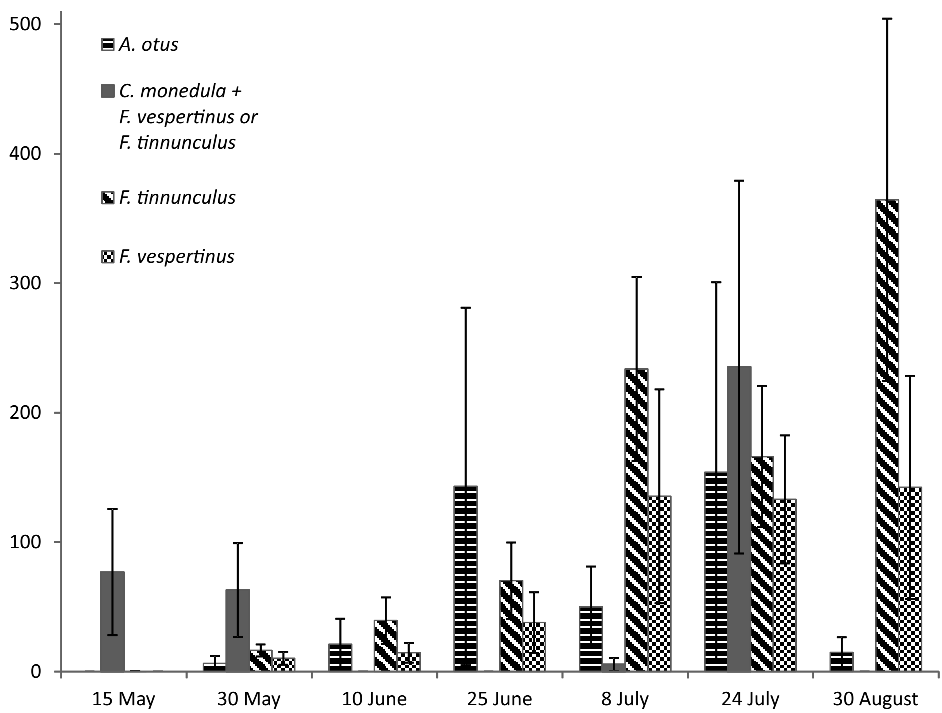

Fig. 2. Phenology of emergence of *Carnus hemapterus* imagoes from three years old accumulated nest material (collected in 2009), grouped by the last breeding bird species (n = number of nest boxes) within the nest (mean ± SEM)

(Palatitz *et al.* 2015). The adjoining arthropod communities in the accumulating nest material and the potential harms they may cause to the nestlings, however, are still poorly known. There are only a few studies dealing with the dipteran communities of the nests of raptor birds (Philips & Dindal 1990, Kaľavský *et al.* 2009). In our study we sampled the Diptera assemblages of these artificial nest boxes and our aim was to survey the entire dipteran fauna connected to the nest boxes with a special focus on parasitic flies.

Our investigations have been carried out in two separate nest box colonies installed for Red-footed Falcons. During the two years of sampling from 76 nest box materials, in which four bird species bred, altogether 45,487 dipteran specimens belonging to 42 species were reared. These numbers, regarding both the number of species and individuals, are remarkably higher than found in raptor bird nests by the former investigations (Philips & Dindal 1990, Papp & Paulovics 2002, Kaľavský *et al.* 2009, Lesko & Smallwood 2012, Lange 2015). A possible reason for this difference is the different breeding habit of the birds, as most raptors are solitary breeders, while the Red-footed Falcon tends to breed colonially. Colonial species may experience higher prevalence of ectoparasites as compared to solitary breeders (Rózsa *et al.* 1996, Brown & Brown 2004).

Analysing the frequency of the dipteran species in our samples, we found that 90% of the species (38 species) were rare (i.e., less than 0.01% of the whole sample). This ratio is very similar to that of found in case of free-living dipteran species utilizing point-like food sources, such as dung, fermenting fruit etc. (Papp 1998). The majority of the reared individuals were *C. hemapterus*, a well-known blood-sucking parasite of bird chicks. Due to ethical reasons, we collected nest materials only after all birds left the colony, and probably this is the reason why we found no parasitic Calliphoridae and Muscidae specimens.

