Parasites and population change of rock ptarmigan in Iceland

Ute Stenkewitz

Faculty of Life and Environmental Sciences
University of Iceland
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Ute Stenkewitz

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Philosophiae Doctor degree in Biology

Advisor
Ólafur Karl Nielsen

PhD Committee
Karl Skírnisson
Gunnar Stefánsson

Departmental Coordinator
Páll Hersteinsson†
Snæbjörn Pálsson

Opponents
Steve Albon
José Alves

Faculty of Life and Environmental Sciences
University of Iceland
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Faculty of Life and Environmental Sciences
University of Iceland
101 Reykjavik
Iceland

Telephone: +354 525 4000

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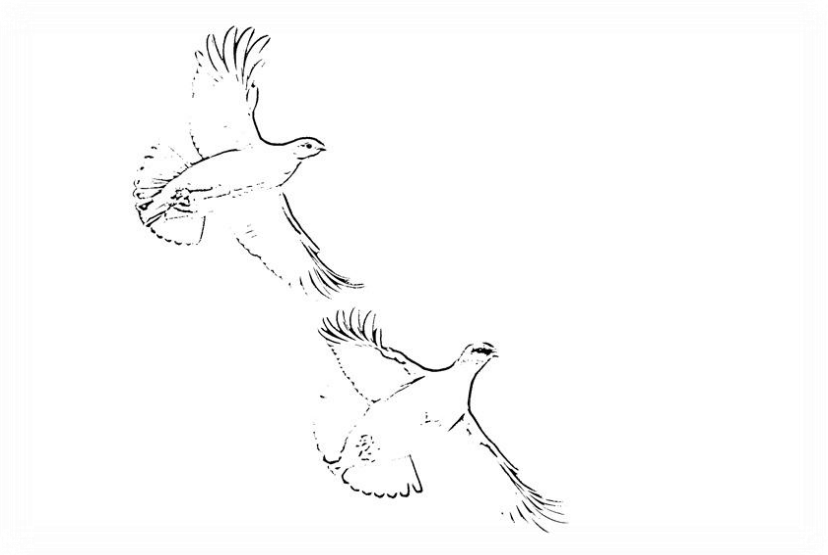
Abstract

The parasite fauna of the Icelandic rock ptarmigan *Lagopus muta* had just been described when engaging in this project in 2010. The purpose was to study the influence that parasites exhibit on ptarmigan population change over a period of 7 years (2006–2012). The cycles that the Icelandic ptarmigan population has recently been undergoing peak every 5–6 years. Host-parasite interactions are known as one possible regulator of cycling host populations. Measures of the parasite community and pathogenic parasites were analysed. Ptarmigan population density was particularly associated with the prevalence of a coccidian parasite named *Eimeria muta*. Annual aggregation levels of this eimerid fluctuated inversely with its prevalence, with lows at prevalence peak and vice versa. Both prevalence and aggregation of *E. muta* tracked ptarmigan population density with a 1.5 year time lag. The time lag could be explained by the host specificity of this eimerid, host density dependent shedding of oocysts, and their persistence in the environment from one year to the next. *E. muta* prevalence was also negatively associated with ptarmigan body condition, marginally negatively with fecundity, and positively with mortality, indicating their pathogenicity. Further, there were significant associations between fecundity and the chewing louse *Amyrsidea lagopi* prevalence (negative), excess juvenile mortality and the nematode *Capillaria caudinflata* prevalence (positive), and adult mortality and the skin mite *Metamicrolichus islandicus* prevalence (negative). Though this study is correlational, it provides strong evidence that the microparasite *E. muta* has the potential to destabilize rock ptarmigan population dynamics in Iceland.

Útdráttur

Sníkjudýrafánu íslensku rjúpunnar *Lagopus muta* hafði nýlega verið lýst þegar rannsóknir mínar hófust árið 2010. Markmið mitt var að rannsaka hvaða áhrif sníkjudýr hafa á stofnbreytingar rjúpunnar og rannsóknatíminn var 7 ár (2006–2012). Stofnsveifla rjúpunnar hefur breyst á síðustu árum og nú líða um 5–6 ár á milli hámarka. Einn af þeim þáttum sem vitað er að hafa áhrif á stofnsveiflur eru tengsl hýsils og sníkjudýrs. Við greininguna voru skoðuð lýsigildi fyrir sníkjudýrasamfélagið í heild sinni og einstakar meinvirkar sníkjudýrategundir. Þéttleiki rjúpna sýndi sterkt samband við smittíðni hnísilsins *Eimeria muta*. Dreifing þessarar hnístategundar innan rjúpnastofnsins breyttist í tengslum við breytingar á smittíðni, hnappdreifing þeirra var mest þegar smittíðnin var lægst og svo öfugt. Ferlarnir sem lýsa breytingum á bæði smittíðni og dreifingu *E. muta* fylgdu ferlinum sem lýsti stofnbreytingum rjúpunnar en með eins og hálfs árs töf. Töfin endurspeglar hýsilsérhæfingu þessa sníkjudýrs, þéttleikháðum útskilnaði þolhjúpa hnísilsins, og langtíma virkni þolhjúpanna, en þeir geta lifað á milli ára í umhverfinu. Meinvirkni *E. muta* lýsti sér m.a. í neikvæðu sambandi við holdafar fuglanna, og nær marktæku neikvæðu sambandi við frjósemi þeirra annars vegar og jákvæðu sambandi við afföll þeirra hins vegar. Enn fremur voru marktæk neikvæð tengsl á milli frjósemi og smittíðni naglúsarinnar *Amyrsidea lagopi*, jákvæð tengsl á milli umframaffalla ungfugla og smittíðni þráðormsins *Capillaria caudinflata*, og neikvæð tengsl á milli smittíðni húðmítilsins *Metamicrolichus islandicus* og affalla fullorðinna fugla. Þó svo að þessi rannsókn byggi á fylgni þá bendir hún sterklega til þess að sníkjudýrið *E. muta* hafi alla burði til að skapa óstöðugleika í stofnstærðarstjórnun rjúpunnar á Íslandi.



hoc opus, hic labor
Virgil

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1 The Scene

Wildlife population cycles are curious phenomena that occur in populations of various boreal and arctic bird, mammal, and insect species (Kendall et al. 1998, Berryman 2002). They are particularly well documented for species of grouse (Keith 1963, Hudson et al. 2002, Martínez-Padilla et al. 2014). What drives these cycles has long puzzled researchers (Elton 1924, Keith 1963). Possible explanations include intrinsic factors such as kinship, behavior, life-history features, or physiological responses (Berryman 2002, Mougeot et al. 2005) as well as biotic extrinsic factors such as herbivore–plant, predator–prey, or host–parasite interactions (Newton 1998) and/or abiotic extrinsic factors such as climate, moon cycles, or sunspot activity (Archibald 1977, Sinclair et al. 1993, Ims & Fuglei 2005).

The Icelandic rock ptarmigan *Lagopus muta* population exhibits such cycles, and peaks in numbers have occurred in relatively regular 10–12 year intervals until 2003 (Guðmundsson 1960, Nielsen & Pétursson 1995, Brynjarsdóttir et al. 2003). Following a hunting ban in 2003 and 2004 and changed harvest regulations the dynamics of the ptarmigan population have changed and population peaks are now 5 years apart (Sturludóttir 2015, Icelandic Institute of Natural History unpublished data). The purpose of this study has been to investigate the role of parasites in the population dynamics of rock ptarmigan. It follows in the footsteps of a project on gyrfalcon *Falco rusticolus* – rock ptarmigan predator–prey interactions (Nielsen 1999a, 2011).

This thesis consists of a Synopsis and Publications section. The Synopsis illuminates the structure and frame of this study. The Publications depict the main stages of this study covering the years 2006–2012. First, I investigated how parasites relate to spleen and bursa of Fabricius size, two organs of immune function. Second, I examined how mallophagan chewing lice – in particular one named *Amyrsidea lagopi* – relate to feather holes. Third, I explored how parasites relate to ptarmigan body condition, demographic parameters (mortality and fecundity), and population density. Fourth, I give a detailed overview over the parasite community with regard to age, sex, and year distribution using combined and individual parasite measures.

2 Rock ptarmigan

Rock ptarmigan (hereafter ptarmigan) – the archetypal arctic bird – lives in circumpolar regions of the northern hemisphere (Storch 2007). It is the most widely distributed of any grouse, with the northernmost populations to be found in Greenland (Höhn 1980) and the southernmost in Bulgaria (Storch 2007). In Iceland, ptarmigan (Figure 2.1) is of great cultural and natural value; it is the most important upland game bird, a revered christmas dish, common breeding bird, and a key species in the heathland ecosystem. It carries an important position within the food-web being the dominant wild vertebrate herbivore and important prey. Without it, its specialized main predator, gyrfalcon, would disappear and other predators like Arctic fox *Vulpes lagopi* would suffer.

Figure 2.1 *Icelandic rock ptarmigan male (left) and female (right). Pictures by Daniel Bergmann.*

Habitat

Ptarmigan inhabit dry tundra and alpine habitats with rocky ridges or outcrops and mostly sparse vegetation dominated by grasses, lichens, and mosses (Storch 2000). In Iceland, ptarmigan live in heathland, scrub, and well vegetated lavafields, from the seashore to the mountains (Ólafsson 1991, Nielsen 1993, Baldursson 2014).

Ecology

Icelandic ptarmigan move seasonally within the country. In the autumn, it often gathers in flocks and move uphill to stay above the snowline as long as the lowlands are free of snow. When the land covers with snow, it seeks food in birch stands (Garðarsson 1971, 1988). In

spring (starting in April), first the cocks and 2–3 weeks later the hens return to their breeding grounds.

The territorial period of ptarmigan cocks begins in late April and ends in early June. At this time, they perch on high places to defend their territories and display to hens. After the territorial period, cocks stay on the breeding grounds, but they stop defending territories and do not take any part in family duties. Hens raise the chicks which are independent by August. Ptarmigan reach maturity in their first year of life (Holder & Montgomerie 1993). Mortality rates in the population are high and few birds exceed the age of 4 years (Gardarsson 1988, Icelandic Institute of Natural History ringing data).

Moulting of body feathers happens three times a year, but the white flight feathers and black tail feathers are moulted only once a year (Salomonsen 1939). In winter and spring, the body feathers are white and in summer and autumn they are mainly brown with grey and yellow flecks and specks (Salomonsen 1939).

Icelandic population

From 1981–2015, ptarmigan population densities ranged between 2.5 and 12.5 cocks/km² in northeast Iceland compared to 0.2 and 5.0 cocks/km² in the southwest (Icelandic Institute of Natural History, monitoring data). The difference between peak and low mean annual density in the northeast was 5.4 fold (Nielsen 2011).

Traditionally the ptarmigan population has shown multi-annual cycles spanning 10–12 years (Nielsen & Pétursson 1995). Until 2003, the cycles have occurred in relatively regular intervals (Guðmundsson 1960, Nielsen & Pétursson 1995, Brynjarsdóttir et al. 2003) and were characterized by two demographic factors, namely (a) juvenile excess winter mortality lagging the ptarmigan population by 2–4 years, and (b) the negative impact of population size on chick production, the lag being 2 years (Magnússon et al. 2004). The latter factor combines two, age related chick production and chick removal by gyrfalcon predation in late summer (Magnússon et al. 2004, Snæþórsson 2012). Gyrfalcon, the resident specialist ptarmigan predator, provides the required link between ptarmigan numbers and the time lags in excess autumn and winter mortality of the juvenile ptarmigan as well as chick production, and has thus been suggested to be the primary driver of the ptarmigan population cycles in Iceland (Nielsen 1999a, Magnússon et al. 2004). The predation destabilizes the ptarmigan population, by accelerating the decline, accentuating the amplitude of the cycle, and influence the length of the low phase, but it is not responsible for the start of the decline (Nielsen 1999a). There are, however, aspects to the ptarmigan-falcon population model that cannot be explained (Nielsen 1999a, Magnússon et al. 2004) leaving space for further speculation on what additional factors may drive the ptarmigan population to cycle.

A total hunting ban in 2003 and 2004 and changes in management post 2004 led to drastic

changes in both ptarmigan population cycle and demographics (Sturludóttir 2015). The population now experiences a shorter span of the cycle with peaks every 5 years and population change is now characterized by total adult mortality (natural and hunting), that reflects previous year ptarmigan population density (Sturludóttir 2015). New management regulations include a ban on market hunting and reduction in the number of hunting days from 69 to 12 days. Harvest rate has fallen to 11–17 % from 34–54 % prior to the hunting ban. With respect to ptarmigan numbers, there were peaks in 2005, 2010, and 2015. My study, 2006–2012, thus relates to the period with changed population dynamics of the ptarmigan, and covers one peak year (2010), one bottom year (2007), three years of population decline, and three years of growth.

History of ptarmigan research in Iceland

Ptarmigan in Iceland have been studied for a long time. In the beginning, food habits, molt, movement pattern, and changes in numbers were studied (Guðmundsson 1937, 1951, 1960, Salomonsen 1939, Garðarsson 1971). In 1963, a project to study the ptarmigan population cycle was initiated (Guðmundsson 1964, Guðmundsson & Garðarsson 1970, Garðarsson 1971, 1988). Two further studies were established later, namely the ptarmigan monitoring program and a study on predator–prey interactions between gyrfalcon and ptarmigan (Nielsen 1986, 1999a). Currently, the monitoring program consists of censuses in different parts of the country, measurements of age ratios three times a year, and collection of hunting statistics, the latter through the Environment Agency of Iceland (Nielsen 1999b, Nielsen et al. 2004, http://www.ust.is/the-environment-agency-of-iceland). The monitoring data has been used to study the demography of the population, model population changes and calculate population size (Brynjarsdóttir et al. 2003, Magnússon et al. 2004, Magnússon 2005, Sturludóttir 2015). Additional studies on habitat selection (Nielsen 1995), effects of hunting on survival rates (Nielsen 2000, Nielsen 2001), phylogeny (Arnason 1972, Holder et al. 2004), surveying techniques (Stenkewitz 2006), and reproductive success and survival (Snæþórsson 2012) have been carried out. In 2006, the Ptarmigan Health Project, a research program on the relationship between health related parameters and population change was established (Nielsen & Skírnisson 2009). The health (or condition) factors studied have included parasite burden (this PhD project), body condition, stress levels, immunological defences, and condition of the preen gland. The main questions give attention to the interrelation between these indices of the birds' health and population change and demographics. A number of papers and dissertations have already come out of this project such as on the ptarmigan parasite fauna (Þórarinsdóttir 2009, Þórarinsdóttir et al. 2010, Skirnisson et al. 2012), morphology and systematics of parasites (Skirnisson & Thorarinsdottir 2007, Bochkov & Skirnisson 2011, Skirnisson et al. 2016a, b), morphology (progress reports by Nielsen et al. 2013, 2014), ectoparasite defence (González 2014), diet (Dépré 2014), or body reserves, grit, gizzard and gutlength (Guðmundsson 2015).

