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Ecology of *Proctophyllodes megaphyllus* and *Analges* sp. of the *Prunella modularis* in the West Carpathian region

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Abstract. This study describes the ecology of the dominant feather mite species found on the dunnock (*Prunella modularis).* By comparing mean abundance, prevalence, and intensity during different seasons throughout the annual life cycle of the dunnock, the life cycle of *Proctophyllodes megaphyllus* and *Analges* sp. was examined. Thanks to the collection of feather mites from dead host specimens, it was possible to compare differing abundance on certain parts of the body and thus better understand the population dynamics of both species. Each species have been shown to have different life strategies. In *Analges* sp., population dynamics are adapted to vertical transmission, while *Proctophyllodes megaphyllus* has adapted its to horizontal transmission despite the unusual social behavior of the dunnock. According to our results, feather mites are likely to adapt their lives to their environment, respectively of their host. This may also provide some insights in response to the question of whether feather mites should be called parasitic or ectosymbionic organisms.

Key words: dunnock, ectoparasites, ectosymbionts, acari, ecology, population dynamics

Introduction

This research studies ecology and population dynamics of the two most common feather mite species of dunnock (*Prunella modularis* Linnaeus 1758) - *Analges* sp. and *Proctophyllodes megaphyllus* (Trouessart 1885). These species live in friable layer of feathers, primary flight feathers and basal body parts (Trouessart 1885). The species are symbionts and there is no clear evidence of competitive behaviour between them. Feather mites cannot live on dropped feathers. Their inability to move rarely allows them to survive outside the body of the host (Dubinin 1951). Increasing preening in the spring and autumn influences the behaviour, movement of population, and ecology of each of these ectoparasites (Janiga and Romanová 1996).

Feather mites occupy four main types of microhabitats on the body of birds: plumulaceous down feathers; vane surfaces of contour feathers; the interior of the quills of flight and tail feathers; and the surface of the skin. The dominant species found on *P. modularis* are *P. megaphyllus* and *Analges* sp. (Dabert and Mironov 1999). *Analges* sp. mostly resides in the friable layer of down feathers, while *P. megaphyllus* generally live in primary feathers. It is therefore assumed that there is no spatial or resource competition between the species. The relationship between feather mites and avian hosts like *P. modularis* is still very unclear. Opinions on whether feather mites are considered parasites of ectosymbionts vary considerable. Ecology of feather mites is generally under-studied compared to species such as chewing lice, which also live on bird hosts (Behnke *et al.* 1995). However, with the chewing lice there is a proven detrimental impact on fitness of the host, because of their consumption of blood and paria. Thus, they are considered parasites.

Factors such as seasonal variation, reproduction, social behavior, and patterns related to yearly cycles of dunnock are an important variable in life and population dynamics of ectosymbionts. The reproduction period is referred to as the period with the most load for feather mites. Studies suggest that the life of the host is affected by the ecology of feather mites in large measure. There is no research yet dedicated to the population dynamics and ecology of feather mite species and *P. modularis*. Similar research has been conducted on *Prunella collaris* Scopoli 1786. (Janiga and Kubašková 2000; Kašlík and Janiga 2016), which inhabits exclusively alpine environments. Parasite populations are typically aggregated among their host individuals, but the degree of aggregation varies greatly over time and among populations and species of parasites.

The nature of ecological interactions between mites and their bird hosts is still very controversial today. Many studies consider all symbiotic organisms to be parasites. According to this hypothesis, symbionts are also associated with host characteristics and they are factor in the choice of sexual partner (Blanco *et al.* 1999). While no way yet been explained by which feather mites can harm their host, some authors assume that feather mites are clearly parasites and they can hurt their host and they also provide correlation and experimental evidence for this hypothesis (Pérez-Tris *et al.* 2002; Figuerola *et al.* 2003). According to some research, feather mites can have a detrimental impact on the host. It is likely that some host species are selectively adapting to this

relationship by decreasing the size of their uropygial gland. This leads to a reduction in intensity of feather mite species (Galván *et al.* 2008).

On the contrary, other studies suggest that feather mites bring benefits to their hosts (Campos *et al.* 2011; Dona *et al.* 2018) or have no impact (Dowling *et al.* 2001). Feather mites consume uropygial oil and maintain its quantity at optimal levels required for function. Old uropygial oil acuumulates on plumage and caused it to lose its insulating ability (Blanco and Frías 2001). Feather mites can increase the effectiveness of preening by removing excess uropygial oil (Hubálek 1994; Burtt and Ichida 1999; Blanco and Frías 2001). In addition to uropygial oil mites feed on fungal spores, algae, bacteria that damages feathers and in some cases, on pollen (O'Conor 1982). Feather mites can also control the number of pathogenic microoganisms (O'Conor 1982; Blanco and Frías 2001). Therefore, the nature of the interaction between mites and their hosts remains an unanswered question, the resolution of which would have diverse evolutionary implications, given that mites are present in the feathers of almost all bird species (Proctor 2013).

