Parasitology Research (2019) 118:2643–2650
https://doi.org/10.1007/s00436-019-06380-0

IMMUNOLOGY AND HOST-PARASITE INTERACTIONS - ORIGINAL PAPER

Quill mite infestation of rock ptarmigan *Lagopus muta* (Aves: Phasianidae) in relation to year and host age, sex, body condition, and density

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Received: 1 April 2019 / Accepted: 19 June 2019 / Published online: 5 July 2019

Abstract

A total of 1209 ptarmigan were examined for *Mironovia lagopus*, including 721 juvenile birds (ca. 3 months old) and 488 adult birds (15 months or older). A total of 88 birds or 7.3% (n = 1209, 95% cl 5.9–8.9%) were infested with *M. lagopus*. There was an age difference in prevalence of infection, and more adults (10.7%, n = 488, 95% cl 8.2–13.7%) than juveniles (5.0%, n = 721, 95% cl 3.6–6.8%) were infested. There was a significant age effect in the mean intensity index, and adult birds had more advanced infestations compared with juvenile birds. There were no significant changes in either the interannual prevalence of infection or the mean intensity index of infection. Of the feather types inspected, there was no age-related difference in selection of feathers, nor was there any preference of mites for any one of the inspected feather types. Body dispersants were all adult females. There was an age-related difference in mean intensities of infection of body dispersants; it was higher in adult birds. The methods used to determine presence or absence of *M. lagopus* were not 100% accurate especially for juvenile hosts, and this at least partly explains the difference in prevalence among age groups. There was no relationship between host body condition or host density and infection by *M. lagopus*.

Keywords *Mironovia lagopus* · *Lagopus mutus* · Quill infestation · Intensity · Body condition

Introduction

Feather mites (Acari) are a diverse and abundant group of arachnid arthropods that have adapted to different microhabitats on the avian body (Dabert and Mironov 1999; Mironov 1999; Skoracki 2011). One offshoot of this group is the so-called quill mites, highly specialized permanent parasites that live inside feathers (Kethley 1970; Skoracki 2011). Two subfamilies of quill mites have been described: Syringophilinae Lavoipierre and Picobinae Johnston and Kethley. Syringophiline mites inhabit quills of primaries, secondaries, tertials, retrices, and wing coverts and occasionally also body feathers, but picobiine mites live predominantly inside body feathers (Skoracki 2011). Currently, about 400 valid species of quill mites, belonging to 62 genera, had been described, and over 700 host species identified (95 families, 24 orders) (Zmudzinski and Skoracki 2018). The quill mites feed on the body fluids of the host by piercing through the calamus wall and into the living tissue with their long and needle-like chelicerae (Casto 1974; Kethley 1970, 1971).

A total of 18 syringophilid quill mite species have been reported for 21 host species of galliform birds (Skoracki and Sikora 2011). Five of the mites belong to the genus *Mironovia* (Chirov and Kravtsova 1995; Bochkov et al. 2004; Skoracki and Sikora 2004; Bochkov and Skirnisson 2011). The quill mite *Mironovia lagopus* is known to parasitize both rock ptarmigan *Lagopus muta* (Montin) and the willow ptarmigan *Lagopus lagopus* (Linnaeus) (Bochkov and Skirnisson 2011; Skoracki and Sikora 2011).

We have 12 years of data on prevalence and intensities of *M. lagopus* parasitizing a rock ptarmigan population in northeast Iceland. We explored how *M. lagopus* infestations are related to sex, age, and body condition of the host and host densities. Our

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predictions, based on what is known of quill mite—host interaction and quill mite transmission pattern (Skoracki 2011)—are that both prevalence and intensities of infection should show no relation with host body condition and that there should be no age-related difference in infection pattern. The arguments for these predictions are that quill mites are generally not pathogenic, and transmission is mainly vertical (from parents to chicks).

Material and methods

Ptarmigan sample

A total of 1209 rock ptarmigan (hereafter ptarmigan) were collected by shooting in autumn 2006–2017 from upland areas west, east, and north of Lake Mývatn, northeast Iceland (65° 37′ N, 17° 00′ W) (Table 1). All the juvenile birds (721) and 424 of 488 adult birds were collected during the first week of October under a license issued by the Icelandic Institute of Natural History. The remaining 64 adults were shot during the hunting season 2 to 4 weeks later in 2006–2009. The birds were collected for an in-depth study on the health of the ptarmigan in Iceland.