3 Population cycles and host-parasite interactions

3.1 Theory

Population cycles

Population cycles are phenomenona where populations rise and fall over a given period of time. They are well known for herbivorous species of northern latitudes including lepidopterans, hares, lemmings, voles, and grouse (Keith 1963, Berryman 2002), and are particularly well documented for species in the genus *Lagopus* (Weeden 1965, Nielsen & Pétursson 1995, Moss & Watson 2001, Holmstad et al. 2005b). There is no consensus among researchers about what drives population cycles. Long-term studies show that it can be a combination of intrinsic (species innate) and extrinsic (trophic interactions, environmental) factors (e.g., Newton 1998, Martínez-Padilla et al. 2014). Intrinsic factors include genetic variation, behavior, life-history features, or physiological responses (Berryman 2002, Mougeot et al. 2005). Extrinsic factors include trophic interactions such as herbivore–plant (Haukioja & Hakala 1975, Fox & Bryant 1984), predator–prey (Korpimäki & Krebs 1996, Valkama et al. 2004), host–parasite interactions (Anderson & May 1980, Hudson et al. 2002), or climate, sunspot activity, or moon cycles (Archibald 1977, Sinclair & Gosline 1997, Post & Forchhammer 2002).

The underlying mechanism that often serves to explain population cycles is delayed density dependence. It describes a situation where additions and losses of a population correlate with the size of the population in an earlier year or generation (Newton 1998). A population grows above its normal capacity until a negative feedback mechanism brings it back down, with the negative feedback mechanism operating with a time lag (Newton 1998, Berryman 2002). Predators or parasites are examples for negative feedbacks.

Host-parasite interactions

Host-parasite systems are intimate relationships between two different species. There is a biochemical interaction between host and parasite – that is, they recognize each other – ultimately at the molecular level, and host tissues are stimulated to react in some way (O'Donoghue 2010). Even more though, the genetic program of the one is inevitably tied to the genetic program of the other (Russell 2013). The host is ideally kept alive, at least until the parasite can reproduce (Russell 2013). Interestingly, in such systems, while intimacy is high and antagonism low, compartimentalisation is high and connectance low, although the

latter is in dispute (van Veen et al. 2008, Pires & Guimarães 2012). Each parasite species has its space in the „house“, that is its habitat in or on the host.

Host-parasite interactions driving population dynamics

There are three main regulating or destabilizing qualities that parasites can have on host population dynamics: (1) wide dispersion of parasites within the host population as opposed to highly aggregated, (2) parasite-induced host mortality and reduction of host reproductive potential, and (3) time-lags of host population size in relation to parasite abundance (that is, delays in parasite transmission and reproduction). The conceptual ideas were compiled, modelled, and developed by Anderson & May (1978) and May & Anderson (1978), commonly referred to as the Anderson-May models. A lion‘s share of recent studies about the influence of host–parasite interactions on host population dynamics (both stable and unstable), are based on them. Here are some examples of such studies; (A) – (D) are experimental and (E) and (F) are correlational:

(A) In red grouse *Lagopus lagopus scoticus* in the UK, the parasitic nematode *Trichostrongylus tenuis* drives the 4–8 year cycles of grouse by reducing fecundity and survival (Dobson & Hudson 1992, Moss et al. 1996, Hudson et al. 1998, 2002, Cattadori et al. 2005). There is a delayed density dependent relationship between grouse numbers in one year and worm burdens in the subsequent year (Dobson & Hudson 1992). The explanation is that in the nematode life cycle infective larval stages introduce time delays in the recruitment of adults into the breeding parasite population. That is, the larvae need time to develop within the body of the host to a breeding adult worm, and this causes the time delay. It is also suggested that ingested larvae enter an arrested state of development rather than being recruited directly into the adult population. When anthelmintic drugs were administered against *T. tenuis*, population crashes could be halted (Hudson et al. 1998). More recent studies on the red grouse system suggest that parasites are not a necessary cause for red grouse cycles and highlight that behavioral and parasite-mediated mechanisms are interrelated; long-term experiments show that parasites and aggressiveness interact (e.g., Hudson 2001, Mougeot et al. 2005, Martínez-Padilla et al. 2013).

(B) In mountain hares *Lepus timidus* in Scotland, the parasitic nematode *Trichostrongylus retortaeformis* is the main driver of unstable dynamics of the the hare population (Newey & Thirgood 2004, Newey et al. 2004, 2005, 2007). The low degree of aggregation of *T. retortaeformis* and significant negative effect of intensity of infection on body condition are thought to destabilise the hare population. *T. retortaeformis* also reduces the fecundity and survival of female hares, and infective larval stages introduce time delays in the recruitment of adults into the breeding parasite population from one year to the next. That is, the time lag is created just like in red grouse by the time it takes the larvae to develop into a breeding adult worm. However, recent models combining theory and observation predict that the hare cycles are not driven by the parasite (Townsend et al. 2009), but that

the effect of the parasite on the hares likely forms part of a complex set of interactions that lead to population cycles (Townsend et al. 2011). Other factors most likely significantly influencing the hare population are said to be dispersal, harvesting, and population control (Townsend et al. 2011).

(C) In forest insects, microsporodian protozoan and baculovirus infections may drive 5- to 12-year population cycles (Anderson & May 1980). For instance, some forest Lepidoptera population dynamics in Canada are strongly influenced by nucleopolyhedrovirus (DNA virus) infections (Myers & Cory 2013, 2015). The virus are transmitted both horizontally through contact and vertically through the environment. Infections with this virus result in mortality. Susceptible larvae become infected if they ingest virion-containing occlusion bodies on foliage previously released by dead infected larvae. What provides the lag that is required for cyclic dynamics is suggested to be reduced host fecundity.

(D) In the irregularly fluctuating endemic Svalbard reindeer *Rangifer tarandus* population (CAFF 2001), a model using experimental and observational data implies that the nematode *Ostertagia gruehneri* and its effect on fecundity is sufficient to regulate reindeer densities (Albon et al. 2002). The degree to which parasites repress fecundity is positively related to parasite abundance the previous October, and this in turn is related to host density two years earlier.

(E) In willow ptarmigan *Lagopus lagopus lagopus* in Norway, parasites affect demographic parameters such as body condition, breeding success, or growth rates of the host population, and were hence negatively associated with changes in the ptarmigan population (Holmstad et al. 2005a, b).

(F) In the bank vole *Clethrionomys glareolus* populations on small islands in central Finland, the coccidian *Eimeria* spp. relate inversely to density changes (Hakkarainen et al. 2007). The parasites affect the body condition of vole mothers and their offspring.

3.2 The Icelandic system

Hypotheses

Based on the Anderson-May models and a correlative study on parasites, grouse, and population dynamics in Norway (Holmstad et al. 2005a, b) that I initially used as a model for this study, predictions were made for the Icelandic ptarmigan system. The aim was to evaluate whether the parasite community or any individual parasite potentially contributes to the regulation of the dynamics of the ptarmigan population. This was done by testing the following specific hypotheses:

- Trajectories of the host population size and parasite abundance and aggregation are related. To have a regulatory effect, these trajectories should show a time-lag. That is, parasite abundance should track ptarmigan population density with a time delay.
- Aggregation of parasites are low in the host population at peaks of parasite abundance. That is, parasites should become more evenly spread throughout the ptarmigan population when there are more of them around.
- There are direct relations between body condition, individual and demographic parameters such as ptarmigan mortality, and/or fecundity and the parasite community or pathogenic parasites.

Influence of parasites on body condition

Host-parasite interactions work through the effect on host body condition and thus reproduction and survival (e.g., Anderson & May 1981, Loye & Zuk 1991, Grenfell & Chappell 1995, Bush et al. 2001, Combes 2001, Berryman 2002). Assessing host body condition is therefore important and in this study I use a Body Condition Index (BCI) as an indicator for ptarmigan condition to investigate its relation to measures of immune function, parasites, fecundity, survival, and population density.

Parasite infections – cause or consequence of body condition?

My study is based on the assumption that host body condition and demographics is a consequence of parasite levels. This however has been questioned: do parasite levels depend on body condition and population densities (e.g., Holmstad et al. 2005a)? Since this is a correlational study, neither of these viewpoints can be judged entirely. But the above assumptions are based on mathematical models that have shown parasites *can* destabilize host numbers when they exhibit (a) low degrees of aggregation, (b) time-lags with respect to host population size, and (c) reductions in host fecundity and survival (Anderson & May 1978, May & Anderson 1978). All these points apply to the ptarmigan system.

4 Parasites of rock ptarmigan

The parasite community of ptarmigan has recently been described (Þórarinsdóttir 2009, Skirnisson et al. 2012), and this study is carried out based on these fundamental descriptions. A total of 17 parasite species are known for the ptarmigan in Iceland, 7 endoparasites and 10 ectoparasites. The endoparasite fauna consists of protozoans and worms (Table 4.2) and the ectoparasite fauna of mites, lice, fleas, and flies (Table 4.1). The ptarmigan body is a habitat for a diverse ensemble of parasite species – a clear example of biodiversity on the micro scale. Each of these species has its specific niche with respect to where they live (Figure 4.1), what to feed on, and how to disperse. Examples are the five species of mites: one species is confined to the space between the barbs of distinct wing feathers, another is found in the down, two in the skin, and one in the quills (Skirnisson et al. 2012). Some of these mites feed on feather wax and keratin, others on skin debris and body fluids (Johnson & Clayton 2003, Proctor 2003, Clayton et al. 2008). Dispersal can be direct, from bird to bird, or by phoresis whereby the hippoboscid fly serves as vector for mallophagans and mites (Keirans 1975, Macchioni et al. 2005, Harbison et al. 2009, Marcelino et al. 2009, da Cunha Amaral et al. 2013). For ptarmigan, adult females of the mite *Myialges borealis* surrounded by eggs were found attached to the abdomen of the hippoboscid *Ornithomya chloropus* (Figure 4.2). Two more mite species though foreign to ptarmigan were found on *O. chloropus*, one of them attached to the wings of the hippoboscid (Guðmundsson et al. 2013); this scenario, where the host of a parasite is another parasite is hyper-parasitism. Most of the parasites mentioned are definitive to ptarmigan, but it occasionally happens that parasites with different final hosts are detected in ptarmigan. One such parasite is the tapeworm *Mesocestoides canislagopodis* whose natural final host is the Arctic fox *Vulpes lagopus* (Skírnisson et al. 1993). It is found in ptarmigan body cavities and just now it was discovered that ptarmigan serves as a second intermediate host (Skirnisson et al. 2016a, b).

Pathogenicity

Pathogenicity is the capability of a pathogen to cause disease. The following parasites are thought to be the most pathogenic to ptarmigan:

Eimeria muta and *E. rjupa* are intestinal microparasites, and *E. muta* was found to be involved in coccidiosis (Ólafur K. Nielsen and Karl Skírnisson, pers. comm.). The primary symptom of coccidiosis is diarrhoea and in severe cases it can lead to death (Atkinson et al. 2008). For instance, Ring-necked pheasants *Phasianus colchicus* experimentally infected with low numbers of *Eimeria phasiani* (10,000 oocysts) developed only diarrhoea, but

when exposed to 100,000 oocysts, the birds exhibited ruffled feathers, incoordination, mucoid diarrhoea, and weight loss (Trigg 1967). Similarly with infections of Ring-necked pheasants with *Eimeria colchici*: birds with low infections (20,000 oocysts) survived, but none survived exposure to 80,000 or 320,000 oocysts (Norton 1967). However, the highly species specific eimerids differ in their degrees of pathogenicity (Rommel et al. 2000).

Table 4.1 *Habitat, size, and life cycles of the ectoparasites of Icelandic rock ptarmigan. Pictures by Karl Skírnisson.*

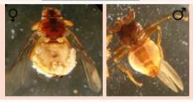
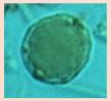
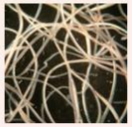
Group	Scientific name	Appearance	Habitat Average size Life cycle Final host
Acari (mites)	*Metamicrolichus islandicus*		Skin ♀ 362 µm ♂ 276 µm Indirect?
	Mironovia lagopus		Quills 640 µm Direct
	Myialges borealis		Skin, plumage? ♀ 283 µm Indirect? *Ornithomya chloropus*?
	Strelkoviacarus holoaspis		Down ♀ 346 µm ♂ 256 µm Direct
	Tetraolichus lagopi		Vanes ♀ 405 µm ♂ 262 µm Direct
Mallophaga (lice)	*Amyrsidea lagopi*		Skin, plumage ♀ 2.1 mm ♂ 1.4 mm Direct
	Goniodes lagopi		Plumage ♀ 2.6 mm ♂ 2.2 mm Direct
	Lagopoecus affinis		Plumage ♀ 1.8 mm ♂ 1.4 mm Direct
Diptera (flies)	*Ornithomya chloropus*		Plumage ♀♂ 6.1 mm Direct
Siphonaptera (fleas)	*Ceratophyllus garei*		Plumage, skin 3 – 5 mm Direct

Table 4.2 *Habitat, size, and life cycles of the endoparasites of Icelandic rock ptarmigan. Pictures by Karl Skírnisson.*

Group	Scientific name	Appearance	Habitat Average size Life cycle Intermediate host
Sporozoa (coccidians)	*Eimeria muta*		Small and large intestines, Ceca 25 × 17 µm Direct
	Eimeria rjupa		Small and large intestines, Ceca 25 × 22 µm Direct
Heterocontophyta	*Blastocystis* sp.		Small and large intestines, Ceca 5 – 14 µm Direct
Cestoda (tapeworms)	*Passerilepis serpentulus*		Duodenum ≤ 75 mm Indirect (requires 2 hosts) Beetle
	Mesocestoides canislagopodis		Body cavity, Liver 2.7 × 1.4 mm Indirect (requires 3 hosts) 1st IH Arthropods? 2nd IH Insectivorous vertebrates (mammals, birds, reptiles, amphibians)
Nematoda (roundworms)	*Capillaria caudinflata*	 	Small intestines, Ceca 7 – 36 mm Indirect (requires 2 hosts) Earthworm
	Trichostrongylus tenuis		Ceca 8 – 10 mm Direct

Capillaria caudinflata is a hairworm (nematode) of the lower intestinal tract. Infections can cause thickening of the mucosa, erosion or ulceration, intraluminal fluid accumulation, petechiae, exudates, and diarrhea, but low numbers of worms are usually asymptomatic (Atkinson et al. 2008). The severe disease is called capillariasis.

Trichostrongylus tenuis is an intestinal nematode that is known to cause trichostrongylosis, also known as "grouse disease" (Atkinson et al. 2008). Hosts with high intensity of these worms can show appetite loss, malnutrition, diarrhea, and emaciation (Atkinson et al. 2008). This nematode was shown to be the regulator in Red grouse *Lagopus lagopus scoticus* population dynamics (Hudson et al. 1998). However, in Icelandic ptarmigan max. 28 worms (2006–2012) were detected in one bird, so it appears unlikely this would elicit severe disease. In populations where this helminth has serious impact, it occurs in thousands (Hudson 1986).