Prevalence and intensity of feather mites on Passeriformes

Differences in feather mite prevalence are related to seasonal changes in the host's physiological state associated with migration. Changes in dispersion and methods of aquisition are related to an increase in host social activity prior to migration. During this period, the hormonal activity that affects the formation of uropygial oil increases. Conversely, the physiological condition of the host after breeding season is stagnating or decreasing, which means there is less sustenance in the form of uropygial oil for mites. Thus, most species have adapted their reproduction to the season, which will provide them with the greatest amount of food and increase the chances of wider dispersion and horizontal transmission (Blanco and Frías 2001).

Research on the prevalence and intensity of feather mites in Passerines (119 bird species) found that these values differ between species (Diaz-Real *et al.* 2014). Differences between habitats were negligible, which means that local factors (breeding season, weather, habitat, spatial autocorrelation and researcher identity) play a secondary role. Almost 100% prevalence was found in Linnet, *Linnaria cannabina* (Linnaeus 1758) with no differences between gender or age groups (Blanco *et al.* 1999). Repeated prevalence and lower intensity values were found in Passeriformes (Diaz-Real *et al.* 2014).

Feather mites living on wings were examined on Portuguese Passeriformes in 1995. A correlation between body mass and abundance values was found. Intensity levels positively correlated with host body size - more body mass provides a larger habitat (Behnke *et al.* 1995). On the other hand, research from 2018 statesvthat there is no relationship between feather mite abundance and body size or fitness, independent of host species and sex (Matthews *et al.* 2018).

In 2013 and 2014 Passerines were studied in the Azores. 19 feather mite species belonging to the superfamily Analgoidea, including the Analgidae and Proctophyllodidae families were detected. In most of the bird host species the prevalence of Analgoidea was very similiar to their prevalence in european passerine species, including *Turdus merula, Pyrrhula murina* and *Fringilla* sp. Prevalence of this species reached 100% in both Analgoideae and Proctophyllodidae families (Rodrigues *et al.* 2015).

Cooperative breeding means that one or more individuals of a social group take care of offspring regardless of lineage. These helpers or auxiliaries are non-breeding adults that help to care for offspring. This care includes feeding, nest construction, and even incubation, which may influence the vertical transmission of mites (Stacey and Koenig 1990). Transmission of mites from parent to child, during or after birth, is called vertical transmission. Horizontal transmission is caused by physical contact between two or more individuals (Biosci 2000). Cooperative breeding is also assumed to result in higher ectoparasitosis levels. Poinani's (1992) comparative analysis investigated this hypothesis in Australian Passerines. This research has shown that in non-migrating species, cooperative breeding increases the number of parasites per host. Conversely, migrating non-cooperative breeding species are characterized by less dense transferable ectoparasites per host. Generally, the number of ectoparasites increases in proportion to the host's weight and relative abundance.

Factors shaping the community and population structure

In symbiosis ecology, understanding why host species vary greatly in ectoparasite or symbiont counts and how this may depend on ecological host and symbiotic characteristics is a major question. Some symbiotic taxa may be specialized in tracking changes in the quantity and quality of food sources that the host provides to improve reproduction and dispersal. Some species can therefore adapt their lifestyle strategy, activity and conditions of reproduction to specific stages in the host's life, such as retching or nesting (Blanco and Frías 2001).

Recently, there has been a hypothesis that mites are ectosymbionts of birds living on the skin, in feathers or on the surface of feathers (Campos *et al.* 2011). Depending on the taxon, they feed on uropygium oil, dead skin, fungi, bacteria and, to a lesser extent, the feathers themselves. Feather mites are a diverse group of ectosymbionts that occur on most bird species. We know of more than 2000 described species (Mironov and Proctor 2011). The size of the individual has been shown to correlate with the size of the mite population on its body (Proctor 2013). Thus, the body weight of the host may also affect mite diversity. Larger hosts provide more resources and therefore support larger ectosymbiont populations (Poulin 2007).

Another factor affecting abundance is the size of the uropygial gland. Since uropygial oil is an important source of food, its production directly correlates with infestation values. This correlation is also associated with mating seasonality. The relation-

ship of infestation and gland size varies between migrating and residential species (Galván and Sanz 2006; Galván *et al.* 2008).

