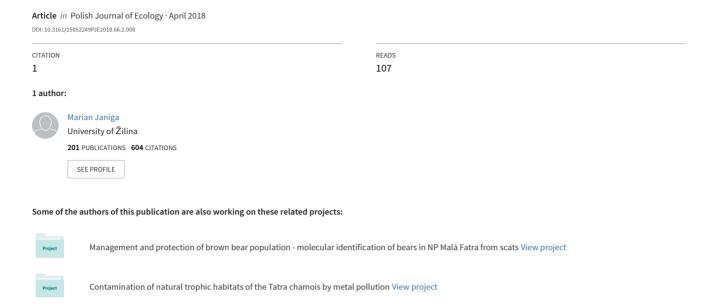# Different Coevolutionary Breeding Strategies of Ischnoceran Lice on Prunella collaris and P. modularis in High Mountains

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Different coevolutionary breeding strategies of Ischnoceran lice on *Prunella collaris* and *P. modularis* in high mountains

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ARTICLE INFO	ABSTRACT
	Alpine accentors (*Prunella collaris*) and dunnocks (*P. modularis*) are closely related species of Prunellidae, which often breed in polygynandrous groups and have specific types of mating behaviour. The alpine accentor lives at high altitudes, in an extreme alpine environment; the dunnock is widely dispersed from lowland to tree line in the mountains. Both species are hosts of the related species of wing lice *Philoptersus emiliae* and *Ph. modularis,* respectively. Behavioural differences between these two host species may have resulted in different breeding and seasonal adaptations by their parasites. The main goal of this paper was to test this hypothesis. Sixty five alpine accentors *Prunella collaris* (Scopoli, 1769) and eighty four dunnocks *Prunella modularis* (Linnaeus, 1758) were examined for Ischnocera lice in the West Carpathians, Slovakia from 1988 to 2001, and from 2007 to 2010, respectively. Birds were found to be infested with two species of Ischnoceran lice: the parasite species are not competing as they each have their own host *Philopterus emiliae* Balát, 1955 /*P. collaris* and *Philopterus modularis* (Denny, 1842) /*P. modularis*. Significant differences in abundance and prevalence existed between these two species of lice. High number of *Ph. modularis* nymphs in the comparison to *Ph. emiliae* nymphs reflects the different ecological, behavioural and phylogenetic trajectories of their host bird species. This work is the first to assess the louse breeding strategies on two closely related bird species in the high mountain environment.

INTRODUCTION

Ischnoceran feather lice are permanent parasites of birds. They feed on feathers and/or dermal debris of the host (Ash 1960, Marshall 1981a). The lice can be harmful to their individual host; the feeding damage caused by feather lice can decrease the host's attractiveness to mates by altering plumage quality, and negatively affecting thermoregulatory and flying capabilities (Vas *et al.* 2011). Heavy louse loads may result in increased effort in preening, reducing time available for obtaining food or mates (Brown *et al.* 1995). Lice, in turn, have coevolved adaptations to the morphological features, behaviour and ecology of their hosts (Clayton *et al.* 2015).

Many species of lice are host specific (Price *et al.* 2003) They move onto new hosts mainly during periods of direct contact between host individuals, such as between parent birds and their offspring in the nest (Janiga and Mičková 2004). Because alpine accentor and dunnock lice are very dependent on vertical (parent-offspring) transmission, selection may favor lice that prefer female hosts. In this study, this hypothesis is tested for lice from two closely related species of hosts. Lice have a prominent role in co-speciation studies and it had been widely accepted that comparative studies take evolutionary history of co-species into account, as traits of related taxa are statistically non-dependent (Page 2003). Ecological barriers responsible for specifity

can reinforce macroevolutionary processes that generate host-parasite phylogeny. Ecological factors of different habitats of genetically closely host species may dictate different breeding pattern of their parasites and influence parasite population genetic structure. Unfortunately, few studies have explored two parallel associations in a single host-parasite system. In this study I compare the seasonal breeding histories of two species of feather lice that parasitise genetically closely related and ecologically different species of birds. I tested the hypothesis that the louse species which breeds in seasonal predictable environment show the different seasonal breeding trajectories than lice living in seasonally more unpedictable habitats.