Processing of sampled ptarmigan and the body condition index

Each bird was tagged immediately after collecting, then wrapped in absorptive paper, placed in a closed paper bag, cooled to 4 °C, transported to the lab, and dissected within 3 days. The 64 adults collected during the open season were derived from hunters' bags, and most of them had been in physical contact with other ptarmigan carcasses after death. Birds were sexed using both the loral stripe and size and color of the combs (Montgomerie and Holder 2008), and aged based on pigmentation of the primaries (Weeden and Watson 1967). Sex and age were confirmed during dissection by inspection of the gonads, and presence or absence of bursa of Fabricius (*Bursa fabricii*). Two age classes were recognized: juvenile birds (ca. 3 months old) and adult birds (15 months and older).

We weighed the intact carcass to the nearest 1 g using a digital scale (= gross body mass). During dissection, we removed and weighed the content of the crop. Net body mass was defined as gross body mass minus the crop content. To obtain an index of body condition, we took the following external and internal morphometrics for each bird: (1) wing length, measured to the nearest millimeter with a ruler from the carpal joint to the tip of the flattened and straightened wing; (2) head + bill length, measured to the nearest 0.1 mm with calipers from the hindmost point of the head to the tip of the bill; (3) sternum length, measured to the nearest millimeter with calipers from the tip of the spina externa along the center line to the margo caudalis; and (4) sternum–coracoid length, measured to the nearest 0.1 mm with calipers from the center line of the margo caudalis to the cranial end of the coracoideum. Anatomical terms are according to Baumel (1979). The four body measures were highly correlated with each other. A principle component analysis (PCA) on the four morphometrics was used to derive an index of structural size, namely, factor 1 from the PCA. Factor 1 explained 76.7% of the variance in the original variables and was highly related to them (loadings: wing = 0.866, head + bill = 0.835, sternum = 0.894, sternum–coracoid = 0.907). To obtain the index of body condition, net body mass was regressed on structural size, and the residuals were used as a body condition index.

Collection and processing of parasites

Prior to dissection, a handheld vacuum cleaner, *Princess Turbo Tiger, Type 2755*, was used to collect external parasites. The

Table 1 Age and sex of rock ptarmigan *Lagopus muta* hosts analyzed for *Mironovia lagopus* infestations in northeast Iceland 2006–2017

Year	Ad female	Ad male	Ad total	Juv female	Juv male	Juv total	Grand total
2006	20	20	40	30	30	60	100
2007	21	22	43	30	30	60	103
2008	21	20	41	30	30	60	101
2009	20	20	40	30	30	60	100
2010	13	27	40	30	30	60	100
2011	16	25	41	30	30	60	101
2012	9	31	40	30	30	60	100
2013	15	26	41	30	30	60	101
2014	15	26	41	31	30	61	102
2015	18	23	41	30	30	60	101
2016	16	24	40	30	30	60	100
2017	11	29	40	30	30	60	100
Grand total	195	293	488	361	360	721	1209

vacuum cleaner was connected to an external collection chamber fitted with a circular sack-like filter (92 cm^2, diameter of pores 2–30 μm). Each bird was vacuumed systematically, covering the whole body in ca. 2 min. Filter samples and wings were kept frozen in individually marked plastic bags at − 20 °C. Later, the content of each filter was flushed into a 400-ml glass jar. The jar was left to stand overnight, but the first seven drops of the surfactant TritonH X-100 were added to the liquid to promote particle settling. Parasites were collected under a stereoscope and embedded on a slide in Hoyer's medium (Anderson 1954).

Wing feathers, rectrices, and adjacent coverts as well as several larger coverts from five infested birds were systematically examined for the presence of quill mites at the onset of the study. The mites were almost exclusively detected in shafts of the secondary and tertiary flight feathers and in the adjacent large coverts. In a single case, infestation was detected in the quill of a primary flight feather. All alula quills appeared to be free of infestation. It was decided to search for quill mites in seven feathers from the middle of the wing, namely, (a) upperwing greater primary coverts (PUC) number 4 and 5 (numbered distal to proximal) and (b) secondary flight feathers (S) number 3 to 7 (numbered distal to proximal) (Fig. 1a). The feathers were plucked from the wing and examined one by one under a stereoscope at 16-fold magnification and using illumination from below. To increase transparency, the calamus was submerged in 70% ethanol in a 5-ml glass jar during inspection; this way, single mites, eggs, and even excrements of the mites became visible (Fig. 1b).

Infested feathers were designated to two groups based on the number of mites per quill: (a) recent infestations, up to nine mites present in the quill, usually a single female (foundress) and her developing offspring's, scored as "1," and (b) old infestations, 10 or more mites in the quill, with mass of excrements and decanting material, scored as "2." The scores for the different feathers were summed up for each individual and the sum used as an index of the intensity of infection.

Infected quills were sometimes cut open and the mites counted and mounted according to Anderson (1954) for microscopic examination. Identification of *M. lagopus* and determination of sex and developmental stage were based on Bochkov and Skirnisson (2011).