For nearly every bird species there is a specific species of parasite. These can be endoparasites or ectoparasites. Endoparasites, and in this case haemoparasites that inhabit a host's bloodstream, can be one of the factors affecting the life of mites in a bird host. In 2004, it was found that many bird species which were free of haemoparasites, were highly infested by ectoparasites. Forbexample, some Procellariiformes and alpine swifts, were highly infested with ectoparasites but free of haemoparasites. Often, haemoparasites kill their host, or adversely affect them, thereby creating undesireable conditions for feather mite life (Gonzalez-Solis and Abella 1997; Merino and Minguez 1998; Tella *et al.* 1998; Martinez-Abrain *et al.* 2004).

One important factor that is often overlooked in investigating ectosymbionic diversity is the influence of the host's abiotic environment (Malenke *et al.* 2011). In particular, the diversity of arthropods on the body of birds can be affected by many climatic factors (Møller 2009). Kruskal – Wallis tests were used to support the feather mite migration hypothesis of *Proctophyllodes stylifer* species in blue tits (*Cyanistes caeruleus*). The findings revealed that during cold environmental conditions, feather mites actually aggregate on tertiary remiges. In addition, *P. stylifer* not only spread to remiges of blue tits during warm weather conditions, but statistical data revealed that feather mites prefer to aggregate on the host's primary remiges. Thermal imaging supports the hypothesis, that tertiary remiges are actually warmer or better insulated than primary and secondary remiges (Schmit 2011). This may also apply to the migration of the feather mites throughout the body from colder to warmer body parts.

One of the aims of this study is track how the incidence and social behaviour of *P. modularis* affects the population dynamics and the life strategy of its dominant feather mite species. We will compare population dynamics of the feather mite species sharing the host - *P. megaphyllus* and *Analges* sp. – similar to *Analges pollicipatus* which commonly infests Alpine accentors (*P. collaris).* They are morphologically close to the dunnock, due to joint membership of the family Prunellidae (Haller 1882). One of the goals of our study is to describe the ecology of feather mites compared to seasonal activities of the host species, including preening, breeding, nesting and migration, as well as to find out how mite aggregations are related to environmental conditions.

Material and Methods

Study area

All bird samples were collected between 1998 – 2016. The birds were found dead – either as roadkill, or in the ornithological nets used during previous research. Hosts were collected in characteristic habitats for *P. modularis*; mountain and submountain zones of the Western Carpathians, located in Slovakia. This included localities in: The High Tatra mountains (Veľká Studená dolina, Velická dolina, Dolina Bielych plies); Low Tatra mountains (Demänovská dolina, Chopok, Stredná hoľa, Veľký Choč); Western Tatras (Červenec), Belianske Tatras (Tatranská Javorina, Podspády, Ždiar); Great Fatra mountains (Suchý vrch); and the Oravské Beskydy mountains (Oravská priehrada, Babia hora). All locations are between 665 – 1719 m a.s.l.

Collecting the ectoparasites

All bird samples were stored in a deep-freezer, so it was neccesary to melt them before the mites were extracted. Frozen individuals thawed for a minimum of half an hour at room temperature in a Petri dish. Maturity and sex were determined after complete thawing. Gender was determined by examining cloacal protuberancies and surrounding feathers (Janiga, pers. observation). In the case of young individuals or unclear prominences, the sex was determined by autopsy. For the extraction of feather mites, birds were moved to a soft polystyrene pad for the extraction of parasites. Using pins and preparation needles, different areas of plumage were scanned. Mites were collected using feather forceps and transferred to an Eppendorf with 90% ethanol. Species, gender, and the area of the host's body it inhabited were recorded for each mite (Mironov 2012). Mites found in the Petri dish or on the polystyrene pad may not have been included because of the inability to determine the original body part they came from. Mite sites were divided as follows: head, right wing, left wing, chest, back and tail. Mites were stored in an Eppendorf filled with ethanol and placed in the refrigerator for next use (Balát 1959; Zlotorzycka 1972).

Statistical processing of the data

The matrix of data consists of a feather mite identifier (numbers were used), site, feather mite species, sex, maturity (whether feather mite was adult or juvenile), identifier of a dunnock (PMx), date and location of sampling, sex, maturity, altitude and mercury level. The intensity, abundance and prevalence during the periods April-May, June-July, and August-September were evaluated using Quantitative Parasitology 3.0 (Rózsa *et al.* 2000). To understand this study, it is important to be familiar with the terminology of QP3.0 software. This terminology is often used in connection with study of the parasitic relationship. Site refers to the exact location of feather mites on the body of a bird host. Locality is the region or geographic location where the host was found. Prevalence is a very common term used in the field of parasitology. It shows the proportion of hosts infected with a particular species of parasite and the number of individuals examined for this species. It is expressed as a percentage, but in mathematical operations it is used in the form of a ratio, or respectively, a fraction. QP3.0 uses two methods to determine the confidence level for prevalence. It is recommended to use 95% confidence limits for prevalence in most cases. Mean intensity is the average number of parasites found in all hosts excluding the uninfected specimens, which are de-

scribed as zero values. The median number of examined parasites, therefore, represents a typical level of infestation. Unlike mean intensity, this quantity is not affected by extremely infected hosts. The mean number of parasites found in all host specimens is called the mean abundance. This measure includes uninfected subjects as well (Rózsa *et al.* 2000).