The alpine accentor is a passerine species living in high altitude montane regions above the timber line where alpine meadows and rocky outcrops predominate. The species breeds between the tree land and snow line of to 4–5000 m in Central Asia, in the West Carpathians, it breeds from 1600 to 2600 m, of-

ten near the highest peaks (Dyrcz and Janiga 1997). Regardless of region, alpine accentors are closely associated with high mountains where habitats are not continuous, but rather have a patchy distribution. The size of the habitat patches available to accentors is determined by the physical and geographic characteristics of each individual mountain range. Host features like morphology, age, health status, life history variables have a major influence on the ecology, evolution of their lice (Vas *et al.* 2011, Clayton *et al.* 2015). Size, shape and abundance of alpine accentor´s lice may differ among different seasons of a year (Janiga and Kubašková 2000, Janiga and Mičková 2004). For lice, alpine habitat of their hosts is seasonally variable but for their generations in the following years, the environment is highly predictable – alpine zone of mountains (Fig. 1). In contrast to alpine accentors, dunnocks have an extremely large range, from seaside gardens in Scandinavian or Mediterranean countries, throughout the European mixed and coniferous forests, up

Fig.1. Preening of the young alpine accentor. Favourite habitat of lice (*Philopterus emiliae* – upper right corner) is the interbarb space of wing feathers. Lice are approximately one mm long, the length of host averages at 180 mm. Photo: M. Janiga

to the treelines of the high mountains. In our research area in the tree line zone of the West Carpathians, the nests of dunnocks are inside of dense dwarf pine forest, what probably means more seasonally stable environment for their lice than for lice of alpine accentors. But regarding the development of lice generations in the following years, the habitat for lice is highly unpredictable because yearlings and some females of hosts may transmit the lice to very different habitats, from lowland to mountains. In both species of birds, it has been shown that differential migration by sex and age occurs during the non-breeding season. Approximately half of the young disperse outside their breeding areas, and females are more likely to leave than males, females of alpine accentors usually do not spend winter in the mountains. The life cycle of both species is driven year-round by marked differences in ecological and social constraints among sexes and age classes (Davies 1990, Henry 2011). Because both male and female birds breed when one year old (Davies 1990), for their louse parasites depending mainly on vertical transmission, it means radically different situation. While *Ph. emiliae* every year releases its offspring in patchy predictably alpine environment, for the generations of *Ph. modularis* the environment is, from a year to year, highly unpredictable.

Lice have a major influence on the ecology and evolution of their avian hosts (Clayton and Moore 1997). Much work has been done on the importance of basic host features like morphology, health status, social and life history variables (Vas *et al.* 2011, Clayton *et al.* 2015) but relatively little work has been devoted to the influence of host phylogenetic history on the breeding performance of lice. The alpine accentor is phylogenetically more conservative species than dunnock. The monophyletic family Prunellidae appears to split from outgroup families app. 14.8 Ma in middle Miocene, and was divided into two strongly supported clades, one comprising two large accentors (including *P. collaris*) and the other comprising eleven smaller members of the family (including *P. modularis*). The divergence of the large and small accentors occurred approximately 7.3 Ma during the late Miocene, and the two largest species *P. collaris* and *P. himalayana* definitely diverged

from each other app. 3 Ma during the Pliocene in Himalayan or the central Palearctic region. The small group of accentors experienced a period of rapid radiation in the early Pleistocene (2.1–1.69 Ma), the definitive node separating *P. modularis* from its sister species is dated to 1.81 Ma in average (Drovetski *et al.* 2013). Thus the alpine accentor is probably an older species than the dunnock, and lives in more predictable alpine habitats. It may be assumed that the phylogenic history of hosts may influence host-specific parasite long term load but not all ecological systems are suitable for such a research. This work discusses the comparative phylogeny of two *Prunella* species and its potential influence on louse breeding strategies in the high mountain environment.

STUDY AREA

The study was conducted at two different times – 1988–2001 for alpine accentors and 2007–2010 for dunnocks in the same mountain ranges of the High Tatra, Low Tatra, Great Fatra and Choč Hills mountains (the West Carpathians - area limited by borders, (49.06N×19.29E, 49.23N×20.27E, 48.91N×19.53E and 48.88N×20.14E).