Ptarmigan population index

Territorial male ptarmigan were counted on six plots each spring starting in 1981. The total size of these plots was 26.8 km^2 (range 2.4–8.0 km^2). Each plot was surveyed once during 10–24 May. The survey was conducted on foot by at least two observers in the early morning (05:00–10:00) or late afternoon (17:00–24:00) (see Stenkewitz et al. 2016 for details).

Statistical analysis

We performed statistical analyses using the software packages Statistica (Dell Inc. 2015) and Quantitative Parasitology (Rózsa et al. 2000). Prevalence was defined as the proportion of birds with *M. lagopus*. A bird was considered infected if *Mironovia* was found in quills checked or in the vacuum filter. The Sterne method was used to calculate the 95% confidence limits for prevalence (Rózsa et al. 2000). Fisher's exact test was used to compare prevalence among groups. Cross-correlation analysis was used to study how time series for prevalence and mean intensity index related to host body condition and host density. Prior to analysis, the different time series were de-trended using the "trend subtract" function within the Time Series module of Statistica. To study interannual changes in prevalence of *M. lagopus*, we used generalized linear models with binomial distribution and logic link function. We used Mann–Whitney *U* test and Kruskal–Wallis ANOVA to compare among age groups and years the mean intensity index. We used chi-square tests to compare host age frequency classes for some infestation characteristics, and also

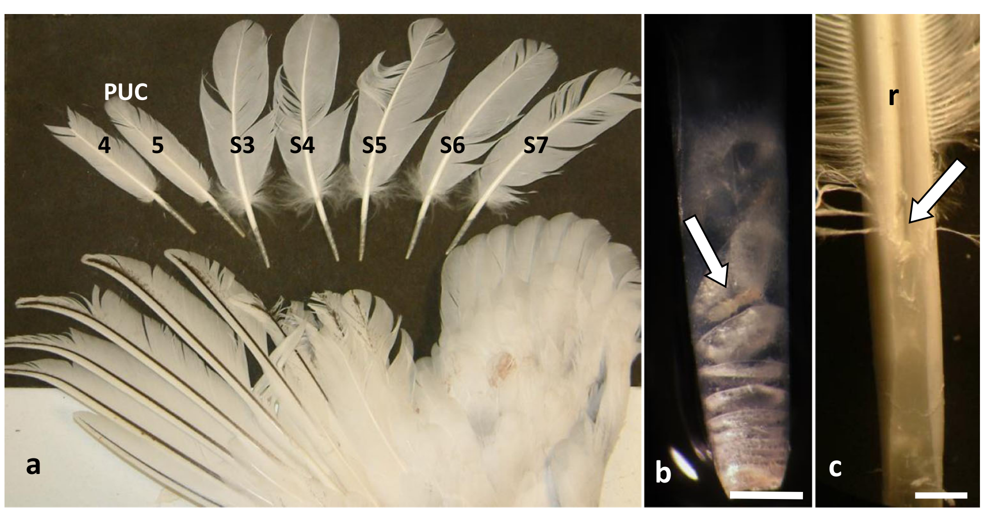

Fig. 1 Rock ptarmigan *Lagopus muta* wing feathers and quills. **a** Seven feathers pulled out of the wing prior to search for quill mite infestations (upper greater coverts of primaries, PUC 4 and 5; secondary flight feathers S3 to S7). **b** Quill of a secondary flight feather recently infested with a single *Mironovia lagopus* foundress (arrow). **c** The entrance site (arrow) for quill mites into the hollow shaft is a narrow opening (*umbilicus superior*) located at the base of the rachis (r). Scale bar 1 mm (**b**, **c**). Photographs: Karl Skirnisson

possible preference of *M. lagopus* for certain feather types. We calculated mean intensities for *M. lagopus* dispersants found in vacuum filters and used the Bootstrap 2-sample *t*-test to compare the age groups (Rózsa et al. 2000). We used the *t*-test to compare the body condition index of infected and non-infected birds. The alpha level, 2-tailed, was set at $p = 0.05$ for all tests.

Results

Prevalence of infection

A total of 1209 ptarmigan were examined for *M. lagopus*, and 88 birds or 7.3% (95% cl 5.9–8.9%) were infested. The prevalence for adult females was 11.8% ($n = 195$, 95% cl 7.9–17.1%), for adult males 9.9% ($n = 293$, 95% cl 6.9–13.9%), for juvenile females 5.3% ($n = 361$, 95% cl 3.3–8.1%), and 4.7% ($n = 360$, 95% cl 2.9–7.5%) for juvenile males. There was no sex-related difference in prevalence for either adult (Fisher's exact test, $p = 0.550$) or juvenile hosts (Fisher's exact test, $p = 0.865$). There was a significant host age-related difference in prevalence of *M. lagopus* (Fisher's exact test, $p < 0.001$); the mean prevalence for adult birds was 10.7% ($n = 488$, 95% cl 8.2–13.7%) and for juvenile birds 5.0% ($n = 721$, 95% cl 3.6–6.8%). Infested adult hosts were found all years, but no infested juvenile hosts were detected in either 2010 or 2011 (Table 2). The interannual differences in prevalence for the combined sample was not significant (year, df = 11, Wald stat. = 16.934, $p = 0.11$).