In former investigations, only 8 dipteran species, *C. hemapterus*, *Cynomya mortuorum*, *Meoneura neottiophila*, *Ornithomya avicularia*, *Potamia littoralis*, *Protocalliphora avium*, *Scenopinus fenestralis* and *Scoliocentra brachypterna* were known to occur in the nests of the four bird species involved in our study (Red-footed Falcon, Common Kestrel, Jackdaw and Long-eared Owl) (Hicks 1959, Hicks 1962, Bohm 1978, Rotheray 2012, Amat-Valero *et al.* 2013, Sumasgutner *et al.* 2014, Lange 2015). We found only three of these species (*C. hemapterus*, *M. neottiophila*, *S. fenestralis*), therefore, all the other 39 species are new for the nest fauna of these birds. It is worth mentioning that while the samples collected in 2009 originated from the nests used by four bird species, the samples from 2010 were exclusively from the nest boxes of the Red-footed Falcon. Formerly only *C. hemapterus* was found in the nests of Red-footed Falcon (Hicks 1962, Fehérvári *et al.* 2015) and, therefore, the additional 13 dipteran species recorded from the 2010 samples are reported here for the first time to occur in the nests of *F. vespertinus*. The samples included 8 dipteran species

(*Drosophila bifasciata*, *Drosophila busckii*, *Hydrotaea hennigi*, *Psychoda minuta*, *Coproica hirtula*, *Spelobia pseudosetaria*) which were recorded by us for the first time to occur in avian nests. In addition, one of the species, *Fannia lineata*, is new for the fauna of Hungary. Since formerly only a very few studies targeted the dipteran assemblages of the bird nests in Hungary (Liker *et al.* 2001, Papp & Paulovics 2002), the occurrence of this *Fannia* species in the Hungarian fauna was probably overlooked.

Carnus hemapterus is an obligatory nest-dwelling avian ectoparasite, having been found in the nests of >50 bird species (Grimaldi 1997, Brake 2011) including raptors. Certain studies indicated that *C. hemapterus* infestations had a negative effect on the condition of the chicks of *Colaptes auratus* (Wiebe 2009), *Sturnus unicolor* (Avilés *et al.* 2009) and *Merops apiaster* (Hoi *et al.* 2010), but no significant negative effects were found in case of raptors (Dawson & Bortolotti 1997, Kaľavský *et al.* 2010). However, apart from blood loss and discomfort caused by their bites, these flies are also important as vectors of *Plasmodium* and *Haemoproteus* infections (Vaclav *et al.* 2016).

In the nest litter accumulated through three consecutive years, the number of *Carnus hemapterus* individuals was on average an order of magnitude higher than in the one year old nest materials. The formerly published data on the abundance of *C. hemapterus* (Liker *et al.* 2001, Valera *et al.* 2003, Sumasgutner *et al.* 2014) were roughly similar to our samples from the one-year old nest boxes. This fact indicates a marked increase of *C. hemapterus* abundance during the re-use of nest through consecutive years. Certain investigations pointed out that in the nests of Kestrels (Sumasgutner *et al.* 2014) and Barn Owls (Roulin 1998) the abundance of *C. hemapterus* was higher in nests with accumulated litter than in cleaned ones. Although in these cases there was no significant correlation between the increased parasite numbers and the breeding success, the accumulation periods were shorter and the increase of parasite abundance was much smaller than in our study. In nests not cleaned for years, the increase of *C. hemapterus* abundance is supposedly greater because the pupae may exhibit diapause through several years (Valera *et al.* 2006). Furthermore, the saprophagous larvae may also benefit form greater food resources and higher relative humidity in the accumulating debris of uncleaned nest boxes. The lower competition of larvae for the larger amount of multi-years nest material could also positively influence the development and survival of immatures and, consequently, the number of hatched adults. The nest boxes in the Hungarian breeding colonies are often not cleaned every year, therefore, subsequent studies should clarify the effect of accumulated nest litter on the breeding conditions of birds.