Results

Parasite quantification

Out 30 hosts, 364 specimens of *Analges* sp. and 257 *P. megaphyllus* were found. The total prevalence was 100% (Table 1,2) and was the smallest in males of the symbiont species (93.3%). *Analges* sp. had a mean intensity level of 2.29 in males and 6.83 in females, while the general mean intensity level was 12.10. Females were the most numerous group in our samples, accounting for 56% of the total count. Nymphs and males were responsible for the remaining 26% and 18%, respectively. *P. megaphyllus* mean intensity was 8.57. The lowest mean intensity was 2.0 in nymphal individuals and the variance-to-mean ratio was 0.63 (Table 2). 47% of all specimens were females, 32% males and the smallest group was nymphal and represented 21%.

Seasonality

448% of the feather mites (*Analges* sp.) were collected from hosts found in June - July, 32% in April-May, and 20% in August and September. Mean intensity was significantly higher in August and September compared to April – May and June - July. In June and July prevalence showed a significant increase when compared with other months (Table 3, Table 4). The prevalence values of both feather mite species reached 100% in all months. Mean intensity of *P. megaphyllus* was significantly higher on hosts collected in spring, respectively in April and May. Confidence limits for prevalence were higher in June and July compared to other months (Table 5).

Comparison of sex-relatedgroups

When it comes to sexual variation of *Analges* sp., only male x nymph (Table 6, Table 7) mean intensity was significantly different (p=0.0055). The

	No. of hosts	Infected hosts	Prevalence	Mean intensity	Median intensity	Variance to mean ratio
***Analges* sp. sum**	30	30	100%	12.10	12.0	0.59
***Analges* sp. female**	30	30	100%	6.83	7.0	0.58
***Analges* sp. male**	30	28	93.3%	2.29	2.0	0.67
***Analges* sp. nymphal**	30	30	100%	3.17	3.0	0.46

Table 1. Sumary of *Analges* sp.Collected *Analges* sp. specimens were divided into nymphs, females and males, and a summary of all hosts is included. Prevalence, mean intensity (MI) and median intensity are included. Exact confidence limit levels of confidence range from 95% to 99%.

	No. of hosts	Infected hosts	Prevalence	Mean intensity	Median intensity	Variance to mean ratio
***P. megaphyllus* sum**	30	30	100%	8.57	9.0	0.32
***P. megaphyllus* female**	30	30	100%	4	4.0	0.48
***P. megaphyllus* male**	30	28	93.3%	2.96	1.2	1.14
***P. megaphyllus* nymphal**	30	27	90%	2	2.0	0.63

Table 2. Summary of *P. megaphyllus*. Collected *P. megaphyllus* specimens were divided into males, females and nymphs, and a summary of all of the hosts is included. Prevalence, mean intensity and median intensity are included. Exact levels of confidence range from 97% to 99%.

	Species	MI Bootstrap p-value (two-sided)	MA Bootstrap p-value (two-sided)
Apr-May x June-July	*P. megaphyllus*	0.4165	0.4135
	Analges sp.	0.8085	0.7955
June-July x Aug-Sep	*P. megaphyllus*	0.7740	0.7595
	Analges sp.	0.0870	0.0905
Aug-Sep x Apr-May	*P. megaphyllus*	0.3215	0.3190
	Analges sp.	0.1005	0.1000

Table 3. Tabulated summary of p-values of significantly differing variables in seasons and species. Only statistically significant results displayed. MI = Mean Intensity; MA = Mean Abundance.

	No of hosts	Prevalence	95% Confidence limits for prevalence	Mean intensity	95% (Bca) Bootstrap CL for MI
Apr-May	10	100%	0.7092 - 1.0000	11.7	10.40 - 13.10
June-July	15	100%	0.7778 - 1.0000	11.5	10.27 - 12.40
Aug-Sep	5	100%	0.5000 - 1.0000	15	11.40 - 16.80

Table 4. Mean intensity and prevalence values of *Analges* sp. displayed in different months within the year: April - May, June – July and August – September. Lower and upper confidence limits of prevalences and bootstrap confidence limits (CL) of mean intensities (MI) are included, both at the 95% confidence level.