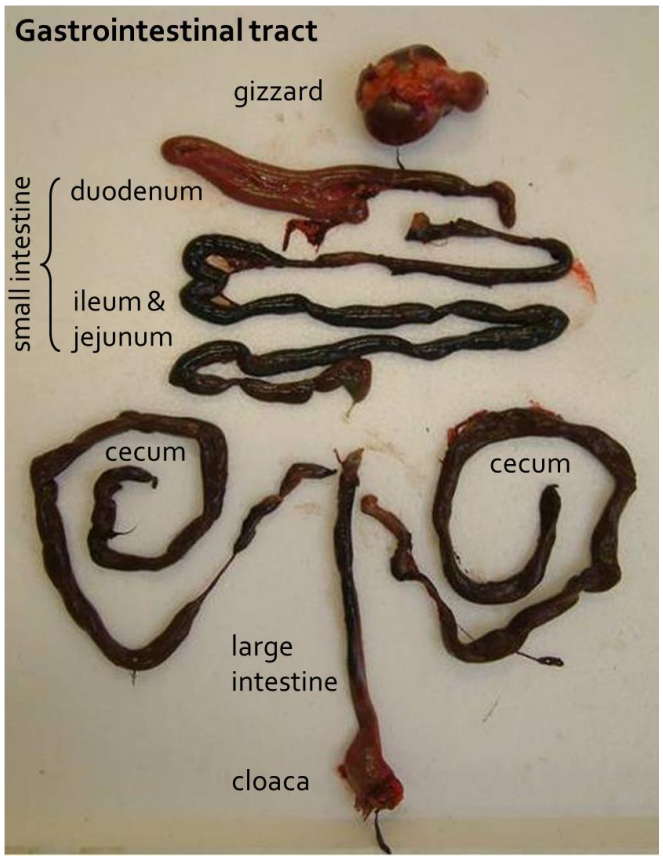


Figure 4.1 *Endoparasitic habitat of Icelandic rock ptarmigan. Picture by Karl Skírnisson.*

Metamicrolichus islandicus is a skin mite that causes mange (Skirnisson et al. 2012). Mange is a skin disease that results in scaly skin, and in severe cases damage and loss of feathers and anemia (Atkinson et al. 2008). In ptarmigan, manged birds are recognized by their scaly skin (Figure 4.2). *M. islandicus* is a species new to science (Mironov et al.

2010). *Myialges borealis* groups with epidermoptid skin mites but its life cycle is still unknown, and also if it contributes to mange on the ptarmigan and yet other bird hosts (Skirnisson et al. 2012).

Amyrsidea lagopi is an amblyceran chewing louse that feeds on host skin and blood by biting the skin or pin feathers, but also by shearing or scraping feathers and skin (Crutchfield & Hixson 1943, Ash 1960, Johnson & Clayton 2003). When present in large numbers, amblycerans can cause extensive feather and skin damage, leading to dermatitis, itching, insomnia, and excessive preening and scratching (Atkinson et al. 2008).

The following parasites are thought to be less pathogenic to ptarmigan:

Goniodes lagopi and *Lagopoecus affinis* are ischnoceran chewing lice that are highly specialized, live in the plumage, and feed primarily on keratin of the barbules (e.g., Johnson & Clayton 2003, Møller & Rózsa 2005, Clayton et al. 2008).

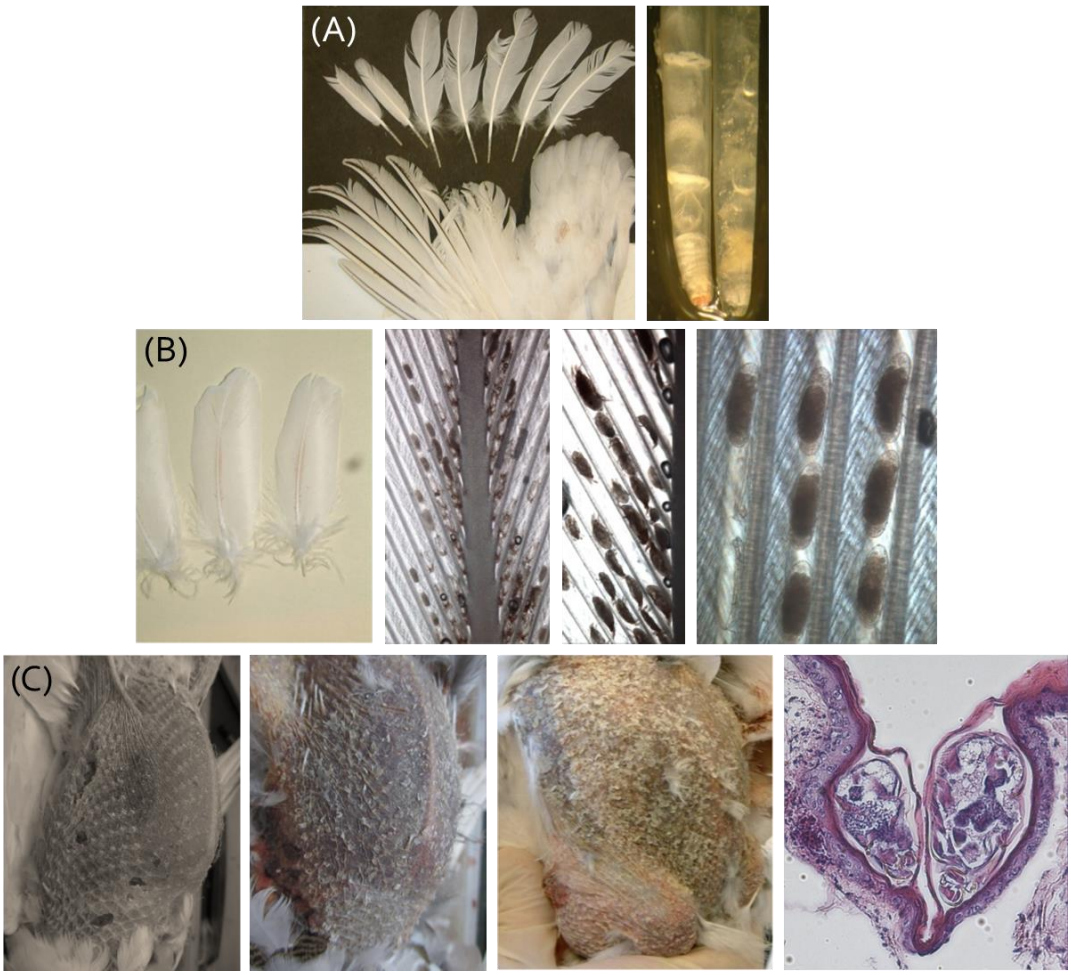


Figure 4.2 *Ectoparasitic habitat of Icelandic rock ptarmigan. (A) Habitat of the quill mite* Mironovia lagopus*. Picture on the right: Left quill uninfested, right quill infested. (B) Habitat of the feather mite* Tetraolichus lagopi *found close to the feather shaft between the barbs. (C) Habitat of the skin mite* Metamicrolichus islandicus*: no infestation, early infestation, heavy infestation with prominent crust on the skin; transverse section through two mites underneath the keratine of an infested bird. Pictures by Karl Skírnisson.*

Mironovia lagopus is a quill mite. It lives inside the feather calmus and pierces the quill wall with long needle-like chelicerae to feed on host tissue fluids on the other side. Infested birds scratch at the feathers in an attempt to relieve the irritation, and this can result in feather loss or secondary infection (Hoefer 1997, Walter & Proctor 2013).

Ornithomya chloropus is a hippoboscid fly that sucks blood from birds (Vastveit 2013) and is known to distribute mites and lice that attach themselves to their body from one bird host to another (phoresy) (Keirans et al. 1975, Harbison et al. 2009, da Cunha Amaral et al. 2013, Bartlow et al. 2016).

Figure 4.3 *Enlarged view of the hippoboscid fly* Ornithomya chloropus *found on Icelandic rock ptarmigan with some adult* Myialges borealis *females and their eggs attached to the abdomen. Picture by Karl Skírnisson.*

Mutual and commensal symbionts

In mutualist relationships individuals of two different species benefit from another. In commensal (meaning "eating at the same table") relationships one species benefits from another whereby the latter remains unaffected. With regard to feather mites, Blanco et al. (2001), Proctor (2003) and Galvan et al. (2012) suggest that in wild birds there is only slight correlative evidence for negative effects (except mange-causing skin mites). Instead, feather mites are commensals or mutualists – so called paraphages – feeding on uropygial oil secretions and removing excess body oils and potentially harmful fungi (Blanco et al. 2001, Galvan et al. 2012). On ptarmigan, the feather mites *Tetraolichus lagopi* and *Strelkoviacarus holoaspis* are believed to act as paraphages. All relationships between these mites and population parameters found on ptarmigan (survival, fecundity) are exclusively positive. In fact, the data support that these mites may be beneficial to ptarmigan.

5 Methods

5.1 Study Area

Iceland

Iceland is a northern European country and situated between the Greenland Sea and North Atlantic Ocean, southeast of Greenland, northwest of the United Kingdom, and at the northwestern most edge of Europe (63–67°N, 18–23°W). It covers an area of 103,000 km², extending c. 500 km east-west and 300 km north-south, and has 329,100 inhabitants from which more than 200,000 live in the capital region in the southwest (Statistics Iceland 2015). Iceland's terrain is mostly flat, interspersed with mountain peaks or ice fields. Large parts of its coast are deeply indented by bays and fjords and glaciers cover about 14 % of the land surface. Elevations range from sea level to 2,110 m above sea level (asl), the highest peak is Hvannadalshnúkur found on Vatnajökull glacier. The climate is cool maritime and milder than its location just south of the Arctic Circle would imply (Einarsson 1984, Icelandic Meteorological Office 2008). This is because the south and west are moderated by a branch of the Gulf Stream that reaches all the way to southeast Iceland (Icelandic Meteorological Office 2008). The north and east are influenced by a branch of the cold East Greenland Current (Icelandic Meteorological Office 2008). Summers are moist and cool and winters mild and windy.

Study Area

The study area is in northeast Iceland centred on Lake Mývatn (65°37' N, 17°00' W; Figure 5.1). The general topography is flat with rolling hills rising from the coast to 400–500 m asl at the southern border, 70 km inland. This relief is broken by isolated mountains, the highest being Bláfjall, 1222 m asl. Two major glacial rivers border the study area, Skjálfandafljót in the west and Jökulsá á Fjöllum in the east. Heath vegetation characterizes the xeric uplands. Important heath plants include dwarf shrubs such as *Betula nana* and *Salix phylicifolia*, and many species belonging to the heather family (Ericaceae) including *Empetrum nigrum* and *Vaccinium uliginosum*. Also important are various species of grasses (Poaceae), sedges (*Carex*), mosses, and lichens. In summer the ptarmigan is common on heath and grassland habitats. Winter habitats include alpine areas, rough lava fields, and *Betula pubescens* shrubs. Ptarmigan for this parasite study were obtained from the entire study area, but ptarmigan numbers from spring counts were obtained from six counting plots located within the study area (Figure 5.1, Table 5.1; Nielsen et al. 2004).

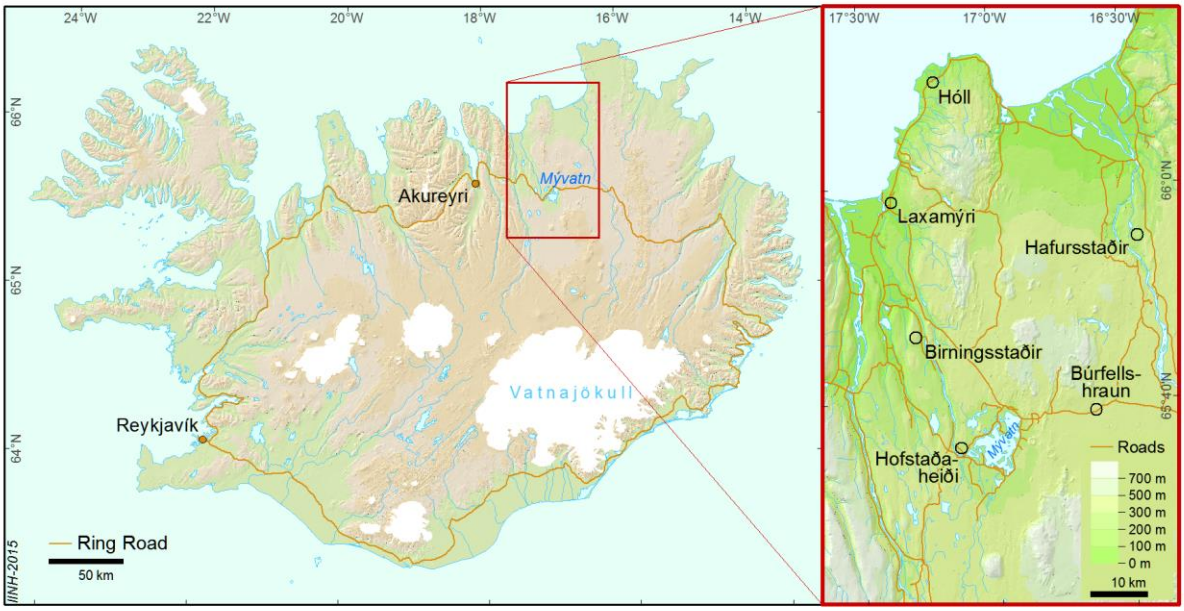


Figure 5.1 *Map of Iceland and the study area of rock ptarmigan in the northeast (red frame). The study area indicates both survey plots of ptarmigan spring counts (circles) and general ptarmigan collection site. Maps by Anette T. Meier at Icelandic Institute of Natural History.*

Table 5.1 *Plots where rock ptarmigan were censused in spring in northeast Iceland.*

Plot	Size	Altitude (asl)	Habitat
Birningsstaðir	3.9×1.5 km 5.7 km^2	140–400 m	Pasture consisting of tussocky heath moors and brushwood, bare mountain peaks, slopes with marshes, grassy meadows, vegetated lava edges, and old hayfields. Moor birch *Betula pubescens* grows north of the farm.
Búrfellshraun	3.8×1.1 km 2.5 km^2	360–400 m	Pasture consisting of tussocky moors of brushwood except lava edges. Common are dwarf birch *Betula nana*, tea-leaved willow *Salix phylicifolia*, and juniper *Juniperus communis*.
Hafursstaðir	4.1×2.4 km 8.0 km^2	220–320 m	Pasture consisting of tussocky moors of brushwood, marshes, grassland, and old hayfields.
Hofstaðaheiði	2.9×2.4 km 4.5 km^2	160–340 m	Area consists of grassland and tussocky moors of brushwood. Common are dwarf birch *Betula nana* and tea-leaved willow *Salix phylicifolia.*
Hóll	3.1×0.9 km 2.4 km^2	90–140 m	Pasture consisting of wet marshes and dry heath moors.
Laxamýri	3.2×1.5 km 3.7 km^2	60–160 m	Pasture consisting of tussocky heath moors of crowberry *Empetrum nigrum*, heather *Calluna vulgaris*, dwarf birch *Betula nana*, and bog blueberry *Vaccinium uliginosum.*

5.2 Parasite collection and quantification

5.2.1 Ptarmigan for parasite analyses

Each year in the 1st week of October, 2006–2012, 100 ptarmigan were collected (shot) in moorlands, lava fields, and alpine areas east, west, and north around Lake Mývatn. The 1st week of October was chosen to: (a) reduce potential seasonal variation in parasite measures and size of anatomical and physiological features of ptarmigan (Atkinson et al. 2008, Bicudo et al. 2010, Þórarinsdóttir et al. 2010) and (b) sample the ptarmigan population at the start of winter as winter survival defines population change (Gardarsson 1988, Magnússon et al. 2004). Ptarmigan are free-flying wild birds and hunters could not select individuals at random. Birds were collected by conventional walk-up hunting where they were shot sitting or flying when encountered. The hunters tagged each bird immediately after collection, wrapped it in absorbent paper to avoid cross-contamination, and placed it in a paper bag. Each bag was sealed by interfolding and stapling. Birds were cooled to 4°C until dissection within 3 days of collection.