Table 2 Prevalence (%) of *Mironovia lagopus* infestations in adult and juvenile rock ptarmigan *Lagopus muta* in northeast Iceland in autumn 2006–2017 with sample size (*n*) and 95% confidence limits (95% cl)

	Adults			Juveniles		
	n	Prevalence	95% cl	*n*	Prevalence	95% cl
2006	40	20	9–35	60	5	1–14
2007	43	19	9–34	60	7	2–16
2008	41	12	5–25	60	2	0–9
2009	40	5	1–17	60	3	1–11
2010	40	8	2–20	60	0	…
2011	41	12	5–25	60	0	…
2012	40	8	2–20	60	5	1–14
2013	41	7	2–19	60	3	1–11
2014	41	7	2–19	61	2	0–9
2015	41	12	2–25	60	10	5–21
2016	40	5	1–17	60	15	8–27
2017	40	13	5–26	60	8	3–18
Total	488	10.7	8–14	721	5	4–7

Index for mean intensities

The mean intensity index was 4.3 ($n = 88$, range 0–13, sd = 3.5) for the combined sample. Note that zero values are birds with body dispersants but with no infection in inspected feathers. The intensity index was much higher for adults than juveniles or 6.2 ($n = 52$, range 0–13, sd = 3.4) against 1.6 for juveniles ($n = 36$, range 0–5, sd = 1.3; Table 3). A Mann–Whitney test indicated that this age-related difference was highly significant ($U = 203$, $p << 0.001$). A cross-correlation analysis of the two trajectories did not give any significant relationships ($p > 0.05$). The highest mean index values were in 2007–2009; the following years, the index got lower but increased again at the end of the study period (Table 3). For the combined sample of infected birds, the interannual differences in the intensity index were not significant (Kruskal–Wallis ANOVA: H (11, $n = 88$) = 16.053, $p = 0.14$). Cross-correlation analysis of mean intensity time series and prevalence time series did not show any significant relationships neither for the combined samples nor for adults and juveniles only ($p > 0.05$).

Development of infestations and host age

The scores, 1 (= recent infestation) or 2 (= advanced infestation), also reflect how advanced or developed an infestation in a quill was. Of 30 juvenile birds with infestations in feathers, five feathers (9%) were scored with advanced infestation and 48 (91%) with recent infestations. For 50 adults, the respective values were 102 (47%) advanced infestations and 117 (53%)

Table 3 The mean intensity index for *Mironovia lagopus* infestations in rock ptarmigan *Lagopus muta*, northeast Iceland 2006–2017. Also given is sample size (*n*) and standard deviation (sd)

Year	Adults			Juveniles		
	Mean	*n*	sd	Mean	*n*	sd
2006	5.0	8	2.3	1.0	3	0.0
2007	8.3	8	3.5	1.5	4	1.3
2008	7.6	5	4.6	5.0	1	…
2009	8.0	2	…	0.5	2	…
2010	7.0	3	2.6	…	0	…
2011	5.8	5	4.1	…	0	…
2012	4.3	3	3.5	1.7	3	1.2
2013	4.0	3	2.0	0.0	2	…
2014	6.7	3	3.1	1.0	1	…
2015	4.6	5	4.7	1.7	6	1.4
2016	5.5	2	…	1.7	9	1.1
2017	6.2	5	3.3	2.4	5	1.1
All Grps	6.2	52	3.4	1.6	36	1.3

Note: standard deviation was only calculated for $n \geq 3$

recent. The difference in the composition among the age groups was highly significant (chi-square = 24.67, df = 1, $p < 0.001$).

Feather selection by quill mites

Seven different types of feathers were analyzed for quill mites. For 50 adults, 219 different feathers were infested and for 30 juveniles 53 feathers. There was no age-related difference with respect to type of feather infested (chi-square = 6.758, df = 6, $p = 0.344$). Therefore, we joined the data for the two age groups and compared the observed distribution with an even distribution of infestations among feathers. There was no apparent selection for any one type of feather (chi-square = 6.765, df = 6, p = 0.34).

Body dispersants

Altogether, 82 *M. lagopus* dispersants were found in vacuum filters from 32 ptarmigan, including 19 adult and 13 juvenile hosts. Mean intensities for adult hosts was 3.58 (range 1–13, 95% cl 2.42–5.47), and for juvenile hosts it was 1.08 (range 1–2, 95% cl 1.00–1.23). This difference in mean intensities of infection among host age groups was significant (Bootstrap 2-sample *t*-test, $t = 3.219$, $p = 0.032$). All dispersants were adult females; larvae, protonymphs, tritonymphs, and adult males were only found inside quills.