	No of hosts	Prevalence	95% Confidence limits for prevalence	Mean Intensity	95% (Bca) Bootstrap CL for MI
Apr-May	10	100%	0.7092 - 1.0000	9	8.30 - 9.60
June-July	15	100%	0.7778 - 1.0000	8.5	7.27 - 9.27
Aug-Sep	5	100%	0.5000 - 1.0000	8.2	6.60 - 9.00

Table 5. Prevalence and mean intensity values of *Proctophyllodes megaphyllus* displayed in different months within the year: April - May, June – July and August – September. Lower and upper 95% confidence limits of prevalence and bootstrap confidence limits of mean intensity (MI) are included.

Samples compared	Species	MI Bootstrap p-value (two-sided)	Exact P-value (two-sided)
Female x Male	*P. megaphyllus*	0.0150	0.492
	Analges sp.	0.0000	0.492
Male x Nymph	*P. megaphyllus*	0.0120	1.000
	Analges sp.	0.0055	0.492
Nymph x Female	*P. megaphyllus*	0.0000	1.000
	Analges sp.	0.0000	0.237

Table 6. Tabulated summary of p-values of significantly differing variables in sex and maturity of each species. Only statistically significant results displayed. MI = Mean Intensity; MA = Mean Abundance.

	No of hosts	Prevalence	95% Confidence limits for prevalence	Mean intensity	95% (Bca) Bootstrap CL for MI
Female	10	100%	0.7092 - 1.0000	11.0	10.00 - 13.00
Male	10	100%	0.7092 - 1.0000	13.6	11.80 - 15.20
Juvenile	10	100%	0.7092 - 1.0000	11.7	9.90 - 12.80

Table 7. Prevalences and mean intensities of *Analges* sp. on female, male and juvenile hosts. Lower and upper confidence limits fo prevalence and bootstrap confidence limints of mean intensity (MI) are included.

	No of hosts	Prevalence	95% Confidence limits for prevalence	Mean intensity	95% (Bca) Bootstrap CL for MI
Female	10	100%	0.7092 - 1.0000	9.40	8.60 - 10.00
Male	10	100%	0.7092 - 1.0000	8.10	7.00 - 9.10
Juvenile	10	100%	0.7092 - 1.0000	8.20	6.70 - 9.00

Table 8. Prevalences and mean intensities of *P. megaphyllus* on female, male and juvenile hosts. Lower and upper confidence limits fo prevalence and bootstrap confidence limints of mean intensity (MI) are included.

lowest P-value for Fisher's test was between nymphs and females (p=0.237). The population structure of *P. megaphyllus* shows a statistically significant increase in mean intensity in favor of females (Table 6, Table 8).

Relationship between sex, maturity and site

For *Analges* sp. females there is a visible difference in mean abundance, especially on the chest (2.10), while they have the lowest abundance on the back (0.70). Overall, the highest abundances occured on wings (2.20 – 2.80) (Table 9). Most *Analges* sp. males are located on juvenile wings (1.20) and none on female chests (Table 10). Nymphs of *Analges* sp. are the most represented on female chests, (1.70) and juvenile backs (1.80) (Table 11).

	Head	Wings	Chest	Back	Tail
Juvenile	1.1	2.2	0.7	2.0	0.5
Female	0.4	2.8	2.1	0.7	0.6
Male	0.5	2.6	1.7	2.0	0.5

Table 9. Comparison of mean abundance of *Analges* sp. females depending on host maturity, gender and site.

	Head	Wings	Chest	Back	Tail
Juvenile	0.3	1.2	0.6	0.3	0.3
Female	0.2	0.8	0.0	0.2	0.2
Male	0.2	1.0	0.6	0.6	0.1

Table 10. Comparison of mean abundance of *Analges* sp. males depending on host maturity, gender and site.

	Head	Wings	Chest	Back	Tail
Juvenile	0.2	0.4	0.2	1.8	0.6
Female	0.2	0.6	1.7	0.0	0.4
Male	0.8	1.0	1.1	0.6	0.0

Table 11. Comparison of mean abundance of *Analges* sp. nymphs depending on host maturity, gender and site.

	Head	Wings	Chest	Back	Tail
Juvenile	0.5	1.4	0.7	0.7	0.2
Female	0.3	1.7	1.4	0.3	0.4
Male	0.2	1.8	0.7	0.7	0.5

Table 12. Comparison of mean abundance of *P. megaphyllus* females depending on host maturity, gender and site.

	Head	Wings	Chest	Back	Tail
Juvenile	0.1	1.1	0.4	0.7	0.2
Female	0.2	1.3	1.0	0.6	0.3
Male	0.3	1.1	0.5	0.4	0.1

Table 13. Comparison of mean abundance of *P. megaphyllus* males depending on host maturity, gender and site.

	Head	Wings	Chest	Back	Tail
Juvenile	0.1	0.7	0.0	1.1	0.4
Female	0.2	0.5	0.6	0.5	0.0
Male	0.2	0.5	0.2	0.4	0.1

Table 14. Comparison of mean abundance of *P. megaphyllus* nymphs depending on host maturity, gender and site.