Ptarmigan for this study were collected outside the hunting season by a license issued by the Icelandic Institute of Natural History under law 64/1994, chapter 4, article 7 (http://www.althingi.is/lagas/140a/1994064.html). To do all the sampling and analyses required for the study at large it was necessary to sacrifice birds. But it should be noted that the ptarmigan is common in Iceland and a popular game bird and since 1995 between 40 and 160 thousand birds have been shot every year (http://www.ust.is).

The annual sampling goal of 100 birds, 40 adults and 60 juveniles, was achieved in most years for juveniles, but not for adults (Table 5.2). All adults caught each year were analyzed, but juveniles were shot in excess and individuals selected at random while keeping the sex ratio equal.

Ptarmigans were measured and dissected at the Mývatn Research Station (http://www.ramy.is) laboratory by Ólafur K. Nielsen and Karl Skírnisson.

5.2.2 Parasite collection

Parasites for this study were collected by hunters in the field (only hippoboscids) and in the laboratory at the Mývatn Research Station, and quantified in the laboratories of the Institute for Experimental Pathology, University of Iceland (Institute for Experimental Pathology, Keldur) or the Icelandic Institute of Natural History.

Table 5.2 *Ptarmigan sample size used for analyses in this study. Ptarmigan collected in northeast Iceland, early October 2006−2012.*

Year	Adults		Both	Juveniles		Both	Total
	Females	Males		Females	Males		
2006	13	18	31	30	30	60	91
2007	5	15	20	30	30	60	80
2008	13	12	25	28	29	57	82
2009	7	12	19	29	30	59	78
2010	13	27	40	30	30	60	100
2011	16	25	41	30	30	60	101
2012	9	31	40	30	30	60	100
Total	76	140	216	207	209	416	632

Ectoparasite collection

Hippoboscid flies found by the hunter were collected and fixed in 70 % ethanol. In the laboratory, the carcass was taken out of its wrapping and inspected for hippoboscids. To collect lice, fleas, and astigmatan mites, the plumage of the whole bird was vacuum-cleaned with a hand-held vacuum cleaner (Princess, Turbo tiger, Type 2755). The vacuum cleaner was modified for this purpose. The nozzle (4×1.5 cm) was connected to an external collection chamber fitted with a circular sack-like filter (92 cm², diameter of pores 2–30 µm). Each bird was vacuumed systematically for approximately two minutes. The filter was placed in a plastic bag and stored at -20°C until later processing.

Endoparasite collection

The lower gastrointestinal tract was removed and separated into two parts: (a) small intestines including duodenum, jejunum, ileum, as well as rectum and cloaca; and (b) ceca. Each part was placed in a ziplock plastic bag and kept frozen until later processing.
From the rectum, a sample of 1–2 g of fecal material was weighed (with 0.1 g accuracy) and mixed with the twofold volume (1 g diluted with 2 ml) of 3% (w/v) aqueous potassiumdichromate ($K_2Cr_2O_7$) solution in a 20-ml plastic vial. The solution prevented the development of bacteria and fungi. For the sporulation purposes of eimerids the mixture was kept at room temperature for two weeks but after that refrigerated at 3°C. If the rectum was empty, feces were taken from the posterior part of the small intestines.

5.2.3 Parasite quantification

Ectoparasite quantification

The contents of the filters from the vacuum cleaning were examined to obtain counts of lice, fleas, and mites. For this, the contents of the filter from the vacuum cleaner, i.e. feathers, dust and skin particles, and parasites, were transferred to a 400-ml glass jar. The filter was brushed under a gentle stream of water on to a glass Petri dish (diameter 100

mm, depth 10 mm). This mixture was added to the jar, and more water added until the jar contained approximately 100 ml. Seven drops of the surfactant TritonH X-100 were added to the jar to reduce adhesive forces and to promote particle settling. The jar was fitted with a lid and shaken vigorously by hand. Feathers were removed one by one from the mixture and discarded after being flushed with water over the jar. After gently stirring to remove air bubbles and particles from the surface, the sample in the jar was allowed to settle for several hours, preferrably overnight in a cooler by 4°C. Lice and mites were collected from the surface and sediments under a stereoscope at 10–35 magnification, embedded in Hoyer's medium on a microscope slide (Anderson 1954) for later identification and counting purposes.

To quantify the abundance of the prostigmatan quill mite, a scoring system was used. Quills of seven feathers, the upper-wing primary coverts 4 and 5 and secondary flight feathers 3–7 (numbered distal to proximal) were examined. Each feather was scored according to 0 = no mites, 1 ≤ 10 mites present, and 2 > 10 mites present. The scores were summed to derive a value for each individual.

The hippoboscid fly *Ornithomya chloropus* was identified based on Theodor & Oldroyd (1964), the mallophagan lice *Goniodes lagopi* and *Lagopoecus affinis* based on Timmermann (1950), and *Amyrsidea lagopi* based on Scharf & Price (1983), the astigmatan mites *Tetraolichus lagopi*, *Strelkoviacarus holoaspis*, *Metamicrolichus islandicus* and *Myialges borealis* based on Mironov et al. (2010), and the prostigmatan mite *Mironovia lagopus* based on Bochkov & Skirnisson (2011).

Endoparasite quantification

The small intestines and one of the ceca were examined to obtain counts of helminth parasites. For this, the gastrointestinal tract was thawed, opened with a longitudinal incision with a scissors, and the content was washed in a 250-µm mesh in a sink under a gentle stream of water from the tap. The leftover contents of the mesh were transfered into a beaker glass and examined under a microscope by pouring the content bit by bit into a Petri dish. Helminths worms were counted and identified to species level. The worms of each sample were preserved in a small tagged plastic vial containing 70% ethanol. The worm number of the cecum – because only one of the two ceca was assessed – was multiplied by two to estimate the total number of helminths. It was shown that the number of helminths in each cecum does not differ significantly (Wilson 1979, unpublished thesis, University of Aberdeen, Scotland; Wilson 1983), and so examining only one cecum was more time efficient.

A modified McMaster method was used to obtain estimates of coccidian oocycsts per gram feces (opg). For this, 1.5 g sample (0.5 g feces in 1 ml $K_2Cr_2O_7$ solution) was weighed into a vial on a laboratory scale and filled up with water to 15 ml. The mixture was shaken well

and rotated for 3–5 min in a Labofuge at 2200 rounds per minute (rpm). After the rotation, solid substances (including parasite eggs and oocysts) had settled on the bottom of the vial. The leftover liquid was decanted. The solid substance was filled up with Fasol® to 14.5 ml and the mixture carefully shaken by moving the vial up and down avoiding air bubbles to develop. Immediately after this, a sample from the middle of the solution was taken with a pipette and captured into the two counting chambers of a McMaster glass. Parasite oocysts were given time (c. 2 min) to float to the top, then the sample was ready to be inspected under the microscope. Each counting chamber was divided into 10 lanes. Opg values were estimated by counting oocysts in two McMaster counting chambers at 10×12.5 magnification. The average count was multiplied by a constant (50) to obtain the estimate of opg. If no oocysts were found within the 10 lanes, the surrounding area was scanned. If oocysts were found in the surrounding area, the average count was multiplied by another constant (25) to obtain the estimate of opg.

The nematodes *Capillaria caudinflata* and *Trichostrongylus tenuis* were identified based on Madsen (1945), Wehr (1971), and McDonald (1974), the cestode *Passerilepis serpentulus* based on Alexander Galkin at the Russian Academy of Sciences, St. Petersburg, and the coccidians *Eimeria muta* and *E. rjupa* based on Skirnisson & Thorarinsdottir (2007).

5.2.4 Parasite measures

Parasite richness, prevalence, aggregation, mean intensity, and mean abundance are the parasite measures that were utilized. Parasite (species) richness was defined as the total number of parasite species living in or on the host (Margolis et al. 1982, Bush et al. 1997, Schulte-Hostedde & Elsasser 2011). Parasite prevalence was defined as the proportion of birds infected by a particular parasite species (Bush et al. 1997). Mean parasite intensity was defined as the average number of a particular parasite species for infected birds (Bush et al. 1997). Mean parasite abundance was defined as the average number of a particular parasite species for all (infected and noninfected) birds examined (Bush et al. 1997). Parasite aggregation is a measure of parasite distribution within the host population and can be random, clumped (aggregated), or uniform (regular) (Bush et al. 2001).

Both the combined parasite community and individual parasite species were examined. To obtain values describing the combined parasite community of each bird, parasites were ranked (Holmstad et al. 2005a). The parasite data for each species was ranked in ascending order (1 was allotted to the lowest positive finding) and midranks were used for ties. The ranked values of each parasite species were then summed to endoparasites, ectoparasites, and all parasites for each bird. Data for individual parasites were not used for analyses if sample size was too small.

5.3 Body measures

5.3.1 Age and sex determination

Ptarmigan for this parasite study collected in early October were aged based on size or pigmentation of the primaries (Figure 5.2; Weeden & Watson 1967) and sexed using both the loral stripe and the size and colour of the combs (Montgomerie & Holder 2008). During necropsy, age and sex were confirmed by inspecting the gonads and presence or absence of the bursa of Fabricius. Two age classes were recognized: juveniles (about 3 months old) and adults (about 15 months or older). Ptarmigan become mature as 1 year old (Holder & Montgomerie 1993).

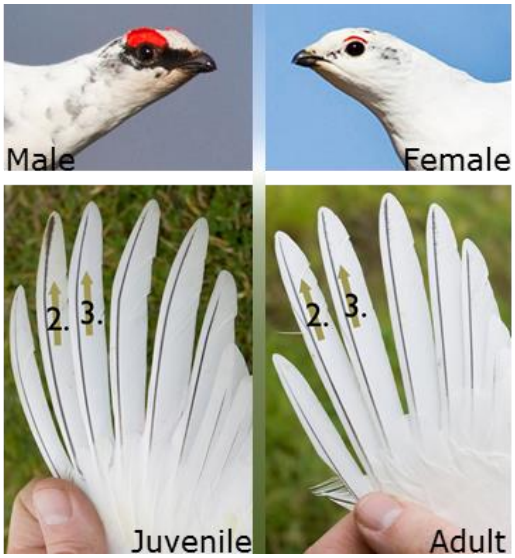


Figure 5.2 *Age determination of rock ptarmigan. From left to right: Pigmentation of primary wing feathers. Juvenile: stronger pigmentation on second primary. Adult: similar or no pigmentation on second and third primary or stronger pigmentation on third primary. Male: bright red combs and black loral stripe. Female: no loral stripe or broken stripe. Picture copies from http://utgafa.ni.is/vefur/rjupan/index.html.*

5.3.2 Body condition

To obtain an index of body condition, body mass was regressed on body size and the residuals used as the index. For body size, six external and internal morphometric measurements for each bird were taken: (a) wing length, measured with a ruler from the carpal joint to the tip of the flattened and straightened wing to the nearest mm; (b) head + bill length, measured with calipers from the hindmost point of the head to the tip of the bill to the nearest 0.1 mm; (c) tarsus length, measured with calipers from the joint between tarsus and toes to the intertarsal joint to the nearest 0.1 mm; (d) tarsus and mid-toe length, measured with a ruler from the joint to the base of the central claw to the nearest mm; (e) sternum length, measured with calipers from the tip of the *Spina externa* along the center

line to the *Margo caudalis* to the nearest mm; and (f) sternum-coracoid length, measured with calipers from the center line of the *Margo caudalis* to the cranial end of the *Coracoideum* to the nearest 0.1 mm (anatomical terms follow Baumel 1979). These six body measures (a–f) were highly correlated with each other. Factor 1 from a principle component analysis (PCA) was used as an index of body size. This Factor explained 61.4% of the variance in the original variables and was highly related to them (loadings: wing = 0.831, head + bill = 0.833, tarsus = 0.528, tarsus + mid-toe = 0.647, sternum = 0.891, sternum-coracoid = 0.899).

5.3.3 Organs of immune function

The immune organs spleen and bursa of Fabricius were used to assess their role in combating parasites. There is a variety of organs of immune function in the avian immune system (Figure 5.3). The spleen and the bursa of Fabricius are two that play an important role in disease resistance (Glick 1956, Cooper et al. 1966, John 1994, Whittow 1999). The bursa is a primary lymphoid organ in which B lymphocytes are produced and mature (Whittow 1999, Boehm et al. 2012). It is a pink pouch connected dorsally to the cloaca and opening into it (Whittow 1999; Figure 5.3). The spleen is a secondary lymphoid organ in which lymphocytes are stored and where they interact with each other and with antigens (John 1994, Whittow 1999, Powers 2000). It looks triangular and pink to red-brown in ptarmigan and is located in the abdomen, situated dorsally between the proventriculus, gizzard, and liver (Powers 2000; Figure 5.3).

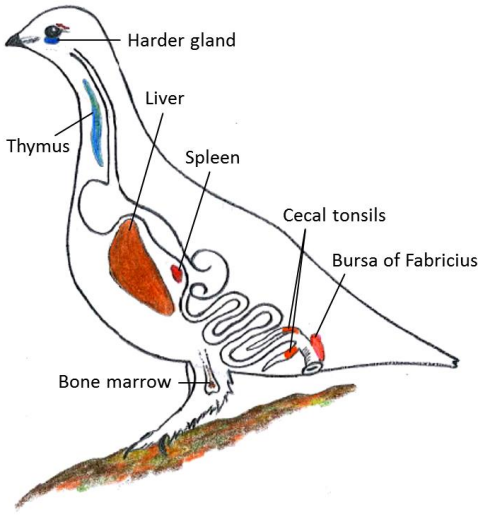


Figure 5.3 *Simplified graphical illustration of organs of the avian immune system.*

Ecologists use spleen size as a measure of the degree of investment in immune defense because its involvement in fighting systemic disease has frequently been observed (Powers 2000). Enlarged spleen size is called splenomegaly and reduced spleen size splenic hypoplasia or atrophy. The bursa is less commonly used as measure of immune defense. It starts to shrink before sexual maturity due to the effects of adrenal and sex hormones and occurs virtually only in juvenile birds (Glick et al. 1956, Whittow 1999, Blanco et al. 2001, Watson & Moss 2008). In most cases, increasing immune function is associated with an increased size of these immune organs, but the opposite has also been shown. Spleen and bursa were removed during ptarmigan necropsy and weighed on a digital scale (accuracy 0.0001 g).

5.4 Demographic parameters

For this study, three sets of population data were used: (1) spring densities of territorial males (Figure 5.4), (2) age ratios in spring, and (3) age ratios in late summer. From those, measures of fecundity and mortality were derived (Figure 5.5).