Ability to detect *Mironovia lagopus* infection

Dispersant *M. lagopus* were found on the body of two adult hosts that did not have infestations in examined quills and also in six juvenile hosts. According to these results, using only the seven feathers to check for presence or absence of *M. lagopus* will underestimate to some degree the prevalence of infection, especially so for juveniles. We can use the data from birds with infestations in quills to estimate the ratio between known infested birds and dispersants on the body. Body dispersants were found in 17 (34%) of 50 adult ptarmigan with infested quills, and on the body of seven (23%) of 30 juvenile ptarmigan with infested quills. There was no age-related difference with respect to the proportion of hosts with infested quills with or without body dispersants (chi-square = 0.559, df = 1, $p = 0.455$). According to this result, 30% of hosts with observed infested feathers had body dispersants. Using this ratio and the number of observed hosts with dispersants but no registered infestation in quill (see above), we assess that the prevalence of juveniles is underestimated by 39% (prevalence observed 5.0% versus prevalence estimated 6.9%) and of adults by 9% (10.7% versus 11.6%).

The cumulative prevalence values based on individual feathers suggests that the seven feathers should be enough to establish infestation in adults. For juveniles, this was not the case and at the seventh feather the trajectory for cumulative prevalence was still rising (Fig. 2).

Annual prevalence changes and host population density

Spring density of ptarmigan on the study area in 2005–2017 varied markedly. There were peak numbers in 2010 and 2015, and low numbers in 2007, 2012, and 2016 (Fig. 3). The difference between high and low numbers was 2.3-fold. The interannual differences in prevalence of *M. lagopus* infection and the mean intensity index were not significant (see above). But the *p* value was low (0.11 and 0.14 respectively) and thus justifying a comparison of these trajectories and the host density trajectory. Cross-correlation analysis of the ptarmigan population trajectory on the one hand and the combined data set for *M. lagopus* prevalence of infection and the mean intensity index on the other hand did not give any significant relationships ($p > 0.05$).

Host body condition and annual prevalence/intensity changes

The body condition index (BCI) was compared for infested ptarmigans versus non-infested individuals. There was no significant difference between the two groups for neither the combined sample ($t = -1.097$, df = 1207, $p = 0.273$) nor the subsamples divided according to host age (juveniles, $t = -0.671$, df = 719, $p = 0.502$; adults, $t = -0.123$, df = 486, $p = 0.902$). The BCI changed significantly between years. To control for these changes, we standardized to zero mean and unit

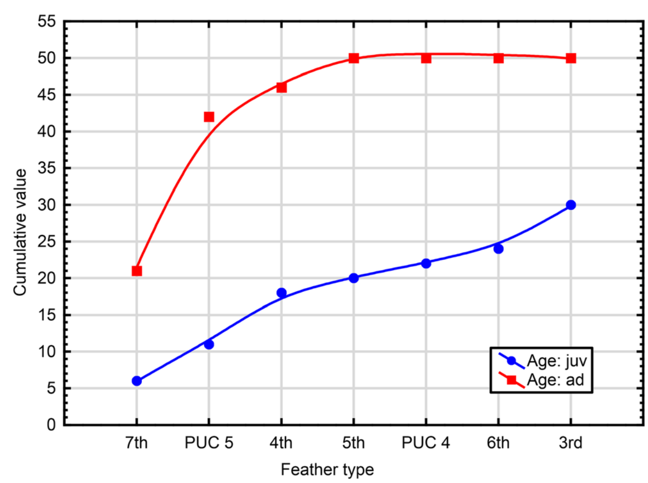

Fig. 2 Cumulative prevalence of *Mironovia lagopus* among 50 infested adult and 30 infested juvenile rock ptarmigan *Lagopus muta* hosts. Seven different types of feathers were checked for presence or absence of *M. lagopus*. The different feather types were arranged in a random order for this analysis. The feather types 3rd to 7th are secondary flight feathers numbered distal to proximal. The feather types Puc 4 and Puc 5 are coverts of primaries 4 and 5 numbered distal to proximal. The trend lines were fitted using distance-weighted least square