	No of hosts	Prevalence	95% Confidence limits for prevalence	Mean intensity	95% (Bca) Bootstrap CL for MI
<1000	4	100%	0.4729 - 1.0000	11.75	10.00 - 13.75
1000-1500	19	100%	0.8245 - 1.0000	12.21	10.95 - 13.42
1500<	7	100%	0.6229 - 1.0000	12.00	10.29 - 14.00

Table 15. Comparison of prevalence and mean intensity of *Analges* sp. specimens depending on high above sea levels.

	No of hosts	Prevalence	95% Confidence limits for prevalence	Mean intensity	95% (Bca) Bootstrap CL for MI
<1000	4	100%	0.4729 - 1.0000	8.75	7.00 – 9.50
1000-1500	19	100%	0.8245 - 1.0000	8.32	7.37 – 8.89
1500<	7	100%	0.6229 - 1.0000	9.14	7.43 – 10.14

Table 16. Comparison of prevalence and mean intensity of *P. megaphyllus* specimens depending on high above sea levels.

P. megaphyllus females are mainly located on wings. On backs there is 1.40 mean abundance of females, which is twice the value of juveniles and males (Table 12). The highest mean abundance of *P. megaphyllus* males is on wings (1.10 – 1.30) and on female chests (Table 13). Most nymphs were found on juvenile backs (1.10) and none on chests, while female chests had the highest mean abundance of all specimens (Table 14).

Changes in prevalence by altitude

Prevalences of both symbiont species was 100% at each altitude interval. Highest mean intensity of *Analges* sp. occured at an altitude of 1000 – 1500 metres (12.21) (Table 15) and for *P. megaphyllus* this value was 9.14 at altitudes higher than 1500 metres (Table 16).

Discussion

The sexual variation of feather mites depending on site

Mean intensity and mean abundance of *Analges* sp. was highest on males. On females and juveniles similar abundance was recorded. *P. megaphyllus* had the highest mean intensity on females. Matthews *et al.* (2018) showed that mean abundance does not depend on the gender of the host (Marini *et al.* 1996; Hamstra and Badyaev 2009; Carleton and Proctor 2010). Our results are inconsistent with these this. It is unknown how interaction between age and sex influence abundance of feather mites. This could be due to the uropygial gland in males, and thus the quantity of uropygial oil available for

mites (Lafferty *et al.* 2006; Matthews *et al.* 2018). The differences in bird sexes can also be reflected in the host´ s body condition and measurements (Rózsa 1997; Galván *et al.* 2008). Despite this, it has been proven that older specimens carry more ectosymbionts than younger ones. In the case of *P. megaphyllus*, this is mostly due to their preferencefor horizontal transmission. Althought *Analges* sp. uses vertical transmission more than horizontal, it is mainly fertilized females and nymphs that are transmitted this way, and thus it takes longer for the population to increase (Dabert and Mironov 1999; Dabert *et al.* 2015).

Females of *Analges* sp. mostly aggregated on wings and chests of female hosts. On the other hand, there was a visible decrease in individual counts found on female backs. High values of mean abundance were also present in nymphs on backs and tails of juveniles. Nymphs of *Analges* sp. aggregated mostly on chests of females and on juvenile backs. Mean abundance of *P. megaphyllus* females on chests and tails of female hosts exceeded mean abundance of nymphs on female host chests. On the contrary *P. megaphyllus* mean abundance reaches highest levels on juvenile backs. This population distribution suggests that feather mites synchronize their aggregation and reproduction with the host species in terms of horizontal transmission (Figuerola 2000; Proctor and Owens 2000). Our results show that *P. megaphyllus* abundace on heads is higher than abundace of *Analges* sp. on heads, and deviate from results found by Lyra-Neves *et al.* (2003), which showed the opposite. This could be proof that *P. megaphyllus* on dunnocks has adapted to special horizontal transmission during cloacal pecking.

This population distribution also seems to depend on the reproductive behaviour of the host and transmission vectors of feather mites. We know that in vertical transmission, predominantly nymphs and fertilized females are transmitted (Dabert and Mironov 1999; Mironov 2012). Our results show that the aggregation of females on lower parts of the host (chest), and nymphs on the back may be the result of vertical transmission, as female chests and juvenile backs are the contact surfaces while nesting. In this period is also possible that nestlings do not form enough uropygial oil, and instead receive oil produced by adult females on their back.