5.4.1 Age ratios (Fecundity)

Age ratios in spring

Spring (May) samples for aging were birds found dead (main cause of death gyrfalcon predation, but also raven *Corvus corax*, Arctic fox *Vulpes lagopus*, and kills in accidents), birds trapped for banding, or birds photographed while flying using high speed cameras (Nielsen 1999b, Nielsen et al. 2004, Icelandic Institute of Natural History unpublished data). Fully grown ptarmigan were aged based on pigmentation of the primaries (Weeden & Watson 1967). Two age classes were recognized, first year birds (juveniles = juv) and older birds (adults = ad).

Age ratios in late summer (Fecundity)

Late summer (last week of July and first week of August) samples for aging were birds actively searched for on foot. Distinguished was between adults (males and females) and chicks according to size, color, and sound (Nielsen 1999b, Nielsen et al. 2004). The age ratio was calculated using total number of females observed and assuming that half of the chicks were females; sex ratio of chicks in late summer was assumed to be even (Gardarsson 1988, Magnússon et al. 2004). This ratio corresponds to ptarmigan brood size and was used as a measure of fecundity.

5.4.2 Mortality rates

Mortality rates were calculated based on Magnússon et al. (2004). For these calculations, a year is defined starting on 1st May and ending 30th April. Two mortality rates were recognized: (1) Z_2 or apparent adult mortality rate. (2) $Z_{X,W}$ or juvenile excess mortality (mortality that juveniles suffer in excess to adults or (1)).

Adult mortality rate (Z_2)

The population abundance index and spring age ratios were used to estimate the Z_2 mortality rate, assuming that spring abundance was proportional to the total number of birds in the study area. It was assumed that any bird alive at the end of winter was either in its second-year or older at the end of the following winter, provided it survived. So, adult mortality from spring to spring was calculated as:

$$\hat{Z}_2^t = \ln(Y^{t-1}) - \ln(Y^t) - \ln(\hat{p}_2^t)$$

where

Y^t = spring abundance index year t

Y^{t-1} = spring abundance index year $t-1$

$\hat{p}_2^t$ = fraction of adult birds in spring year t

Juvenile excess mortality rate ($Z_{X,W}$)

The $Z_{X,W}$ mortality rate describes mortality that first year birds suffer from 1 August to 30 April in excess to adult mortality. The age ratios in late summer and at the end of the following winter were used to estimate excess juvenile mortality as:

$$\hat{Z}_{X,W}^t = ln\left(\frac{\hat{p}_1^{t,s}}{\hat{p}_2^{t,s}}\right) - ln\left(\frac{\hat{p}_1^t}{\hat{p}_2^t}\right)$$

where

$\hat{p}_1^{t,s}$ = fraction of juvenile birds late summer

$\hat{p}_1^t$ = fraction of juvenile birds at end of winter

$\hat{p}_2^{t,s}$ = fraction of adult birds late summer

$\hat{p}_2^t$ = fraction of adult birds at end of winter

Juveniles share Z_2 with the adults or at least a rate that shows the same trend. Accordingly, the total mortality rate of juveniles was taken as the sum of Z_2 and $Z_{X,W}$ rates.

5.5 Ptarmigan spring densities

To derive an annual index of ptarmigan abundance, territorial male ptarmigan were counted on six plots in the study area between 10 and 24 May (Figure 5.1, 5.4, 5.5, Table 5.1). The total size of the plots was 26.8 km^2 (range 2.4–8.0 km^2). Each plot was surveyed on foot by at least two observers once in the early morning (05:00–10:00) or late afternoon (17:00–24:00). The locations of territorial males as well as ptarmigan kills were plotted on a map. A "kill" is the remains of a ptarmigan killed and eaten after arrival on the census plot in spring. The main cause of death was predation by gyrfalcon (84 %), but also raven or fox, or death through accident (Nielsen 1986). The "freshness" of the kill was based on the state of the feathers. The total number of males in spring is composed of the sum of the number of territorial males censused and recently killed. Not all kills could be sexed, so to estimate the proportion of males, the sex ratio of ptarmigan killed by gyrfalcons in spring on the study area was used (73 % males; Nielsen et al. 2004). The ptarmigan population abundance index used for this study was the annual mean density of males on these six plots and covers the years 2004–2013. Nielsen (1996) provides a detailed description of the census plots (Table 5.1) and methods.

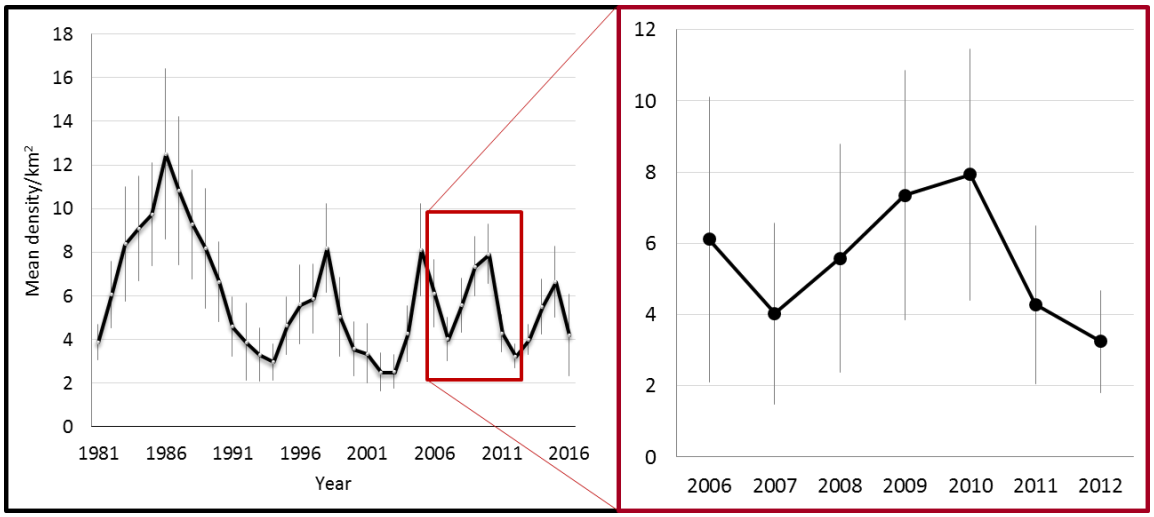


Figure 5.4 *Spring densities (±SE) of rock ptarmigan cocks in northeast Iceland (1981–2015) and closeup of the density data used for the present study (red frame). The data depicts decrease phase, low, increase phase, and peak of one ptarmigan population cycle. Data provided by the Icelandic Icelandic Institute of Natural History.*

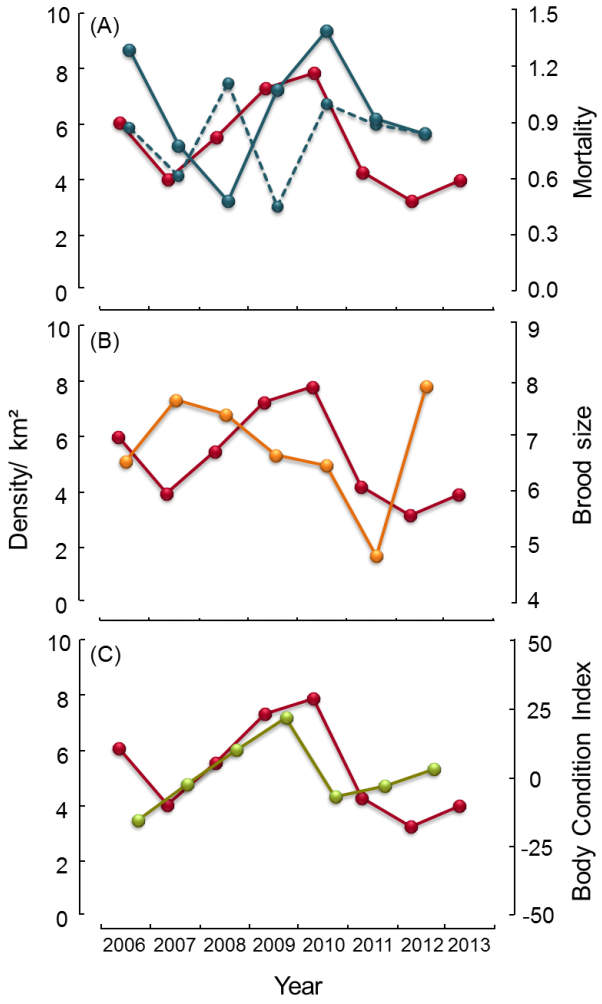


Figure 5.5 *Trajectories of population densities (red continuous line; 2006−2013) and (A) adult mortality Z_2 (blue continuous line), juvenile excess mortality $Z_{X,W}$ (blue dashed line), (B) fecundity (orange continuous line), and (C) body condition index (green continuous line) of rock ptarmigan in northeast Iceland, 2006−2012.*

6 Host-parasite interactions and population change of ptarmigan

The smallest with the strongest connection: *Eimeria muta*

The most significant finding with respect to this study is about one parasite, almost the smallest species found in ptarmigan called *Eimeria muta*, an endoparasite living in the gastrointestinal tract of ptarmigan, that showed a strong positive relationship with population size between 2006 and 2012 (Paper III; Figure 6.1). This relationship included a time delay of 1.5 years where the eimerid lagged behind ptarmigan densities (Figure 6.1). At the same time aggregation levels of this eimerid fluctuated inversely with its prevalence (Figure III.1). That is, this parasite was least aggregated in the ptarmigan population at peak prevalence and vice versa. On top of this, *E. muta* was associated with poorer body condition, increased spleen mass (indicating increased immune function; Paper I), increased mortality, and reduced fecundity of ptarmigan (Figure 6.1). Spleen mass also related positively with ptarmigan density and body condition (Paper I). According to the Anderson & May model (Anderson & May 1979, May & Anderson 1979), these are the exact requirements for a parasite to be of regulating or destabilizing quality to a host population. This gives strong evidence – despite the correlational character of this study – that this parasite is not only very closely connected with ptarmigan, its life cycle and population, but very likely influences its population dynamics as well, may it be direct or indirect.

Ptarmigan may be in poor condition for other reasons than parasites, and this weak condition in turn may make them more susceptible to parasitism. *E. muta* has only relatively recently been detected (Skirnisson & Thorarinsdottir 2007) and it is most probably host-specific to the rock ptarmigan as eimerids are usually to their hosts (Pellérdy 1974). It is not yet known if *E. muta* is sufficiently virulent in itself or if it becomes virulent only or increasingly when the host system is already weakened due to other factors, or possibly due to the combined parasite community. Parasite richness, the overall parasite community, and majority of pathogenic parasites were all directly correlated with body condition of ptarmigan. Whatever the initial trigger may be, data of this study implies that *there is* a strong correlation between ptarmigan condition, population density, and particularly this one eimerid.

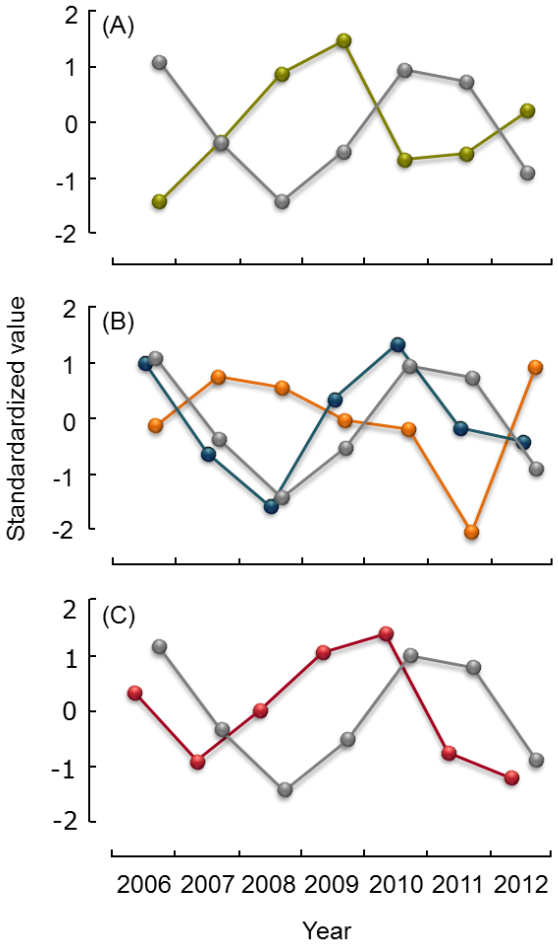


Figure 6.1 *Trajectories of* Eimeria muta *prevalence (grey line) and (A) body condition (green line) of adult rock ptarmigan, (B) adult mortality rate Z_2 (blue line) and fecundity (orange line), and (C) ptarmigan population density (red line) in northeast Iceland, 2006−2012. Values are standardized to (X-μ)/σ.*

How *E. muta* is transmitted from host to the next is thought as follows: Ptarmigan eimerids have a direct life cycle. Oocysts are shed in feces, sporulate in the environment, and hosts become infected through ingestion of the oocycsts. The oocysts are present in the feces year round, but prevalence of *E. muta* peak between October and January (Thórarinsdóttir et al. 2010). Because eimerids are generally host specific (Pellérdy 1974), it is believed that *E. muta* (and also *E. rjupa*) will not persist in species other than rock ptarmigan. What *is* known, is that the prepatent period of similar-sized *Eimeria* species varies between 4 and 6 days with a peak in oocyst shedding within approximately 10 days (Herrick & Ott 1936, Rommel et al. 2000). Thus, oocysts shed by ptarmigan in the first week of October are caused by infections occurring by mid September when ptarmigan are moving to their autumn habitats in alpine areas. At high ptarmigan densities, more oocycsts are released into the environment. Such host density-dependent shedding of oocysts and their subsequent persistence in the environment from one year to the next could be the reason for the observed time-lag between ptarmigan numbers and *E. muta* prevalence. Ptarmigan

hatched in the two years succeeding the peak in their numbers should be exposed to the maximum number of infective oocysts in the environment. Environmental persistence is well known for *Eimeria*: infective oocysts of some species can survive up to 602 days in soil (Farr & Wehr 1949) and stand repeated freeze and thaw cycles (Landers 1953). These life history characteristics are sufficient to maintain eimerid populations (Fuller et al. 2012). Life history characteristics of parasites including the time needed for helminth larval stages to grow to maturity after infection and arrested development of the helminth larvae have been given as explanations for time lags between host and parasite populations in similar systems (see Chapter 3.1; e.g., Dobson & Hudson 1992, Newey et al. 2005). For instance, for red grouse in UK, coupled parasite-host cycles have been described and tested experimentally (Dobson & Hudson 1992, Martínez-Padilla et al. 2014). In this grouse population exhibiting 4–8 year cycles, *Trichostrongylus tenuis* reduced fecundity and survival and there was a density dependent relationship between grouse numbers in one year and worm burdens in the subsequent year (Dobson & Hudson 1992). The fairly low levels of parasite aggregation observed in this system increased the tendency of the system to oscillate (Dobson & Hudson 1992).