MATERIAL AND METHODS

The two species of birds were captured every single year. Spring and summer field sites of alpine accentors lay above the dwarf pine (*Pinus mugo*) line usually between 1800 and 2650 m. The alpine accentor habitat was dominated by alpine meadows and rocky outcrops. Dunnocks were caught at lower elevations than alpine accentors in the dwarf mountain pine forest below the alpine meadows and rocks where accentors were captured. From April to July, 65 specimens of alpine accentors (1988–2001) and 84 dunnocks (2007–2010) were captured; not all birds were parasitized. Both host species were mist-netted or caught with walk-in traps. The birds were individually colour-ringed and measured. Birds were sexed using the shape of the cloacal protuberance (Nakamura 1990), tarsus width, or through the use of multivariate discriminant

function analysis (Heer 1999). Lice were collected from birds by exposing them to chloroform fumes in a glass fumigation chamber, while keeping the head of the bird outside the chamber (Bear 1995). This method allows several birds to be sampled for lice (Walther and Clayton 1997). The method may serve as a reasonably accurate predictor of overall lice abundance (Clayton and Drown 2001). Birds were kept in the fumigation chambers for approximately 15 min. Lice were preserved in 70% ethylalcohol. The species, life stage and sex of lice were determined using an Olympus B 201 microscope connected to a computer running image analysis software (Media Cybernetics) (Balát 1959, Zlotorzycka 1964). Louse nomenclature follows Price *et al.* (2003). Determination of lice was verified by J. Rékasi. After identification, the specimens were deposited in the collection of the Institute of High Mountain Biology of Žilina University.

To study the effects of louse population growth, lice from both host species were divided into two groups, one from spring, immediate period after migration (April-May), and the second from breeding times in June-July (summer). In the West Carpathians, alpine accentor and dunnock males usually appear at the end of March but females usually appear in mid-April, approximately one month before breeding. They usually spend winter at lower elevations in the rocky habitats. The alpine accentor and dunnock are a double-brooded species (Davies *et al.* 1995, Heer 1999, 2013). However in the West Carpathians, two successful broods are rare and only one breeding occurs mainly in alpine accentors due to lost clutches in the snowy periods due or predation. The fledglings from the first broods may occasionally be seen at the end of May and at the beginning of June; those from the second broods of a different female – in the mid July. Lice were sorted according to their age (nymphs – adults), sex and individual host.

In the present paper, the basic recommendations of Bush *et al.* (1997) and Rózsa *et al.* (2000a) were followed regarding how to provide quantitative data on the occurrence of parasites and how to compare these data. For computation the software Quantitative Parasitology ver. 3 was used (Reiczigel and Rózsa 2005). The prevalence, intensity, and abundance were determined for both species of lice. The frequency distribution of the lice collected was calculated using the exponent k (Rózsa *et al.* 2000b). Comparison of prevalences and comparisons of the ratios of adult and nymphal lice were done using a chi-square test for two samples with Yates' correction. Bootstraps two-sample t-test were used for the comparison of mean abundances and mean intensities. Two-tailed p-values were based on 1000 bootstrap replications.

RESULTS

Seasonal distribution

Of the 65 alpine accentors examined, 26 (40%) were infected by *Ph. emiliae* lice. Of the 84 dunnocks inspected, 45 (53.6%) were infested by *Ph. modularis* lice. The prevalence of *Ph. emiliae* in the spring and summer did not differ significantly ($P = 0.5$, Table 1). Nor was there a significant difference in the mean intensity ($P = 0.4$) or mean abundance ($P = 0.4$) of parasites between seasons (Tables 2 and 3). The mean intensity of *Ph. modularis* was significantly higher in spring than in summer ($P = 0.04$). Mean abundance of these lice was also higher in spring than in summer ($P = 0.03$). In contrast, the prevalence of *Ph. modularis* was less affected by seasons ($P = 0.2$). Differences in the abundance, intensity and distribution of parasites from spring to summer (in summer the distribution changed from a bimodal trend in the spring, Table 3) reflect that lice in spring aggregated, many birds had few parasites and a few birds had many lice. These parasites were mainly nymphs and their erruption decreased in summer (Table 4). In *Ph. emiliae* such erruption was not noticed.