The seasonality of feather mites

The results clearly show that the mean intensities are significantly different between species, but there are no big differences in mean intensity between the seasons, except for during August and September in *Analges* sp., and April and May in *P. megaphyllus*. In *Analges* sp., the mean intensity was significantly higher in August and September than in April – May and June – July, when values were very similiar. This may be related to moulting, which starts following the nesting season. Body condition of bird hosts is usually weak during this period (Blanco and Frías 2001) and it can disrupt the life cycle of mites (Dubinin 1951; Jovani and Serrano 2001). Body condition affects production of uropygial gland vaxes, which affects feather mite abundance (Behnke *et al.* 1995; Haribal 2011). On the other hand, 48% of all host specimens were collected in June and July. Between August and November, hosts migrate to Southern localities (Sol *et al.* 2005). The intensity may be higher precisely because of the increase in the average ambient temperature. Schmit (2011) proved that *Proctophyllodes stylifer* migrate to tertiary feathers in cold conditions, while during the warm season they remain predominantly in primary feathers. Abiotic conditions in the host's environment are important not only for choosing microhabitats, but also because temperature and humidity significantly affect life and reproduction of feather mites (Matthews *et al.* 2018; Melendez *et al.* 2014; Wiles *et al.* 2000). It is logical that feather mites migrate to different areas of the host's body, depending on the temperature of different parts of the body. The warmest places are on the head and the lower parts of bird body. The mean intensity of *P. megaphyllus* was similar throughout the year, but highest in April and May. During these months, spring migration to nesting sites takes place (Ferianc 1979), which could lead to an increase in the intensity of the species. Nesting ecology is a very important factor for understanding feather mite abundance (Matthews *et al.* 2018). During nesting season, the nest represents the host environment, particularly for female and juvenile hosts (Dona *et al.* 2017; Matthews *et al.* 2018). This means that feather mites are affected by the nest environment during nesting season and during transmission from female to juveniles (Galván and Sanz 2006; Matthews *et al.* 2018). During this period, the nest is a very suitable environment for feather mites, because the temperature is higher than 20° C and the humidity is significantly higher than during other periods. This leads to an increase in abundance (Marini and Couto 1997; Wiles *et al.* 2000; Moyer *et al.* 2002; Matthews *et al.* 2018).

These results support the theory that feather mites can adapt to the host's life strategy and for vertical transmission during breeding and nesting season (Galván and Sanz 2006; Kašlík and Janiga 2016). Confidence limits for prevalence of both species were highest in June and July; however, they were very similar to those reached in April and May. On the contrary, the lowest confidence levels occurred in August and September. This may be influenced either by the ambient temperature in the summer months or by the fact that the reproduction of *P. modularis* takes place twice a year and lasts from April to July (Ferianc 1979; Sol *et al.* 2005). At the end of breeding season, along with the start of moulting season, decrease in fitness and production of uropygial oil occurs (Neves *et al.* 2000; Lyra-Neves *et al.* 2003; Pap *et al.* 2010), and thus the food source available to mites decreases, impacting abundance in September through August. Feather mites commonly deviate from their regular distribution pattern during this period (Jovani and Serrano 2001).

Feather mites are photosensitive organisms. Another possible factor influencing the prevalence rate and particularly their intensity during the summer months is the length of day and hence the singig, which is a manifestation of hormonal changes similar to *P. collaris* (Proctor 2003; Kašlík and Janiga 2016; Janiga pers. observation). These hormonal changes (as well as mating) can lead to increased formation of uropygial oil and thus an increase in

level of infestation and variations in mean abundances (Galván *et al.* 2008; Blanco and Frías 2001; Diaz-Real *et al.* 2014). Increased confidence limits for prevalence, mean intensity and mean abundance may also be the result of autumn moulting, when feathers are lost along with many ectosymbionts (Markov 1940; Baum 1968; Burtt and Ichida 1999). Some studies claim that feather mites can move between primary, secondary and tertiary feathers in order to avoid feathers that are about fall out in the near future, to prevent population decline during moulting (Dubinin 1951; Burtt and Ichida 1999; Jovani and Serrano 2001). However, the mechanism of moult escape has not yet been explained. For example, when *Analges* sp. inhabit down plumage, there is more loss recorded during this period, because of the smaller magnitude of vibrations of loosened feathers (Dubinin 1951; Kašlík and Janiga 2016). In addition to feather loss, moulting season also brings a decreas in uropygial secretion at the time of migration to winter habitats (Glutz von Blotzheim 1985; Sol *et al.* 2005).