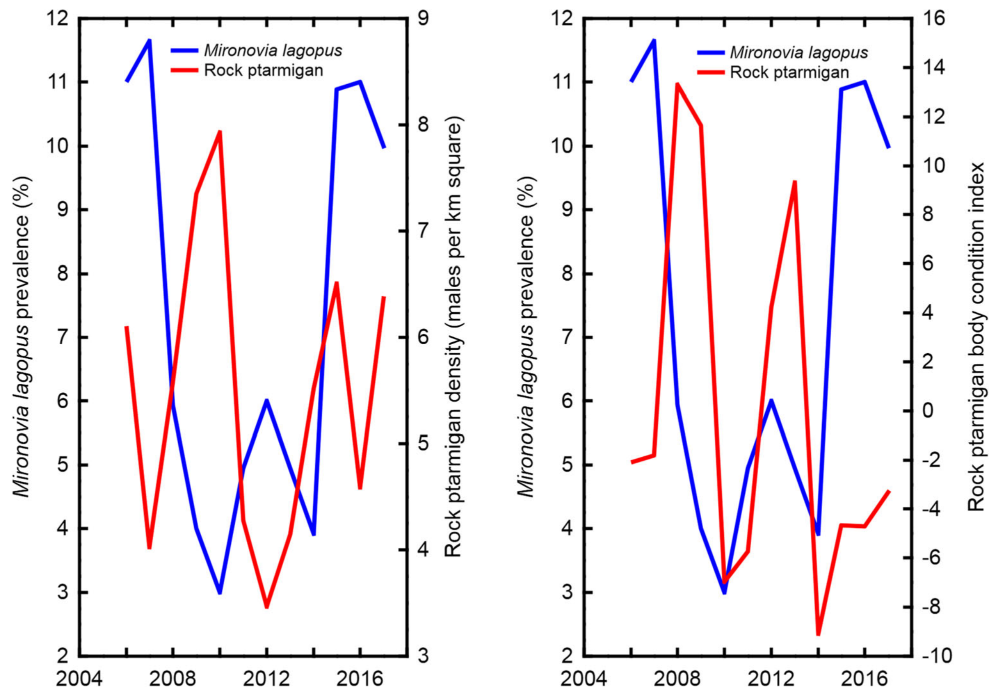

Fig. 3 Comparison of rock ptarmigan *Lagopus muta* spring density and body condition and prevalence of the quill mite *Mironovia lagopus*

variance the values for each year and repeated the comparison but with the same results, namely, no significant difference between the two groups for neither the combined sample ($t = -1.479$, df = 1207, $p = 0.139$) nor the subsamples divided according to host age (juveniles, $t = -1.034$, df = 719, $p = 0.302$; adults, $t = -0.028$, df = 486, $p = 0.977$).

Discussion

General

We found that the quill mite *M. lagopus* occurred at low prevalence in the Icelandic rock ptarmigan population 2006–2017. There was no host sex-related difference in prevalence but a significant age-related difference; juvenile hosts had a significantly lower prevalence of *M. lagopus* infestations (mean 5%) than adult hosts (mean 11%). There was a large change in host density over the years of the study, but neither prevalence of infection nor the mean intensity index of infection did show host density-dependent relationships. There was no relation between host body condition and infection of *M. lagopus*. Below, we want to discuss these and some other issues further.

Dispersal

Transmission of quill mites is thought to be direct and mainly through parent–offspring interaction (vertical transmission; Kethley 1971; Kethley and Johnston 1975; Skoracki 2011). Transmission through interaction of full-grown birds (horizontal transmission) could also play a role. Quill mites are not known to use phoresis for dispersal (Skoracki 2011). We have in our studies examined 520 *Ornithomya chloropus* for phoronts and not found any *M. lagopus* on these louse flies (unpublished data). The louse flies in question were collected from the same pool of ptarmigan as the *M. lagopus* (Table 1).

Vertical transmission, in the case of the ptarmigan, is between the mother and chick as only the hen broods. Ptarmigan chicks are brooded for at least 1 month (Omachi Alpine Museum 1992). In Iceland, this window for vertical transmission would be those from the end of the third week of June (hatch) to the latter part of July.

Horizontal transmission, where mites are transmitted between full-grown birds that come into physical contact, is also a possibility. This would be in spring (late April through May) and between the male and the female (mainly during mating) or between competing males in territorial encounters. The actual length of the contact for both these types of action is brief; each event is measured in seconds not minutes. Physical contact between adults is not known to occur at other times of the year.

Our result, namely, higher prevalence of infection for adult birds, suggests that both vertical and horizontal transmission is involved in the ptarmigan–*M. lagopus* case. This age difference could be at least partly related to the methods applied to register infection though. It is obvious that the seven feathers inspected to determine presence or absence of *M. lagopus* is not enough in the case of juvenile hosts (Fig. 3). This could be further exacerbated by the fact that "colonies" of *M. lagopus* in juvenile host feathers were smaller than colonies in adult host feathers and might therefore be harder to record.

We believe that the main dispersal path for *M. lagopus* is between mother and chick hosts (vertical transmission), but we cannot rule out horizontal transmission. The main dispersal period according to this scenario is in summer from late June into late July (vertical transmission), and possibly also in spring from late April through late May (horizontal transmission).