Occurrence of louse species

The prevalence of lice on dunnocks was greater than that on alpine accentors in the spring ($P = 0.03$) but not in the summer ($P = 0.9$). The mean abundance of lice on dunnocks was also greater than that of alpine accentors in the spring ($P = 0.03$) but not in the summer ($P = 0.2$). Mean abundance is not

Table 1. Prevalence of *Philopterus emiliae* in the alpine accentors and *Philopterus modularis* in the dunnocks in the mountain regions of the West Carpathians.
n – number of birds examined, Prevalence >10 – relative number of birds with more than nine lice, CL – Confidence limits (lower and upper) for the prevalence (Clopper-Pearson) at level 95%

		n	Prevalence	Prev. >10	CL_L	CL_U
Apr.-May	*Philopterus emiliae*	42	36%	2%	0.216	0.520
	Philopterus modularis	33	64%	24%	0.451	0.796
June-July	*Philopterus emiliae*	23	48%	0%	0.268	0.694
	Philopterus modularis	51	47%	12%	0.329	0.615

Table 2. Intensity of *Philopterus emiliae* in the alpine accentors and *Philopterus modularis* in the dunnocks in the mountain regions of the West Carpathians.
n – number of birds examined, MI – mean intensity, CL – lower and upper 95% confident limits for the population mean intensity by the BCa method with 2000 bootstrap replications, Median – median intesity with confidence limits in brackets

		n	MI	CL	Median
Apr.-May	*Philopterus emiliae*	42	5.2	2.47 to 13.8	1(1−6)
	Philopterus modularis	33	12.6	7.02 to 20.2	4(1−17)
June-July	*Philopterus emiliae*	23	1.9	1.00 to 3.18	1(1−1)
	Philopterus modularis	51	4.4	2.50 to 7.71	1(1−3)

Table 3. Abundance and distribution of *Philopterus emiliae* in the alpine accentors and *Philopterus modularis* in the dunnocks in the mountain regions of the West Carpathians.
n – number of birds examined, MA – mean abundance, CL - 95% conf. limits for the population mean abundance by the BCa method with 2000 bootstrap replications, k – negative binomial exponent, *P* – *P*-value from chi-square test of binomial distributions, in spring groups the fit of the negative binomial distribution to data was acceptable, the third summer sample (alpine accentor) was small to test binomial distribution, and the dunnock summer sample does not fit the binomial distribution

		n	MA	CL	k	*P*
Apr.-May	*Philopterus emiliae*	42	1.86	0.786 to 5.89	0.168	0.808
	Philopterus modularis	33	8.00	4.15 to 13.9	0.268	0.343
June-July	*Philopterus emiliae*	23	0.91	0.435 to 1.91	0.652	
	Philopterus modularis	51	2.08	1.060 to 3.93	0.262	0.018*

indepedent of prevalence because it includes uninfested birds. In contrast, mean intensity is indpendent of prevalence because it includes only infested birds. *Ph. emiliae* and *Ph. modularis* did not differ in mean intensity in spring (*P* = 0.09) or summer (*P* = 0.1).

In general, *Ph. modularis* is more abundant on their hosts than *Ph. emiliae* in the spring and that intensity of this dunnock´s parasites decreases from spring to summer. The high abundancy of *Ph. modularis* is caused by rapid population growth in the spring in the comparison to *Ph. emiliae*. The ratio of nymphal to adult lice is significantly

Table 4. Age and sex ratio of *Philopterus emiliae* – louse infesting the alpine accentor *(Prunella collaris)* and *Philopterus modularis* – louse infesting the dunnocks *(Prunella modularis)* in the West Carpathian mountain region. n – number of birds infested

	Species	(n=100%)	No. of lice	% of nymphs	% of males	% of females
Apr.-May	*Ph. emiliae*	(15)	78	16.7%	39.7%	43.6%
	Ph. modularis	(21)	264	70.5%	7.2%	22.3%
June-July	*Ph. emiliae*	(11)	21	20.0%	25.0%	55.0%
	Ph. modularis	(24)	117	64.1%	7.7%	28.2%

higher in dunnock´s than in alpine accentor´s lice ($P = 0.000$) in the spring, this difference slightly decreases but it is still highly significant in summer ($P = 0.002$). In *Ph. modularis*, the ratio of nymphs : imagos was not significantly different between spring and summer ($P = 0.59$). Such difference was also not found in *Ph. emiliae* ($P = 0.83$). A huge erruption of nymphs in *Ph. modularis* produces more louse females than males (Table 4). Sex ratios of two collected lice species were biased towards females but was higher in *Ph. modularis* (1m : 4f) than in *Ph. emiliae* (1m : 2f - $\chi^2 = 9.5$, $P = 0.002$)