Our study indicated that the abundance of *C. hemapterus* was significantly higher when the Kestrel was the last breeder in the nest box, as compared to cases when the Red-footed Falcon was the ultimate breeder. The reason of this difference could be the different size of their broods: the Kestrel is larger-bodied and it has usually 5–6 nestlings, while the Red-footed Falcon is smaller and it has only 3–4 chicks. Supposedly, a larger mass of chicks in Kestrel broods may maintain more parasitic flies, that can lay more eggs and, therefore, the abundance of the next generation of flies may be larger as well.

The synchronisation of the *C. hemapterus* generations to bird breeding was recorded in different nestling developmental stages of the same bird species (Liker *et al.* 2001, Calero-Torralbo *et al.* 2013), as well as to different bird species breeding in the same area, but not in the same nests (Valera *et al.* 2003). This synchronisation is inevitable for the flies because the freshly hatched adults die without feeding within 2–3 days (Calero-Torralbo *et al.* 2013). We also observed synchronisation to 2 bird species subsequently occupying the same nest within a single breeding season. In the samples hatching in 2010 there were two peaks of *C. hemapterus* abundance (in May and in July) in the nest boxes used by Jackdaws and *Falco spp.*, while there was only one summer peak in the other nests used only by *Falco* spp. (Fig. 2). This likely indicates that some of the flies synchronised their life cycle to Jackdaws, while others to the Common Kestrels and Red-footed Falcons that breed remarkably later.

Our study demonstrates that the nest boxes installed for the Red-footed Falcons and used by more bird species are inhabited by surprisingly diverse dipteran assemblages. We plan future studies to investigate the behaviour of parasitic dipterans and to compare the composition of fly assemblages in colonial versus solitary nest boxes. Moreover, the comparison of the assemblages of these nest boxes and the natural breeding sites in Rook colonies would provide further important information about the accommodation of these dipteran groups to the different nest types. Finally, further studies would be necessary to clarify the possible effect of the accumulation of nest litter to the composition and abundance of the dipteran assemblages inhabiting avian nests.

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REFERENCES

Amat-Valero, M., Calero-Torralbo, M. A. & Valera, F. (2013): Temperature during the free-living phase of an ectoparasite influences the emergence pattern of the infective phase. – *Parasitology* **140**: 1357–1367. https://doi.org/10.1017/S0031182013000929

Avilés, J. M., Pérez-Contreras, T., Navarro, C. & Soler, J. J. (2009): Male spotless starlings adjust feeding effort based on egg spots revealing ectoparasite load. – *Animal Behaviour* **78**: 993–999. https://doi.org/10.1016/j.anbehav.2009.07.020

Bohm, R. T. (1978): Protocalliphora infestation in great horned owls. – *Wilson Bulletin* **90**: 297.

Brake, I. (2011): World catalog of the family Carnidae (Diptera, Schizophora). – *Contributions to the Systema Dipterorum (Insecta: Diptera). Myia* **12**: 113–169.

Brown, C. R. & Brown, M. B. (1986): Ectoparasitism as a cost of coloniality in cliff swallows (Hirundo pyrrhonota). – *Ecology* **67**: 1206–1218. https://doi.org/10.2307/1938676

Brown, C. R. & Brown, M. B. (2004): Empirical measurement of parasite transmission between groups in a colonial bird. – *Ecology* **85**: 1619–1626. https://doi.org/10.1890/03-0206

Calero-Torralbo, M. A., Vaclav, R. & Valera, F. (2013): Intra-specific variability in life-cycle synchronization of an ectoparasitic fly to its avian host. – *Oikos* **122**: 274–284. https://doi.org/10.1111/j.1600-0706.2012.20374.x

Cantarero, A., López-Arrabé, J., Rodríguez-García, V., González-Braojos, S., Ruiz-De-Castañeda, R., Redondo, A. J. & Moreno, J. (2013): Factors affecting the presence and abundance of generalist ectoparasites in nests of three sympatric hole-nesting bird species. – *Acta Ornithologica* **48**: 39–54. https://doi.org/10.3161/000164513X669982

Dawson, R. D. & Bortolotti, G. R. (1997): Ecology of parasitism of nestling American kestrels by Carnus hemapterus (Diptera: Carnidae). – *Canadian Journal of Zoology* **75**: 2021–2026. https://doi.org/10.1139/z97-835

Fehérvári, P., Harnos, A., Neidert, D., Solt, S. & Palatitz, P. (2009): Modeling habitat selection of the red-footed falcon (Falco vespertinus): a possible explanation of recent changes in breeding range within Hungary. – *Applied Ecology and Environment* **7**: 59–69.