Killer worms? *Capillaria* and *Trichostrongylus*

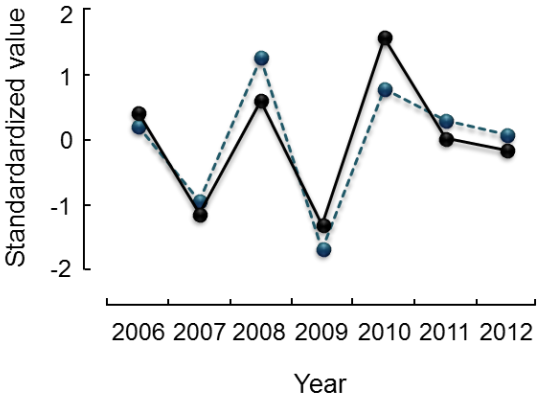


Figure 6.2 *Trajectories of excess winter mortality $Z_{X,W}$ (blue dashed line) and* Capillaria caudinflata *prevalence (black continuous line) of juvenile rock ptarmigan in northeast Iceland, 2006–2012. Values are standardized to (X-μ)/σ.*

In addition to the *Eimeria* relations, I further found close relationships between mortalities of juvenile birds and prevalence of the endoparasitic nematode *Capillaria caudinflata* (Paper III; Figure 6.2). *Capillaria* are known to cause severe symptoms such as diarrhoea, weakness, weight loss, and a drop in egg production (capillariasis; Atkinson et al. 2008). *C. caudinflata* has an indirect life-cycle with earthworms as intermediate hosts (Morehouse 1942). Ptarmigan chicks have a mixed diet of plants and invertebrates such as earthworms, but adult birds eat mainly plants (Garðarsson 1971). Excitingly, adult birds in this study also show *C. caudinflata* infections. One reason for this could be that some of the adults carry infections acquired as juveniles; the life span of *C. caudinflata* is c. 10 months (Olsen 1974). High prevalence among adults however suggest that birds beyond these 10 months get also infected frequently. This suggests that adult must occasionally be ingesting earthworms. Nevertheless, more juveniles suffer from *C. caudinflata* infections than adults, and so these seem to be one of the drivers of the mortality that juveniles suffer in excess of adults in

autumn and winter. That juveniles suffer more from *C. caudinflata* infections than adults may have to do with varying levels of immune function to resist or treat infections (Paper I).

Trichostrongylus tenuis plays a strong role in red grouse because it determines their population cycles (Hudson et al. 1998) and is associated with reduced body condition in willow ptarmigan in Norway (Holmstad et al. 2005a). In this study however, this helminth nematode occurred in numbers such low (≤ 28 worms) that it seems unlikely that it could have evoked any serious harm (Hudson 1986). Yet, this parasite did show an inverse relationship with body condition in adult birds and the 1.5 year time lag was near significant for both age groups (Paper III).

… and the internal parasites altogether?

The combined parasite community correlated with ptarmigan condition, but only endoparasites were also positively correlated with annual mortality in juveniles, probably mostly attributable to *E. muta* (Paper III). Comparatively, though none of the parasites in Norwegian willow ptarmigan had a significant impact on their own, the parasite community was negatively related with host fitness, and this in turn was suggested to promote effects on host body mass and chick mortality (Holmstad et al. 2005a).

Chewing lice & feather holes: the primesuspect *Amyrsidea*

I found a reverse relationship between prevalence of the amblyceran chewing louse *Amyrsidea lagopi* and fecundity (Paper III; Figure 6.3). This is interesting because the data also implied that *A. lagopi* is very likely associated with the creation of feather holes (Paper II). It is well known that feather lice can be severely damaging to their host (summaries of various studies in Clayton et al. 2015), including by reducing fecundity (DeVaney 1976, Clayton 1990, Moreno-Rueda & Hoi 2012). The amblyceran mallophagan *Menacanthus stramineus* in high intensity, for instance, was related with reduced egg production (Watson 1965). Or, feather wear of parent collared flycatchers *Ficedula albicollis* were traded-off by parental activity, and the degree of feather wear was associated with survival of the flycatchers (Merilä & Hemborg 2000). This is however no rule of thumb, and there are other studies where

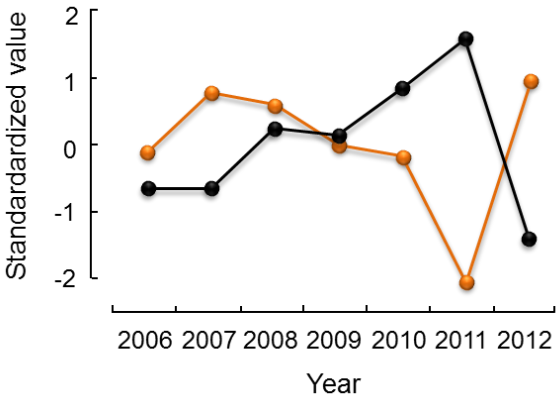


Figure 6.3 *Trajectories of fecundity (orange line) and* Amyrsidea lagopi *prevalence (black line) of juvenile rock ptarmigan in northeast Iceland, 2006–2012. Values are standardized to (X-μ)/σ.*

controlled experiments did not show any effects of lice on reproductive success of common swifts *Apus apus* and rock doves *Columba livia* (Clayton & Tompkins 1995, Tompkins et al. 1996). If the association between *A. lagopi* and feather holes in this study happens through trade-offs between host reproduction and self-maintenance or for other reasons is yet another mystery to be solved and deserves to be tested experimentally.

With respect to the two other ischnoceran chewing lice of ptarmigan, *Goniodes lagopi* and *Lagopoecus affinis*, bursae – an immune organ in juvenile birds – were lighter when both these lice were present and *G. lagopi* occurred in greater intensity (Paper Ⅰ). Both these lice feed primarily on feathers and dead skin whereas the more mobile amblyceran *A. lagopi* feeds on living tissue, such as skin and blood (Price et al. 2003, Clayton et al. 2008). It is peculiar that there is a relationship between the two ischnoceran chewing lice that feed on dead host tissue and immune function, but not with *A. lagopi*, the actually damaging chewing louse (Paper Ⅰ). Møller & Rózsa (2005) in comparison found no relationship between host immune response and ischnoceran chewing lice, contrary to that found for amblycerans. There should be more effective defences than internal immune function against lice such as preening behavior and/ or the use of preen oil from the preen gland (Moyer et al. 2003, Clayton et al. 2010).

'Mutual Core': the two skin mites *Metamicrolichus* and *Myialges*

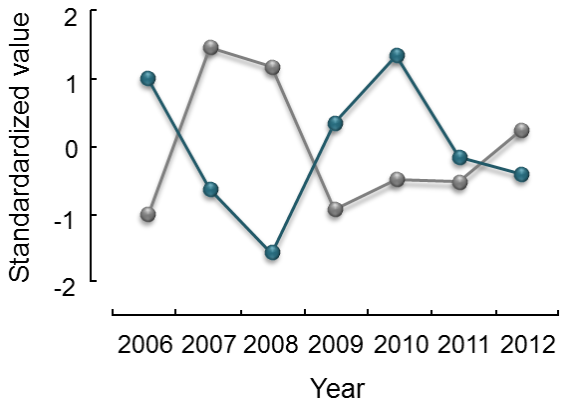


Figure 6.4 *Trajectories of mortality Z_2 (blue line) and* Metamicrolichus islandicus *prevalence (grey line) of adult rock ptarmigan in northeast Iceland, 2006–2012. Values are standardized to (X-μ)/σ.*

I found a reverse relationship between prevalence of *Metamicrolichus islandicus* and adult mortality, but interestingly when mortality was high, then fewer birds were actually infested with this mite (Paper Ⅲ; Figure 6.4). Also, heavier infestations came along with larger spleens, a sign for this mite provoking immune function (Paper Ⅰ). Possibly, energy for immune defense was fully available and this compensated for the effects of disease (mange). Otherwise, I have no explanation for such counter-intuitive pattern other than what Schulte-Hostedde & Elsasser (2011) in their study on male American mink *Neovison vison* suggested, that males with higher intensity of parasites are in better condition because parasites might be drawn to hosts in good condition due to an abundance of resources.

There is another mite, *Myialges borealis*. Less is known about this species than *M. islandicus*, but it is a skin mite although it usually occurs in very close connection with *M.*

islandicus (Paper IV, unpublished manuscript). These two mites nearly always co-occur on infected hosts. This suggests that (1) infestations, once acquired, persist, indicated by their occurence in juvenile *and* adult hosts and (2) that these two mites might be mutually dependent (one not be able to live without the other). The way for *M. borealis* to reach another host is on the hippoboscid fly *O. chloropus* that serves as final host (and ptarmigan as intermediate host) and on the abdomen of the fly is where its eggs are found.

While I could give account of many more findings, those above form the heart of this study. The highlights are more debaucherously depicted in the four Papers (three published, one manuscript) and found in the second part of this thesis. They carry the following titles:

I The relationship between parasites and spleen and bursa mass in rock ptarmigan

II Feather holes of rock ptarmigan are associated with amblyceran chewing lice

III Host-parasite interactions and population dynamics of rock ptarmigan

IV The parasite fauna of rock ptarmigan in Iceland:
Community structure and co-occurrence within the host population

7 Conclusions & Outlook

In this study, I focused on the relationship between parasites and their rock ptarmigan host, and the influence this system would exert on changes of population numbers of the ptarmigan. It is the first study – correlational in character – on host-parasite interactions of a cycling terrestrial resident Arctic bird species in Iceland.

The findings of this study should come as surprise, not only to our research team and the Icelandic scientific community, but to parasitologists and investigators in the field of wildlife population dynamics worldwide. *Eimeria muta*, an intestinal coccidian parasite, showed strong correlation with one full cycle of the ptarmigan population. This connection encompasses a 1–2 year time lag as well as significant relationships with multiple demographic parameters and body measures of ptarmigan; very strong evidence for some regulatory influence of this parasite species on its host population.

A strong relationship of this kind in Icelandic rock ptarmigan is known only between ptarmigan and gyrfalcon, its main specialist predator (Nielsen 1999a). Without questioning the primary influence that gyrfalcon has on its main prey, the new findings of my study put the specialized predator-prey relationship and its driving the ptarmigan population cycles into new perspective; for parasitism in the ptarmigan population may act directly and/or sublethal parasitism may act synergistically with predation by acting upon different population parameters (Morehouse 1942) or by making the ptarmigan more prone to gyrfalcon predation (Hughes et al. 2012, Keymer & Read 1991, Thomas et al. 2010).

The next step building upon my study could be served various ways: (A) to include findings of this study into the ptarmigan population model, (B) to investigate how ptarmigan-parasite and gyrfalcon-ptarmigan interactions relate to illuminate any cross-specific and interaction connections, (C) to explore how ptarmigan diet is related with parasite levels to illuminate any medicinal link, (D) to experimentally infect birds with *Eimeria* and with controls to study effects on condition.

Whole parasite communities of rock ptarmigan are rarely studied. So, it would be fascinating and exciting to me to investigate this further and keep on examining rock ptarmigan and their parasites from other areas within Iceland, but also from adjacent places such as Greenland, northern Europe including Svalbard, North America, the Russian Arctic. What differences are there between ptarmigan from high Arctic realms and those living further south yet higher up? Is there overlap with allied species like White-tailed ptarmigan or Willow ptarmigan? Unsolved mysteries.

With respect to ptarmigan population dynamics, I feel concern, the population cycle has changed both in amplitude and length over the past decades (Williams et al. 2004, Ims et al. 2008; Figure 7.1). Until 2003, the cycles occurred in c. 10–12 year intervals (Guðmundsson 1960, Nielsen & Pétursson 1995, Brynjarsdóttir et al. 2003). But since 2003, the cycle period has shortened to c. 5 years (Nielsen 2015; Paper III, Figure 7.1). The peak of amplitude in 1955 was 3-fold higher than the one in 1985, and 2-fold higher in 1985 than the one in 2015. Already Nielsen et al. in 2004 reported a significant negative trend in population size equaling 4% per annum or 33% over 10 years based on a model by Brynjarsdóttir et al. (2003). In fact, this continual downward trend of the population warranted the inclusion of ptarmigan on the Icelandic Red Data List in the "vulnerable" category already at a much earlier point (Nielsen 2006). Taking this together, then for rock ptarmigan in Iceland it seems cyclic dynamics are diminishing and population size leveling out at low numbers; prognoses predicted also by climate change theory (Walther et al. 2002, Ludwig et al. 2006, Post et al. 2009).

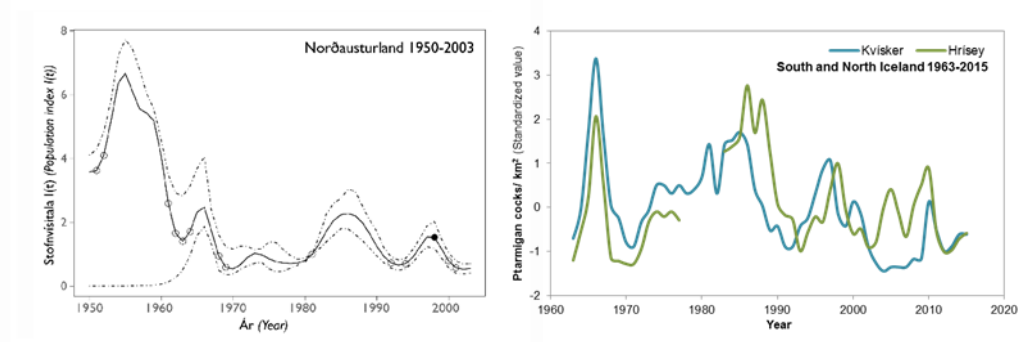


Figure 7.1 *Rock ptarmigan numbers in Iceland since 1950s (Nielsen et al. 2004, Icelandic Institute of Natural History 2016).*

This opens up a much broader picture which indicates that even if predator-prey or host-parasite interactions play key roles in ptarmigan population dynamics, then in the long run there is a force much stronger and subtle that influences the event "ptarmigan population cycle". So, having been able to study a population dynamic has got something sincerely gracious and precious to it. I hope, for changes seem to happen comparatively quickly now, there will be an Icelandic ptarmigan dynamic that can be sustained!

Publications

Paper I Stenkewitz U, Nielsen ÓK, Skírnisson K & Stefánsson G. 2015. **The relationship between parasites and spleen and bursa mass in Rock Ptarmigan *Lagopus muta***. Journal of Ornithology 156: 429–440.

Paper II Stenkewitz U, Nielsen ÓK, Skírnisson K & Stefánsson G. 2017. **Feather holes of rock ptarmigan are associated with amblyceran chewing lice.** Wildlife Biology: In Press.

Paper III Stenkewitz U, Nielsen ÓK, Skírnisson K & Stefánsson G. 2016. **Host-parasite interactions and population dynamics of rock ptarmigan.** PloS ONE 11(11): e0165293. doi:10.1371/journal.pone.0165293.

Paper IV Stenkewitz U.
The parasite fauna of rock ptarmigan *Lagopus muta* in Iceland: Community structure and co-occurrence within the host population. Unpublished Manuscript.