DISCUSSION AND CONCLUSION

The intriguing question is what conditions can facilitate such abundance erruption of nymphs in dunnock´s lice in the comparison to alpine accentor´s lice? The results are discussed from the point of view of three – probably the most important factors which may influence separate breeding strategies between *Ph. emiliae* and *Ph. modularis*: local environment and its microclimate, mating and breeding behaviour of hosts, and habitat.

Local environment in the same mountain valleys

In the West Carpathians, the alpine accentors live always above timberline and often near the highest peaks under conditions of extreme variation in humidity and temperature; the weather varies from very dry windy or sunny to very wet and rainy days, dunnocks live at lower elevations than alpine accentors in the dwarf mountain pine forest below the alpine meadows and rocks where the microclimate may be more stable than at the peaks of mountains. Although lice are permanent parasites that complete their entire life cycle on the body of the host, they are also influenced by non-host environmental factors, such as ambient humidity. The number of individual lice on infested hosts is often higher in more humid regions (Moyer *et al.* 2002, Malenke *et al.* 2011). Furthermore, ambient humidity can mediate the dynamics of interspecific competition in lice (Clayton *et al.* 2015). Ambient temperature also influences lice, even though they are closely attuned to the body temperature of the host. For example, intense solar radiation can kill lice on birds (Moyer and Wagenbach 1995). Both the eggs and hatched lice require warm, humid conditions near the host's skin; lice are so dependent on these conditions that they cannot survive for more than a few hours or days away from the body of the host (Tompkins and Clayton 1999). Feather lice recognize the different temperature in microclimate at the body of the host. If they are hungry, some lice tend to move to downy feathers where it is higher temperature than in the wing feathers. But the same spend much of their time on the wings of the host, where they are less exposed to preening (Harbison and Boughton 2014). Some studies show that lice can also be abundant at low ambient humidity; thus, birds in dry environments do not necessarily have fewer lice (Carillo *et al.* 2007). The microclimate around the nests of accentors and dunnocks may be different. At the higher altitudes of the Carpathians, alpine accentors

breed in the ground or rocky holes, while the dunnock build the nest above the ground in dwarf pine dense forests. There are few studies documenting the differences in microclimate variation in the nests of birds related to the bird population ecology, and probably no study exists on microclimate changes in nests of high mountain birds. Different microclimate around the nests between two species of birds may influence the breeding trajectories and vertical transmission of their lice.

Moreover, the supplementary hypothesis to explain the pattern of feather louse breeding strategies including transmission is that lice disperse phoretically on parasitic flies (Harbison and Clayton 2011). This behaviour allows lice to disperse to new individuals of the same and different host species. Little is known about the transmission of lice/flies dispersing between wild birds, but some recent studies on this type of phoresis indicate that phoretic dispersal may occur frequently (c.f. Johnson *et al.* 2002, Bueter *et al.* 2009). But flies may also transmit other parasites including endo-hemoparasites. Haas *et al.* (2012) examined 109 dunnocks for hemosporidia. The prevalence was at the level of 50%. Authors assume that the high mountain forests near treeline may serve as a very favourable place for the transmission of hemoparasites. In contrary, none from 83 alpine accentors examined in the high altitudes of Slovakian mountains contained hemosporidia (Haas and Kisková 2010). Lack of hemoparasites and low abundance and prevalence of lice in *P. collaris* in comparison to lice prevalence in *P. modularis* leads to a speculation that the pine forest not far from tree line may serve as a suitable habitat for phoretic transmission. The treeline rather than any other vegetation lines provides the most clear-cut and direct relationship to regional climate with limited space for ecotones (Myster 2012). Microclimate (including variation in humidity) in shaded dense pine forest is probably more stable and more favourable for rapid louse development than local microclimate around the nests of alpine accentors in alpine rocks and meadows. Egg-laying females of lice are very susceptible to environmental influences. For instance, Murray (1968) reports that significant mortality in the sheep lice may be caused by rapid reversal of temperature gradients in the fleece as sheep walk from shade into sunlight.