Fehérvári, P., Piross, I. S., Kotymán, L., Solt, S., Horváth, É. & Palatitz, P. (2015): Species specific effect of nest-box cleaning on settlement selection decisions in an artificial colony system. – *Ornis Hungarica* **23**: 66–76. https://doi.org/10.1515/orhu-2015-0006

Grimaldi, D. (1997): The bird flies, genus Carnus: species revision, generic relationships, and a fossil Meoneura in amber (Diptera: Carnidae). – *American Museum Novitates* **3190**: 1–30.

Hicks, E. A. (1959): *Check-list and bibliography on the occurrence of insects in birds' nests.* – Iowa State University Press, Ames, 681 pp.

Hicks, E. A. (1962): Check-list and bibliography on the occurrence of insects in birds' nests: Supplement 1. – *Iowa State Journal of Science* **36**(3): 233–348.

Hoi, H., Kristofik, J., Darolova, A. & Hoi, C. (2010): Are parasite intensity and related costs of the milichiid fly Carnus hemapterus related to host sociality? – *Journal of Ornithology* **151**: 907–913. https://doi.org/10.1007/s00265-014-1808-6

Horváth, É., Solt, S., Kotymán, L., Palatitz, P., Piross, I. S. & Fehérvári, P. (2015): Provisioning nest material for Rooks; a potential tool for conservation management. – *Ornis Hungarica* **23**: 22–31. https://doi.org/10.1515/orhu-2015-0002

Kaľavský, M., Fenďa, P. & Holecová, M. (2009): Arthropods in the nests of the Common Kestrel (Falco tinnunculus). – *Slovak Raptor Journal* **3**: 29–33.

Kaľavský, M. & Pospisilova, B. (2010): The ecology of ectoparasitic species Carnus hemapterus on nestlings of common kestrel (Falco tinnunculus) in Bratislava. – *Slovak Raptor Journal* **4**: 45–48.

Lange, L. (2015): The carnid fly Carnus hemapterus in the Steinburg district (Itzehoe, Schleswig-Holstein) also found on the eagle owl. – *EulenWelt* **2015**: 38–39.

Lesko, M. J. & Smallwood, J. A. (2012): Ectoparasites of American Kestrels in northwestern New Jersey and their relationship to nestling growth and survival. – *Journal of Raptor Research* **46**: 304–313. https://doi.org/10.3356/JRR-11–56.1

Liker, A., Markus, M., Vozar, A., Zemankovics, E. & Rozsa, L. (2001): Distribution of Carnus hemapterus in a starling colony. – *Canadian Journal of Zoology* **79**: 574–580. https://doi.org/10.1139/cjz-79-4-574

Martínez-De La Puente, J., Martínez, J., Rivero-De-Aguilar, J., Del Cerro, S. & Merino, S. (2013): Vector abundance determines Trypanosoma prevalence in nestling blue tits. – *Parasitology* **140**: 1009–1015. https://doi.org/10.1017/S0031182013000371

Martínez-Padilla, J., Martínez, J., Dávila, J., Merino, S., Moreno, J. & Millán, J. (2004): Within-brood size differences, sex and parasites determine blood stress protein levels in Eurasian kestrel nestlings. – *Functional Ecology* **18**: 426–434. https://doi.org/10.1111/j.0269-8463.2004.00874.x

Møller, A. P., Allander, K. & Dufva, R. (1990): Fitness effects of parasites on passerine birds: a review. Pp. 269–280. – *In: Population biology of passerine birds*. Springer.

Nakazawa, M. (2015): fmsb: Functions for Medical Statistics Book with some Demographic Data. R package version 0.5.2. https://CRAN.R-project.org/package=fmsb

Palatitz, P., Fehérvári, P., Solt, S. & Horváth, É. (2015): Breeding population trends and pre-migration roost site survey of the Red-footed Falcon in Hungary. – *Ornis Hungarica* **23**: 77–93.