Clarification of contribution

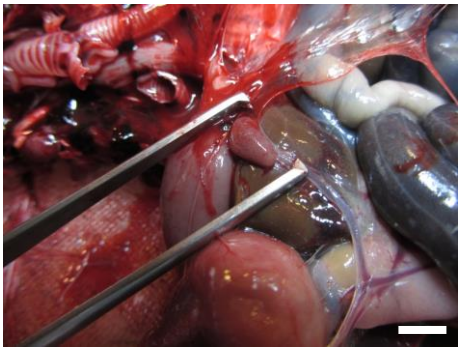
I, Ute Stenkewitz (US), declare that the following papers of this thesis are my work done under mentoring of Dr Ólafur K Nielsen (ÓKN), Prof Karl Skírnisson (KS), and Prof Gunnar Stefánsson (GS). The contributions of the authors to the papers consist of:

Conceptualization	US ÓKN KS
Correspondence (publication process)	US
Data curation	US
Formal analysis	US ÓKN GS KS
Funding acquisition	ÓKN US KS
Investigation	ÓKN KS US
Methodology	US ÓKN KS
Project administration	ÓKN KS US
Resources	ÓKN KS US
Supervision	ÓKN KS GS
Visualization	US
Writing ± original drafts	US
Writing ± review & editing	US ÓKN KS

Paper I

The relationship between parasites and spleen and bursa mass in Icelandic rock ptarmigan *Lagopus muta*

Ute Stenkewitz, Ólafur Karl Nielsen, Karl Skírnisson, Gunnar Stefánsson.
Journal of Ornithology 156: 429–440. 2015.



Spleen

Abstract

The spleen and bursa of Fabricius in birds are organs that play an important role in fighting parasite infections. The size of these organs can be used by ecologists as a measure of immune investment, with larger size implying greater investment. The bursa only occurs in juvenile birds during the development of the B cell repertoire, whereas the spleen, which is the main site of lymphocyte differentiation and proliferation, is present in both juveniles and adults. We investigated spleen and bursa mass in relation to parasite measures for 541 rock ptarmigan *Lagopus muta* collected in northeast Iceland during October from 2007 to 2012. Of these 541birds, 540 carried at least one parasite species. Juveniles had heavier spleens than adults, and adult females had heavier spleens than adult males, but there were no sex differences in juveniles. Spleen mass increased from 2007 to 2009, then decreased up to 2011, before slightly increasing again in 2012. Spleen and bursa mass in juveniles increased with improved body condition, but decreased in adults, and this effect differed significantly among years. Spleen mass in juveniles was positively associated with parasite species richness and abundance, in particular endoparasite abundance, with coccidian parasites being the main predictors. Bursa mass was negatively associated with elevated ectoparasite abundance, with two chewing lice being the main predictors. These two immune defense organs appeared to relate to different stimuli. Mean annual spleen mass of juveniles changed in synchrony with ptarmigan body condition and population density over the years of this study. The only parasite measure that showed any relation to density was coccidian prevalence in juvenile birds, with an approximately 2-year time-lag, suggesting that factors other than parasites are probably more important in triggering changes in spleen mass.

Introduction

The spleen and the bursa of Fabricius (hereafter referred to as „bursa“) in birds are immune defense organs that play a major role in disease resistance (Glick 1956, Cooper et al. 1966, John 1994, Sturkie and Whittow 1999). The bursa is a primary lymphoid organ in which B lymphocytes are produced and mature (Sturkie and Whittow 1999, Boehm et al. 2012), while the spleen is a secondary lymphoid organ in which lymphocytes are stored and where they interact with each other and with antigens (John 1994, Sturkie and Whittow 1999, Powers 2000a). The production and maintenance of immune organs is considered to be costly, and birds in good condition should be able to invest more of their resources in immune function than birds in poor condition (Sheldon and Verhulst 1996, Derting and Compton 2003, Schulte-Hostedde and Elsasser 2011). Infection caused by pathogens can weaken the body condition of the infected organism and also affect the size of the immune organs, leading to depletion (atrophy, hypoplasia, or involution) or enlargement of both the

spleen (splenomegaly) and the bursa (e.g., Glick 1994, John 1994, Møller et al. 1998a, Powers 2000b, Blanco et al. 2001). Ecologists have used spleen size as a measure of the degree of investment in immune defense because its involvement in fighting systemic disease has frequently been observed (Powers 2000a). In most studies, high parasite abundance in birds has been associated with splenomegaly rather than splenic hypoplasia or atrophy (e.g., Møller and Erritzøe 1996, Møller et al. 1998a, Powers 2000b, Blanco et al. 2001, Mougeot and Redpath 2004, Schulte-Hostedde and Elsasser 2011), and increased spleen size has been positively associated with body condition (Møller et al. 1998a).
The size of the bursa has been examined less often than that of the spleen, probably due to its regression prior to sexual maturity and the need to control statistically any observed age-related changes. The bursa starts to shrink before sexual maturity due to the effects of adrenal and sex hormones, and it is virtually absent in adult birds (Glick et al. 1956, Sturkie and Whittow 1999, Blanco et al. 2001, Watson and Moss 2008). Few studies have addressed differences in bursa size and body condition due to parasite infections or the interaction between bursa and spleen size. However, in their study on House Sparrows *Passer domesticus*, Møller et al. (1996) reported that birds with large bursae had more parasites and were in relatively poorer body condition, whereas birds in good body condition had smaller bursae. These authors also found that bursa and spleen sizes were consistently larger in avian species more prone to parasite infections, such as hole versus open nesting birds.

There is an age-related decline in immune function (Ottinger and Lavoie 2007) that is expressed through a decreased size of immune defense organs, such as the spleen. This age effect may be related to a variety of factors, such as immaturity of the immune system of juveniles (young birds may not yet have encountered the full diversity of antigens produced by parasites and other pathogens), trade-off of an investment in immunity for an investment in growth, or the possibility that immune responses may be related to changes in structure and size of the parasite community (Forbes et al. 1999, Hudson et al. 2001, Møller et al. 2003, Hahn and Smith 2011). Investment in immunity can also be sex dependent, reflecting dissimilar exposure to parasites, differences in trade-offs between investment in antiparasite defenses and other activities related to self-maintenance, survival, and reproduction, or to genetic differences in susceptibility (e.g., Zuk and McKean 1996, Zuk and Stoehr 2002, Klein 2004, Møller and Saino 2004, Vicente et al. 2007). There is evidence that specific parasite species or groups elicit specific immune responses rather than responses to the whole parasite community. For example, in Magpies *Pica pica*, ectoparasites are thought to cause a reduction in spleen mass through their effect on nutritional condition (Blanco et al. 2001), with nutritional condition reflecting nutritional status and body condition. Vicente et al. (2007) associated an increased spleen mass of Red Deer *Cervus elaphus* with lungworm *Elaphostrongylus cervi* infections, and Cowan et al.

(2009) reported that the spleen mass of Masked Shrews *Sorex cinereus* increase with bladder nematode *Liniscus maseri* infections.

Parasites have been shown to be possible drivers of population cycles (e.g., Grenfell and Chappell 1995, Bush et al. 2001). According to the Anderson and May models (Anderson and May 1979, May and Anderson 1979), this can happen when (1) parasites show relatively low aggregation within the hosts, (2) parasites impact host fecundity more than host mortality, and (3) transmission or reproduction of parasites shows a time-lag. In Red Grouse *Lagopus lagopus scoticus*, for instance, the parasitic nematode *Trichostrongylus tenuis* increases in response to grouse density, but with a time-lag, and reduces breeding success (Hudson et al. 1998). In vertebrates, however, associations between immune activity and interannual population changes incorporating pathogens or parasites in vertebrates have rarely been examined. In studies on Snowshoe Hare *Lepus americanus* population cycles, the parasites lagged hare density by 2–3 years, and hare spleen weights also changed cyclically, with cycles of spleen weight preceding the hare population cycle by 1.5 years (Cary and Keith 1979). However, other studies have not found correlations between immune organ weights and population densities (Krebs 1962, Acquarone et al. 2002). In Iceland, the population cycles of rock ptarmigan *Lagopus muta* produce peak numbers approximately every 10 years (Nielsen and Pétursson 1995), and parasites could be one of the triggers.

Based on these aforementioned studies in various avian species, we hypothesized that bursa and spleen mass in the rock ptarmigan would provide an indication of their investment in promoting immune responses. We examined 6 years of data and hypothesized that spleen and bursa mass relate to parasite richness, prevalence, and abundance of the parasite taxa that are the main targets of immune responses, and to body condition of the birds. Further, if parasite infections are important in the case of the rock ptarmigan population cycle, we would expect parasites, size of immune organs, and body condition to show a timelag with respect to rock ptarmigan numbers. Birds reach their best physical condition during the „increase phase“ of the cycle, following which condition declines, reaching low 2 or 3 years after the peak in numbers and concurrent with a peak in parasite numbers. This cycle should be more pronounced for juvenile birds because delayed densitydependent winter mortality of this cohort is the demographic driver of the rock ptarmigan population cycle in Iceland (Magnússon et al. 2004).

Methods

The area around Lake Mývatn (65°370N, 17°000W), northeast Iceland, was the focus of the study. Rock ptarmigan (hereafter referred to as ptarmigan) were collected in the first week of October for 6 years (2007–2012) on moorlands, lava fields, and alpine areas west,

east, and north of the lake. The birds were collected by gunshot outside the hunting season under a license issued by the Icelandic Institute of Natural History.

The first week of October was chosen as our reference point to (1) control for seasonal changes in spleen and bursa size, as well as parasite measures (e.g., John 1994, Þórarinsdóttir et al. 2010, Akbar et al. 2012), and (2) sample the ptarmigan population at the onset of winter because winter survival determines population change (Garðarsson 1988). Ptarmigan are free-flying wild birds; consequently, individuals could not be selected at random, but were collected by conventional walk-up hunting. The birds were shot sitting or flying when encountered in areas where they gather during this season. In each year, there was a surplus number of juvenile birds in the catch, and individuals in this group were selected at random for analysis.

A total of 541 ptarmigan (179 juvenile males, 177 juvenile females, 122 adult males, 63 adult females) were analyzed. Each bird was tagged immediately after collection, wrapped in absorbent paper, placed in a paper bag, cooled to 4°C, and transported to the laboratory at the end of the day. All birds were dissected within 3 days of collection. Birds were sexed using both the loral stripe and the size and color of the combs (Montgomerie and Holder 2008), and age was based on pigmentation of the primaries (Weeden and Watson 1967). Sex and age were confirmed during necropsy by inspection of the gonads and presence or absence of the bursa. Two age classes were recognized: juveniles (about 3 months old) and adults (about 15 months or older). Ptarmigan become mature as 1 year olds (Holder and Montgomerie 1993). Mortality rates in the Icelandic ptarmigan population are high, and few birds exceed the age of 4 years (Garðarsson 1988, Icelandic Institute of Natural History ringing data).

To obtain an index of body condition, we took the following external and internal morphometric measurements 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) tarsus length, measured to the nearest 0.1 mm with calipers from the joint between tarsus and mid-toe to the intertarsal joint, (4) tarsus + mid-toe length, measured to the nearest millimeter with a ruler from the „heel“ to the base of the central claw, (5) 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 (6) 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 six body measures [(1)–(6)] were highly correlated with each other. A principle component analysis (PCA) was used to derive an index of structural size using Factor 1 from the PCA. Factor 1 explained 61.4 % of the variance in the original variables and was highly related to them (loadings: wing = 0.831, head + bill = 0.833,

tarsus = 0.528, tarsus ? midtoe = 0.647, sternum = 0.891, sternum-coracoid = 0.899). To obtain the index of body condition, body mass was regressed on body size, and the residuals used as a body condition index.

The spleen is located in the abdomen and is situated dorsally at the angle between the proventriculus, the gizzard, and the liver (Powers 2000a). In ptarmigan, it is triangular and pink to red-brown. The bursa is a pink pouch connected dorsally to the cloaca and opening into it (Sturkie and Whittow 1999). The spleen and the bursa were removed during necropsy and weighed on a digital scale (accuracy 0.0001 g).

Skirnisson et al. (2012) provide a detailed description of collection and quantification methods for ectoparasites and endoparasites (Table I.1). Quantification of the mite species *Tetraolichus lagopi*, *Metamicrolichus islandicus*, and *Mironovia lagopus* was adapted. Scores and direct counts from vacuum filters were combined for total scores. For the feather mite *T. lagopi*, abundance was scored by viewing the underwing coverts of the primary flight feathers and alula feathers against a strong light source. Single mites were seen as reddish dots close to the shaft of the white feathers, but mites also occurred in clumps. Scores from 0 to 3 were used to describe abundance, where 0 = no mites present, 1 = few or some dozens of mites present, seen as isolated reddish dots, 2 = narrow, reddish mite accumulations seen on some affected feathers, and 3 = broad (up to 2–3 mm wide) accumulations of mites seen on infested feathers. Both filter count and score data were cross checked to confirm infestation. If mites were present in the filter, but not observed during scoring, that bird was given a score of 1. Hence, a score of 1 indicated both minor infestation with this mite species and its presence. For the prostigmatan mite *M. lagopus* living in feather shafts on the wing, seven feathers from the middle of the wing (two upper-wing greater primary coverts and five secondary flight feathers) were examined. Each feather was scored, where 0 = no mites present; 1 = ≤10 mites present, and 2 = >10 mites present. The scores were added to derive a value for each individual. Ptarmigan were also scored for mange. Mange is a skin disease caused by skin mites – in the case of ptarmigan, M. islandicus. Infested skin appears dry and scaly. Feathers from the chest, sides, and back of each bird were plucked, and scores of 0–3 were used to describe mange extent, with 0 = no scales, 1 = <25 % of the body covered with scales, 2 = 25–75 % of skin with scales, and 3 = >75 % of skin with scales. Both count and score data were cross checked to confirm infestation of the bird. If mites were present in the filter, but not observed during scoring, that bird was given a score of 1. Hence, a score of 1 indicated both minor scaly skin and the presence of skin mites.

Each spring, territorial male ptarmigan were counted on six plots in the study area. The total size of these plots was 26.8 (range 2.4–8.0) km^2. Each plot was censused once during May (range 10–24 May). This census was conducted on foot by at least two observers in the early morning (0500–1000 hours) or late afternoon (1700–2400 hours). The positions

of territorial males as well as the locations of ptarmigan kills were plotted on a map. A „kill“ indicated the remains of a ptarmigan killed and eaten after arrival on the census plot in the spring. The total number of males counted in the spring census was the sum of the number of territorial males censused and those killed. The ptarmigan index used for this study was the annual mean density of males on these six plots. Nielsen (1996) provides a detailed description of the census plots and methods.