Host breeding behaviour

Ph. emiliae and *Ph. modularis* are morphologically similar and have been considered one species by some authors (Eichler 1953). Behavioural flexibility, which is one type of phenotypic plasticity, may allow parasites to quickly cope with new environmental conditions, to exploit new environments, and potentialy create different morphological and ecological adaptations (Bush 2009). Behavioural flexibility of host birds may cause different adaptations in parasites. Alpine accentors and dunnocks are closely related species of the family Prunellidae, which often breed in polygynandrous groups. In both species, alpha and subordinate males usually help to feed different broods (Davies *et al.* 1995, Hartley *et al.* 1995). In dunnocks, in contrast to alpine accentors, neither alpha nor beta adult males showed a reduction in parental effort in relation to a reduction in mates (Davies *et al.* 1996). Two factors probably contribute to the different male responses in the two species. First, the alpine accentor males have often overlapping home ranges, large group sizes and intensive competition for mates within both sexes (Davies *et al.* 1995, 1996). Female song plays a crucial role to attract a male and obtain maximum paternal care for her offspring (Langmore *et al.* 1996). This system has evolved in alpine accentors because both sexes compete intensively for mates. Males are more likely to help feed young if they gain a greater share of the matings with the mother of the brood (Hartley *et al.* 1995). The lice probably reflect this difference in host behaviour. Parasitism of bird hosts requires a number of specialized morphological, physiological and behavioural adaptations, which have evolved for remaining attached to the host, escaping host defences and feeding on the host (Clayton *et al.* 2003). The average year sex ratio of the whole population of adult *Ph. emiliae* lice was 1:1.3 (males : females) in the adult males, and 1:2.3 in adult females of Alpine accentors (Janiga and Kubašková 2000). Female lice are probably capable of adaptive selection of fe-

males of accentors for the purposes of louse dispersal between generations (cf. Potti and Merino 1995, Rózsa 1997). Male dunnocks usually have, at most, just two females. Thus the opportunity costs of helping, in terms of mating and chick feeding demands elsewhere, are less for a male dunnock than a male alpine accentor (Davies and Hatchwell 1992). Dunnock males are more regular feeders than males of alpine accentors, their feeding activity is less dependent on female song (Davies *et al.* 1996), and male help in dunnocks has a marked influence on chick survival. (Davies 1992, Davies *et al.* 1996). In the louse *Ph. modularis,* female bias was significantly higher than in *Ph. emiliae* (Table 4). The sex difference is probably related to different selection pressures by hosts on the sexes of the parasite, with females of alpine accentors generally being under more intense selection (cf. Tryjanowski and Adamski 2007). Many species of lice have even sex ratios (Marshall 1981b), but some have skewed sex ratios, usually with a female bias (Clayton *et al.* 1992). In an analysis of published data, Marshall (1981b) reported 31 of 50 species of birds (62%) with significantly female biased sex ratios. Because hosts have relatively constant body conditions, lice are capable of breeding throughout the year (Askew 1971, Marshall 1981a). Like many parasites, lice tend to have aggregated populations (Fowler and Williams 1985, Rékási *et al.* 1997, Clayton *et al.* 1999). Rózsa *et al.* (1996) showed that aggregation is reduced in more social species of hosts, presumably because of increased horizontal transmission. The dunnocks are very abundant in the dwarf pine habitats and phoretic transmission of lice cannot be excluded at these sites. Mutual effect between microclimate in dwarf pine forest and greater involvement of males of dunnocks in nesting than in males of alpine accentors may probably lead to the great spring aggregations of dunnock´s lice (Table 3).