Papp, L. (1998): "Outlaws": some evolutionary aspects of rarity in insects. – *Tiscia* **31**: 29–33.

Papp, L. & Paulovics, P. (2002): On the life-habits and developmental stages of Nidomyia cana Papp (Diptera, Borboropsidae). – *Journal of Natural History* **36**: 979–989. https://doi.org/10.1080/00222930110061850

Philips, J. & Dindal, D. (1990): Invertebrate populations in the nests of a screech owl (Otus asio) and an American kestrel (Falco sparverius) in central New York. – *Entomological News* **101**: 170–192.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & Team, R. C. (2017): nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–131. 2017. http://CRAN.R-project.org/package=nlme

R Core Team (2016): A Language and Environment for Statistical Computing. – R Foundation for Statistical Computing, Vienna, Austria 2016. http://www.R-project.org

Richner, H., Oppliger, A. & Christe, P. (1993): Effect of an ectoparasite on reproduction in great tits. – *Journal of Animal Ecology* **62**(4): 703–710.

Rogerson, P. (2001): *Statistical methods for geography*. – Sage. London, 236 pp.

Rotheray, G. E. (2012): Morphology of the puparium and breeding sites of eight species of Heleomyzidae (Diptera). – *Journal of Natural History* **46**: 2075–2102.

Roulin, A. (1998): Reproductive cycle and abundance of Carnus hemapterus a parasitic diptereae in barn own Tyto alba broods. – *Alauda* **66**: 265–272.

Rózsa, L., Rékási, J. & Reiczigel, J. (1996): Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera). – *Journal of Animal Ecology* **65**(2): 242–248.

Seres, G. & Liker, A. (2015): Habitat urbanization and its effects on birds. – *Acta Zoologica Academiae Scientiarum Hungaricae* **61**(4): 373–408. https://doi.org/10.17109/AZH.61.4.373.2015

Smith, K. G. V. & Ferrar, P. (2000): 1.6. Key to families – larvae. Pp. 2001–2239. *In*: Papp, L. & Darvas, B. (eds): *Contributions to a manual of Palaearctic Diptera*, vol. 1. – Science Herald, Budapest.

Sumasgutner, P., Vasko, V., Varjonen, R. & Korpimaki, E. (2014): Public information revealed by pellets in nest sites is more important than ecto-parasite avoidance in the settlement decisions of Eurasian kestrels. – *Behavioral Ecology and Sociobiology* **68**: 2023–2034. https://doi.org/10.1007/s00265-014-1808-6

Tomás, G., Merino, S., Martínez-de la Puente, J., Moreno, J., Morales, J. & Lobato, E. (2008): Determinants of abundance and effects of blood-sucking flying insects in the nest of a hole-nesting bird. – *Oecologia* **156**: 305–312. https://doi.org/10.1007/s00442-008-1001-6

Václav, R., Bétaková, T., Švančarová, P., Pérez-Serrano, J., Criado-Fornelio, Á., Škorvanová, L. & Valera, F. (2016): Nest ecology of blood parasites in the European roller and its ectoparasitic carnid fly. – *Experimental Parasitology* **165**: 71–80. https://doi.org/10.1016/j.exppara.2016.03.014

Valera, F., Casas-Criville, A. & Calero-Torralbo, M. A. (2006): Prolonged diapause in the ectoparasite Carnus hemapterus (Diptera: Cyclorrhapha, Acalyptratae) – how frequent is it in parasites. – *Parasitology* **133**: 179–186. https://doi.org/10.1017/s0031182006009899

Valera, F., Casas-Criville, A. & Hoi, H. (2003): Interspecific parasite exchange in a mixed colony of birds. – *Journal of Parasitology* **89**: 245–250. https://doi.org/10.1645/0022-3395(2003)089[0245:ipeiam]2.0.co;2

Wiebe, K. L. (2009): Nest excavation does not reduce harmful effects of ectoparasitism: an experiment with a woodpecker, the northern flicker Colaptes auratus. – *Journal of Avian Biology* **40**: 166–172. https://doi.org/10.1111/j.1600-048X.2009.04481.x

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