Molt passage

A feather is an ephemeral habitat with respect to the longevity of the host. We assume that a feather shaft becomes inhabitable for a quill mite when it is fully grown and the pulp of the growing feather has been reabsorbed from the feather shaft lumen. The quill mites—for infestation to remain—must infest new feathers following molt, and this has been termed "molt passage" (Kethley 1971; Kethley and Johnston 1975; Skoracki 2011). The life cycle of the quill mite *Syringophiloidus minor* (Berlese) is ca. 40 days (Kethley 1971), and we assume a similar span for *M. lagopus*. The life cycle is spatially restricted to the quill except for the dispersal period. Only fertilized females disperse; males apparently never leave the quills (Kethley 1971; Casto 1974). This is in accordance with our observations for *M. lagopus* where only adult female mites where found in plumage.

The ptarmigan is notorious for frequency of molt, and adult birds have three plumages over the course of the year (Salomonsen 1939). Not all feathers of the plumage of an adult ptarmigan are molted three times, and the sexes differ in the extent of the molt. The secondary feathers, except for the innermost, have only one generation per year, but inner wing greater coverts have two or three generations per year. We know that *M. lagopus* inhabits at least the quills of both these types of feathers. The secondary feathers are mainly molted in July and August. The wing coverts are molted in May through the beginning of October. Molt passages for *M. lagopus* on adult ptarmigan hosts will thus span May through October.

The ptarmigan downy young hatches with the first set of primaries as pinfeathers. Some of the wing feathers are fully grown already when the juvenile bird is ca. 10 days old or at the beginning of July in Iceland, and these could serve as a site of colonization of *M. lagopus*. Dispersants from the first colonies established in early July—assuming ca. 40 days for the mite to complete the life cycle—will be around in the plumage in early August. The juvenile secondaries are molted already in late July and early August, when the bird is ca. 5 weeks old, and replaced by the immature secondaries that are ready for colonization in mid August and are retained until July–August of the following year. The juvenile wing coverts grown during the first week or two in the life of the bird are retained during the post-juvenile molt and shed during the immature winter molt in September. These coverts are replaced synchronously with adult molt the following spring and summer. Thus, for juvenile and immature birds one would expect to observe molt passage for the first generation of *M. lagopus* in early August and the second generation in late September and early October.

There was a clear age-related difference in mean intensities of dispersants on the hosts. Adult hosts had far more dispersants than juvenile birds. Also, there was an age-related difference with respect to how advanced the infestation was; juveniles had a much higher proportion of "recent infestations" as compared with adults. We interpret this as to reflect colonization of novice host by a limited number of dispersants, time since colonization, and also the time required for a buildup of a local population.

Prevalence of infection

The prevalence of infection by quill mites seems generally to be low (Skoracki 2011 and references therein). Examples are gray shrike *Lanius excubitor* parasitized by *Syringophiloidus weiszi* with 3.5% prevalence ($n = 508$; Skoracki et al. 2001), and barn swallow *Hirundo rustica* parasitized by *Syringophiloidus hirundus* with 17% prevalence ($n = 208$; Skoracki et al. 2003). This is comparable with 7.3% prevalence ($n = 1209$) of *M. lagopus* on ptarmigan in our study. The exception to this are gregarious wild birds like house sparrow *Passer domesticus* parasitized by *Syringophiloidus minor* with 82% prevalence ($n = 492$; Casto 1975) and domestic chicken *Gallus gallus* living under crowded condition with 75% prevalence of a quill mite infestation ($n = 1500$; Rebrassier and Martin 1932). Implicit in this is the potential role of horizontal transmission as an agent for higher prevalence of infection of quill mites.

We did not find any significant changes in prevalence of *M. lagopus* infections for ptarmigan over the course of our study. Also, there was no significant relationship with host density. Such questions have not been addressed by other researchers of the quill mite–host relationship as far as we know.

Impact on host fitness

Quill mites are parasites and feed on host tissue fluids and could serve as vectors for viral and bacterial infections. Once infected, the host is considered to have the quill mite for the remainder of its life and the parasite could potentially affect the fitness of its host (Skoracki 2011). We did not observe any signs of pathogenicity of *M. lagopus* infections in ptarmigan. There were no macroscopic lesions on infected feathers and no sign of feather loss, and the body condition index of affected birds did not differ from that of uninfected birds. Skoracki (2011 and references therein) has revived the literature on the possible negative effect of quill mites on host.

The only examples of the pathological effect related to domestic birds and include itching and feather loss.

Acknowledgments We would like to thank the Lake Myvatn Nature Research Station (RAMY) and the Northeast Iceland Nature History Office for logistical support. We are grateful to a number of hunters for collecting the ptarmigan and to several assistants by preparing and sampling the birds. Finnur Karlsson assisted by searching for the quill mites on all birds. We thank two anonymous reviewers for valuable comments on the article.