In August, the nesting season ends (Ferianc 1979; Sol *et al.* 2005) and host fitness is low. Their feathers are significantly worn out and body condition is poor. Hormonal levels are also reduced, which means less food resources for feather mites and thus decreasing mean abundance (Dubinin 1951; Blanco and Frías 2001; Galván and Sanz 2006; Blanco *et al.* 1997). During August ambient temperatures are also high, creating suitable conditions for feather mite reproduction (Wiles *et al.* 2000; Matthews *et al.* 2018). However, this is also moulting season and mites are forced to migrate to tertiary feathers (Neves *et al.* 2000; Schmit 2011; Diaz-Real 2014), the natural microhabitat and territory of *Analges* sp., where competition for food sources can occur (Malenke *et al.* 2011). Thus, the mites do not focus on reproduction during this period, and instead focus on synchronizing reproduction with the breeding season of their host (Diaz-Real *et al.* 2014). Between August and November is also the beginning of pre-winter migration to southern locations (Sol *et al.* 2005). Preening takes place during this time and may be an important factor in feather mite loads as preening involves the removal of parasites. During breeding season, almost no preening occurs, however, in spring and autumn there is a significant increase in preening and bathing because of winter aggregation and nesting aggregation in spring (Ferianc 1979; Janiga and Romanová 1996; Sol *et al.* 2005).

Life strategies of feathermites

Differing strategies of transmision and population dynamics can be impacted by different host sites of each species. *Analges* sp. occupy down feathers, while *P. megaphyllus* live in primary flight feathers. This means that mites may employ both vertical and horizontal transmission (O´ Conor 1982; Kašlík and Janiga 2016). Horizonal transmission can be dangerous for feather mites even though it takes place during breeding season, when the chance of successful transmission is highest. This is confirmed by our results, as most feather mites were found during the nesting period, when birds are in physical contact in the nest temperature and humidity conditions in the nest are favourable (Wiles *et al.* 2000; Moyer *et al.* 2002; Galván and Sanz 2006; Dona *et al.* 2017; Matthews *et al.* 2018).

It is very likely that for *Analges* sp., it is more difficult to switch hosts during mating, due to its short duration. Morphology is adapted to the particular type of feather, in which each feather mite species lives (Dubinin 1951, 1953; Dabert and Mironov 1999). Feather mites have a strong sexual dimorphism. *Analges* sp. females have small legs and males have hypertrophic legs (Nakamura 1990; Dabert and Mironov 1999). This may be one of the reasons, that *Analges* sp. have a predisposition to vertical transmission as opposed to horizontal. Our results have shown high mean abundances of females and nymphs on host female chests and host juvenile backs during breeding and nesting season. It is much easier to switch hosts during nesting and incubation. *P. megaphyllus* seems more actively mobile and is able to practice horizontal transmission as well (Dabert and Mironov 1999; Kašlík and Janiga 2016). Based on the high mean abundance of *Analges* sp. nymphs it is possible that feather mites common to dunnock have adapted so much, that they are able to use cloaca pecking to achieve horizontal transmission in addition to mating.

As mentioned previously, feather mites are photosensitive and it is possible that solar radiation has a harmful effect on feather mite lifespan, and may even have a lethal effect in high enough quantities (Moyer and Wagenbach 1995). To protect themselves from radiation during the summer season, mites migrate into down feathers or onto the skin (Jovani and Serrano 2001). Solar radiation, in addition to moulting, may cause migration of *P. megaphyllus* from primary feathers to the friable layer of plummage. They are able to sense vibrations in feathers prior to moulting, and as a result, migrate to down feathers. These plumage layers are already inhabited by *Analges* sp. There may be increased competition between these species following breeding season, considering the increased amount of food resources. In this case, *Analges* sp. has the advantage of being in its natural environment. This leads to an increase in mean intensity and confidence limits for prevalence of *P. megaphyllus* in late summer and autumn (August and September).

Most host specimens were found at altitudes 1000 - 1500 m a.s.l. Despite expectations, the highest mean intensity occured in specimens collected at 1500 m and higher. We expected that abundance and intensity would decrease proportionally with increasing altitude. This hypothesis was based on the assumption that feather mites are sensitive to low temperatures (Poulin 2006; Schmit 2011; Møller *et al.* 2013) and solar radiation, which is more intense at higher altitudes (Moyer and Wagenbach 1995). Kašlík and Janiga (2016) found much higher mean intensity on *P. collaris*, which inhabits exclusively alpine ecosystems. Thus, we can say that mites are sensitive to temperature and solar radiation but the only result appears to be is migration to other plumage layers and body parts (Schmit 2011). On the other hand, the level of infestation increases with higher altitude. This could be a result of longer lifespans for dunnock in alpine zones due to fewer predators at lower altitudes, and a reduc-

tion in people, traffic and environmental pollution. We cannot say for sure whether feather mites will be able to adapt to such conditions over time. The most likely reason for a decrease in feather mites at lower altitudes is air pollution. Air conditions affect the host´ s fitness, as well as the lifespan of feather mites. If we perceive feather mites as ectosymbionts (Behnke *et al.* 1995; Evans *et al.* 1961), we can say that they are impacted by their host´ s life as it acts as their natural environment.

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