Habitat, history and lifespan of mountain animals

The habitat feature of the alpine accentor is from a year to year predictable but seasonally variable, unfavourable climate. This does not hold for widely distributed dunnock in different European ecosystems. For their lice, the microclimate is less variable during a year than for the lice of alpine accentors, but highly unpredictable from a year to year. In Prunellidae, allopatric speciation is probably the predominant geographic mode of speciation. Reconstruction of the biogeographic history of Prunellidae by Drovetski *et al.* (2013) suggests that the origin of family, including divergence of the two subgenera *Laiscopus (including P. collaris)* and *Prunella* (including *P. modularis)*, and initial diversification happened within the Himalayan region. The subgenus *Prunella* dispersed out of the Himalayan region and across the Palearctic from the mid- to late-Pliocene. This colonization of the Palearctic was followed by a rapid radiation of accentors suggesting the importance of colonizing new biogeographic regions and vicariant events resulting from Pleistocene glacial retreats in their speciation history (Drovetski *et al.* 2013). Thus Prunellidae are today separated to larger and phylogenetically older alpine species (*collaris* and *himalayana*) and smaller accentors associated with shrubs or scrub habitats (Hatchwell 2005). Lice have to follow the life of alpine accentors in predictable patchy habitats and of dunnocks in different unpredictable environment, and natal dispersal of hosts probably plays an important role in the trajectories of louse breeding. Many high montane animal species are under selection for reduced birth rates but longer life spans. This is known from mountain snow voles to mountain marmots in vertebrates as well as in invertebrates. Mountains are in every world region source of ecologically stable high biodiversity. The life of *Ph. emiliae,* parasite of alpine accentors, probably reflects the phylogenic trajectory of its host living in the alpine zone. After migration and during the breeding period of alpine accentors, the ratio of *Ph. emiliae* nymphs to adults is approximately 1:3 while in *Ph. modularis* it is 2:1 (Table 4). The data indicate that the number of dunnock´s louse nymphs appear to be more reduced than of the alpine accentor´s nymphs, and the lice *Ph. emiliae* seem to possess longer lifespan than *Ph. modularis*. The results also indicate that the fecundity and egg rate in dunnock´s lice is higher than in alpine accentor´s lice. Studies on lifespan of lice have rarely been

carried out in *in vivo* conditions but several comparative "*in vivo/in vitro*" studies have shown that adult lice reared *in vivo* (predictable conditions for lice) developed faster than lice reared *in vitro* (unpredictable conditions) and males and females of lice reared *in vivo* survived for longer periods of time than lice reared *in vitro* (Crawford *et al.* 2001, Takano-Lee *et al.* 2003). In unfavourable conditions (*in vitro*), the instars develop longer than *in vivo* but the number of eggs produced during female lifespan is higher *in vitro* than in more favourable environment (Rawat *et al.* 1993, Takano-Lee *et al.* 2003, Gupta *et al.* 2007). This is probably because fertility of louse females declines with their age and their egg production is negligible in the last phase of their survival (Rawat *et al.* 1993, Takano-Lee *et al.* 2003). *Ph. modularis* lice have probably high fecundity because their hosts exploit a wider diversity of 'unpredictable' habitats than less innovative alpine accentors, hosts of *Ph. emiliae* (cf. Overington *et al.* 2011). Bird species with higher measure of innovation abilities tend to have higher densities of potential parasites (Soler *et al.* 2012, Vas *et al.* 2012). Important role in this process may play breeding dispersal of lice. Theoretical studies on dispersal typically assume natal dispersal, where individuals emigrate right after birth. But emigration may also occur during a later moment within in a reproductive season, so called breeding dispersal (Lakovic *et al.* 2015). For example, many species of insect in the diverse mountain patchy environment deposit their eggs in their natal patch before migrating to other sites to continue egg-laying there (possible phoretic dispersion in lice). How breeding dispersal compared to natal dispersal influences the evolution of dispersal of mountain lice has not been explored.

To summarize, louse mountain populations are surely affected by environmental conditions outside the host body such as temperature and humidity and probably by different breeding strategies of their hosts. The daily variation in ambient humidity seems to be the most important factor. But I predict that ectoparasite load should be associated with host habitat, and habitat reflects the host phylogenic history. An evolutionary comparative approach is a potentially useful tool to reveal whether variation in louse population dynamics is caused by habitat reflecting host phylogenetic relationships or only by correlates of host behaviour and environment. The causes and consequences of these effects in the mountains need further study. Up to know only a relatively few comparative studies have been carried out to explore the population dynamics of ectoparasitic lice in the patchy mountain environment.

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