Funding information This study was funded by the Icelandic Centre for Research (grant number 090207021) and the Research Fund of the University of Iceland.

Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

References

Anderson LM (1954) Hoyer's solution as a rapid permanent mounting medium for bryophytes. Bryologist 57:242–244

Baumel JJ (1979) Nomina anatomica avium. Academic Press, London

Bochkov AV, Fain A, Skoracki M (2004) New quill mites of the family Syringophilidae (Acari: Cheyletoidea). Syst Parasitol 57:135–150

Bochkov AV, Skirnisson K (2011) Description of the life stages of quill mite *Mironovia lagopus* sp. nov. (Acari: Syringophilidae) parasitizing the rock ptarmigan *Lagopus muta* (Phasianidae) from Iceland. Parasitol Res 108:715–722

Casto SD (1974) Quill wall thickness and feeding of *Syringophiloidus minor* (Berlese) (Acarina: Syringophilidae). Ann Entomol Soc Am 67:824

Casto SD (1975) The effect of the postjuvenal molt in the House Sparrow on infestations of the quill mite, *Syringophiloidus minor* (Berlese) (Acarina: Syringophilidae). J Med Entomol 12:23–27

Chirov PA, Kravtsova NT (1995) A new genus and new species of mites of the family Syringophilidae. Parazitologiya 29:370–379 [In Russian]

Dabert J, Mironov SV (1999) Origin and evolution of feather mites (Astigmata). Exp Appl Acarol 23:437–454

Dell Inc. (2015) Dell Statistica (data analysis software system)**,** version 13. software.dell.com. Accessed 29 March 2019

Kethley JB (1970) A revision of the family Syringophilidae (Prostigmata, Acarina). Contrib Am Entomol Inst 5:1–76

Kethley JB (1971) Population regulation in quill mites (Acari: Syringophilidae). Ecology 52:1113–1118

Kethley JB, Johnston DE (1975) Resource tracking patterns in bird and mammal ectoparasites. Misc Publ Entomol Soc Am 9:227–236

Mironov SV (1999) Feather mites: general morphological adaptations, phylogeny and coevolutionary relationships with birds. Ekologiya 2:57–66

Montgomerie R, Holder K (2008) Rock ptarmigan (*Lagopus muta*). In: Poole A (ed). The birds of North America online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: https://doi.org/10.2173/bna.51; http://bna.birds.cornell.edu/bna/species/051. Accessed 29 March 2019

Omachi Alpine Museum (1992) Rock ptarmigan — life history and challenge to breeding. Shinano Mainichi Press, Nagano In Japanese

Rebrassier RE, Martin ED (1932) *Syringophilus bipectinatus*, a quill mite of poultry. Science 76:128

Rózsa L, Reiczigel J, Majoros G (2000) Quantifying parasites in samples of hosts. J Parasitol 86:228–232

Salomonsen F (1939) Moults and sequence of plumage in the Rock Ptarmigan [*Lagopus mutus* (Montin)]. Videnskabelige Meddeleser fra Dansk Naturalhistorisk Forening, no. 103

Skoracki M (2011) Quill mites (Acari: Syringophyllidae) of the Palaearctic region. Zootaxa 2840:1–414

Skoracki M, Hromada M, Tryjanowski P (2001) Description of a new species of quill mite *Syringophiloidus weiszii* sp. n. (Acari, Prostigmata, Syringophilidae) from Great Grey Shrike *Lanius excubitor*. Acta Parasitol 46:30–34

Skoracki M, Møller AP, Tryjanowski P (2003) A new species of parasitic mites of the genus *Syringophiloidus* Kethley, 1970 (Acari: Syringophilidae) from the Barn Swallow *Hirundo rustica* Linnaeus, 1758. Parasite 10:17–20

Skoracki M, Sikora B (2004) A new genus and four new species of quill mites (Acari: Prostigmata: Syringophilidae) from phasianid birds (Galliformes: Phasianidae). Parasite 11:379–386

Skoracki M, Sikora B (2011) Quill mites (Acari: Syringophilidae) associated with galliform birds (Aves: Galliformes). Zootaxa 2966:13–30

Stenkewitz U, Nielsen OK, Skirnisson K, Stefánsson G (2016) Host-parasite interactions and population dynamics of Rock ptarmigan. PLoS One. https://doi.org/10.1371/journal.pone.0165293

Weeden RB, Watson A (1967) Determining the age of rock ptarmigan in Alaska and Scotland. J Wildl Manag 31:825–826

Zmudzinski M, Skoracki M (2018) An updated check-list of the family Syringophilidae (Acariformes: Prostigmata). Available at: https://sites.google.com/site/syringophilidae/. Accessed 28 March 2019