Statistical analyses

Statistical analyses were done using the software package R (Core Team 2011, ver. 2.14.1). All tests were two-tailed, and differences were deemed significant at $P \leq 0.05$. The frequency distributions of spleen and bursa mass were assessed using a Shapiro–Wilk test. Spleen mass was right skewed and thus log transformed to ensure normal distribution of the data. Year was treated as a factor (i.e., categorical variable). The parasite data for each species were ranked in ascending order (1 was allotted to the lowest positive finding) and midranks were used to account for ties (Holmstad et al. 2005). The ranked values of each parasite species were then summed to derive the total parasite, ectoparasite, and endoparasite abundance for each individual host and so enable the different counting units of the parasite groups to be combined. For the parasite groups „coccidians“, „helminths“, and „lice“, the original parasite count data of the respective parasite species were summed for each individual host. Parasite richness was defined as the total number of parasite species living in or on the host (Margolis et al. 1982, Bush et al. 1997, Schulte-Hostedde and Elsasser 2011). Parasite prevalence was defined as the proportion of hosts infected by a particular parasite species (Bush et al. 1997, Schulte-Hostedde and Elsasser 2011). Mean parasite abundance (hereafter referred to as parasite abundance) was defined as the sum of individuals of a particular parasite species in a sample of hosts divided by the number of hosts examined (Bush et al. 1997). Parasite count data of *Amyrsidea lagopi* and *Ceratophyllus garei* for adult birds and *C. garei* for juvenile birds were not used in further analyses due to small sample sizes. Helminths were analyzed as a group due to small sample sizes of the different species. Linear models were used to test whether spleen and bursa mass were related to body size, age, sex, year and body condition index and to investigate interactions between these variables. The stepwise backwards procedure was adopted, i.e., the least important variables (highest P values) were removed from the model until only the significant ($P \leq 0.05$) variables remained. Following this analysis, parasite measures and individual parasite species or groups, each tested separately, were added to the model, and it was reanalyzed controlling for the significant variables in the preceding model. Alpha levels ($P \leq 0.05$) were adjusted using Holm–Bonferroni corrections. Linear models were used to test whether spleen mass was associated with bursa mass, controlling for body size and ptarmigan population density.

Results

Parasites

Of the 541 ptarmigan analyzed, 540 had at least one parasite species, with 540 carrying ectoparasites and 449 carrying endoparasites. The parasites included four species of astigmatan feather mites and one prostigmatan quill mite (Acari), two ischnocerid and one amblycerid chewing lice (Mallophaga), two coccidians (Sporozoa), three helminths (two Nematoda and one Cestoda), one fly (Diptera), and one flea (Siphonaptera; Table I.1). All parasite species were more abundant in juvenile birds, with the exception of the nematodes *Capillaria caudinflata* and *Trichostrongylus tenuis*, which were more abundant in adult birds (Table I.1). Most prevalent was the mite *Tetraolichus lagopi*, followed by the coccidian *Eimeria muta* and the louse *Goniodes lagopi* (Table I.1).

Table I.1 *The ecto- and endoparasite fauna of rock ptarmigan (*Lagopus muta*) in northeast Iceland during each October 2007−2012.*

Parasite group	Scientific name	Number of infected hosts		
		Prevalence all (N = 541)	Prevalence juveniles (N = 356)	Prevalence adults (N = 185)
Ectoparasites				
Acari (mites)	*Metamicrolichus islandicus*	29.1	31.9	21.6
	Myialges borealis	14.4	18.6	5.3
	Mironovia lagopus	5.9	2.8	12.3
	Strelkoviacarus holoaspis	42.5	55.0	27.8
	Tetraolichus lagopi	99.2	100.0	98.3
Chewing lice (lice)	*Amyrsidea lagopi*	13.1	18.5	2.7
	Goniodes lagopi	71.8	84.0	48.1
	Lagopoecus affinis	51.2	64.2	25.4
Diptera (flies)	*Ornithomya chloropus*	37.3	39.4	35.7
Siphonaptera (fleas)	*Ceratophyllus garei*	0.4	0.6	0.0
Endoparasites				
Sporozoa (coccidians)	*Eimeria muta*	75.4	77.5	71.7
	Eimeria rjupa	12.8	13.4	11.5
Cestoda (tapeworms)	*Passerilepis serpentulus*	1.2	1.1	0.0
Nematoda (roundworms)	*Capillaria caudinflata*	28.4	27.5	32.5
	Trichostrongylus tenuis	2.7	2.3	2.9

Blastocystis sp. was present, but not quantified

Spleen and bursa mass

Spleen mass ranged from 0.024 to 0.243 g and was not significantly related to body size ($F_{1,539} = 0.04$, P = 0.840; Table I.2). Variation in spleen mass was due to age and year (age: $F_{1,534} = 62.80$, $P < 0.001$, year: $_{F5,534} = 2.57$, $P = 0.026$), as well as to the interaction of age and body condition ($F_{2,538} = 11.77$, $P < 0.001$). Consequently, juveniles had heavier spleens than adults, and mean spleen mass increased from 2007 to 2009, then decreased to 2011, before slightly increasing again in 2012 (Figure I.2, Table I.2). While spleen mass increased in juveniles with increasing body condition, it decreased in adults (Figure I.1).

Variation in spleen mass of juvenile birds was due to body condition ($F_{1,353}$ = 12.10, P < 0.001), as well as to the interaction of body condition and years ($F_{1,349}$ = 2.21, P = 0.042). Accordingly, spleen mass increased with improved body condition (Figure I.1), but the effect of body condition differed among years. While with improved condition, spleen mass increased in almost all years, it decreased in 2009 and decreased slightly in 2012. There was no significant variation in spleen mass among the sexes ($F_{1,353}$ = 1.60, P = 0.207; Table I.2).

Variation in the spleen mass of adult birds was marginally due to sex ($F_{1,183}$ = 3.81, P = 0.053), as well as to the interaction of body condition and years ($F_{6,172}$ = 2.45, P = 0.027). As such, adult females tended to have heavier spleens than males (Table I.2), and the effect of body condition differed between years. While spleen mass decreased in almost all years with improved body condition, it increased in 2009 and 2012.

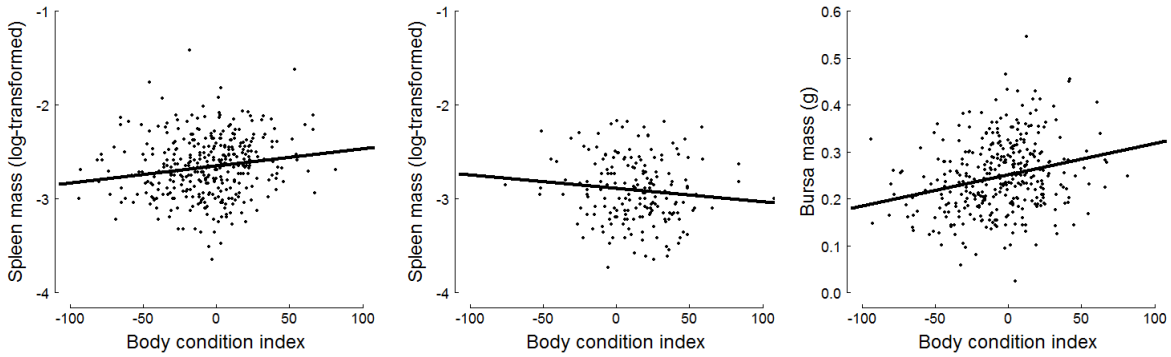


Figure I.1 *Effect of body condition on spleen mass (log-transformed) in juvenile (left) and adult (middle) rock ptarmigan (*Lagopus muta*), as well as bursa mass in juvenile rock ptarmigan in northeast Iceland each October between 2007 and 2012. Lines are linear regression lines.*

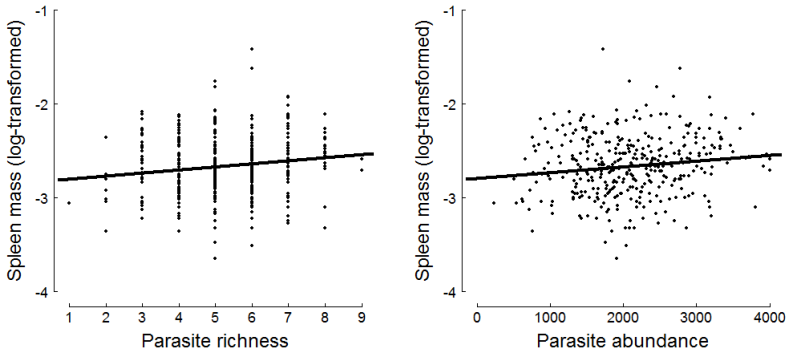


Figure I.2 *Associations between spleen (log-transformed) mass and parasite richness and abundance of juvenile rock ptarmigan (*Lagopus muta*) in northeast Iceland each October between 2007 and 2012. Lines are linear regression lines.*

Table I.2. *Association between mass of bursa and spleen (log-transformed) and parasite species richness, parasite abundance, and prevalence of rock ptarmigan in northeast Iceland during each October 2007−2012.*

Factors	**Bursa juvenile** (df = 349)		**Spleen juvenile** (df = 348)		**Spleen adult** (df = 182)	
	t	*p*	*t*	*P*	*t*	*p*
Parasite richness	-1.58	0.116	2.81	**0.035***	0.66	0.513
Parasite abundance	-1.66	0.098	2.63	**0.036***	0.54	0.594
Endoparasite abundance	0.35	0.177	3.24	**0.010***	0.55	0.584
Coccidians	0.28	0.783	1.23	0.221	-0.04	0.967
Eimeria muta	-1.16	0.249	1.39	0.167	-0.03	0.976
Eimeria rjupa	1.29	0.200	0.44	0.658	-0.14	0.888
Helminths	0.17	0.869	0.76	0.450	0.23	0.822
Ectoparasite abundance	-2.76	**0.036**	1.13	0.261	0.24	0.814
Acari						
Metamicrolichus islandicus	-1.93	0.066	2.52	**0.036***	0.11	0.912
Myialges borealis	-0.61	0.545	1.44	0.150	1.21	0.230
Strelkoviacarus holoaspis	0.93	0.354	0.71	0.477	-0.94	0.351
Tetraolichus lagopi	-2.13	0.034	0.21	0.831	-0.22	0.830
Mironovia lagopus	-1.63	0.104	-0.88	0.379	1.08	0.280
Chewing lice	-1.50	0.135	-0.96	0.339	1.26	0.210
Goniodes lagopi	-2.15	0.066	-0.39	0.696	0.57	0.569
Lagopoecus affinis	-1.40	0.161	-1.75	0.082	1.92	0.056
Amyrsidea lagopi	1.15	0.252	-0.12	0.907	-	-
Hippoboscids						
Ornithomya chloropus	1.72	0.087	-0.39	0.697	0.46	0.648
Parasite presence/absence						
Coccidians	-0.32	0.752	4.28	< **0.001***	0.74	0.460
Eimeria muta	-0.91	0.365	4.19	< **0.001***	0.21	0.833
Eimeria rjupa	0.72	0.474	3.13	< **0.001***	1.59	0.114
Helminths	1.63	0.104	-0.13	0.901	-0.58	0.565
Acari						
Metamicrolichus islandicus	-1.31	0.190	2.79	**0.036***	-0.70	0.487
Myialges borealis	-0.91	0.364	1.66	0.098	0.39	0.698
Strelkoviacarus holoaspis	0.13	0.894	0.23	0.822	0.03	0.980
Mironovia lagopus	-1.24	0. 216	-0.94	0.347	1.01	0.314
Chewing lice	-3.32	<**0.001***	-0.81	0.419	1.40	0.165
Goniodes lagopi	-2.95	**0.024***	-0.78	0.435	0.94	0.349
Lagopoecus affinis	-3.25	**0.010***	-0.92	0.359	0.93	0.355
Amyrsidea lagopi	0.31	0.758	0.27	0.790	-	-
Hippoboscids						
Ornithomya chloropus	0.74	0.462	0.09	0.926	-0.74	0.462

** Significant at P < 0.05 after Holm-Bonferroni correction*

The linear models were corrected for year, sex, body size, or body condition index. Ranked data were used for total parasite, endoparasite and ectoparasite abundance. Analyses for T. lagopi prevalence were omitted as these Acari were present on at least 98.3% of the birds. For other omitted values, the sample size was too low

Bursa mass ranged between 0.059 and 0.466 g and was significantly positively related to body size ($F_{1,344}$ = 4.75, P = 0.030; Figure I.1). Variation in bursa mass was due to body condition ($F_{1,344}$ = 20.02, P < 0.001; Table I.2) as well as the interaction of body condition and year ($F_{6,345}$ = 5.23, P < 0.001). Therefore, bursa mass increased with improved body condition in all years, but the slopes differed between years. There was no significant variation in bursa mass among the sexes ($F_{1,344}$ = 0.52, P = 0.471; Table I.2).

Spleen and bursa mass in relation to parasite measures

Spleen mass in juvenile birds increased significantly with increasing parasite species richness (Figure I.2) and abundance; this was particularly true for endoparasite abundance and the abundance of the skin mite *M. islandicus* (Table I.3). Regarding parasite prevalence, spleen mass was significantly greater when coccidians and the skin mite *M. islandicus* were present (Table I.3). Spleen mass in adult birds had no significant relationship with parasite measures (Table I.3).

Bursae were significantly lighter when ectoparasites were more abundant, and particularly when the chewing lice *Lagopoecus affinis* and *G. lagopi* were present (Table I.3).

Spleen versus bursa mass

Spleen and bursa mass, corrected for body size, were not related ($F_{1,350}$ = 0.65, P = 0.420).

Table I.3 *Mean spleen and bursa mass of rock ptarmigan (*Lagopus muta*) in north-east Iceland during each October 2007−2012.*

Organ	Age	Sex	Year	Sample size (N)	Mean mass (g)[a]	Range (g)
Spleen	Juvenile	Both	2007	60	0.070 ± 0.019	0.035 - 0.110
			2008	57	0.076 ± 0.026	0.036 - 0.162
			2009	59	0.084 ± 0.031	0.039 - 0.243
			2010	60	0.076 ± 0.030	0.030 - 0.197
			2011	60	0.067 ± 0.019	0.031 - 0.119
			2012	60	0.071 ± 0.025	0.026 - 0.172
		Female	All	177	0.075 ± 0.027	0.026 - 0.243
		Male	All	179	0.073 ± 0.024	0.024 - 0.197
	Adult	Both	2007	20	0.052 ± 0.020	0.029 - 0.114
			2008	25	0.057 ± 0.019	0.034 - 0.107
			2009	19	0.084 ± 0.031	0.024 - 0.113
			2010	40	0.056 ± 0.020	0.027 - 0.102
			2011	41	0.060 ± 0.022	0.026 - 0.111
			2012	40	0.058 ± 0.019	0.033 - 0.113
		Female	All	63	0.063 ± 0.023	0.024 - 0.114
		Male	All	122	0.056 ± 0.019	0.027 - 0.113
Bursa	Juvenile	Female	All	174	0.231 ± 0.070	0.059 - 0.412
		Male	All	178	0.262 ± 0.076	0.101 - 0.466

[a] *Data are presented as the mean ± standard deviation*

Spleen and bursa mass in relation to ptarmigan density

Spleen mass ($F_{1,539} = 5.57$, $P = 0.019$), but not bursa mass ($F_{1,351} = 0.03$, $P = 0.872$), was significantly positively related with ptarmigan density (Figure I.3, Table I.4). The 2009 autumn peak in spleen mass and body condition was succeeded by a peak in ptarmigan density in spring 2010, i.e., spleen mass tracked population change synchronously (Figure I.3).

Table I.4 *Mean densities of rock ptarmigan (*Lagopus muta*) on six census plots in north-east Iceland during each May 2007−2013.*

Year	Mean density	Standard error
2007	4.03	0.992
2008	5.58	1.247
2009	7.35	1.362
2010	7.93	1.373
2011	4.28	0.864
2012	3.53	0.698
2013	4.00	0.749

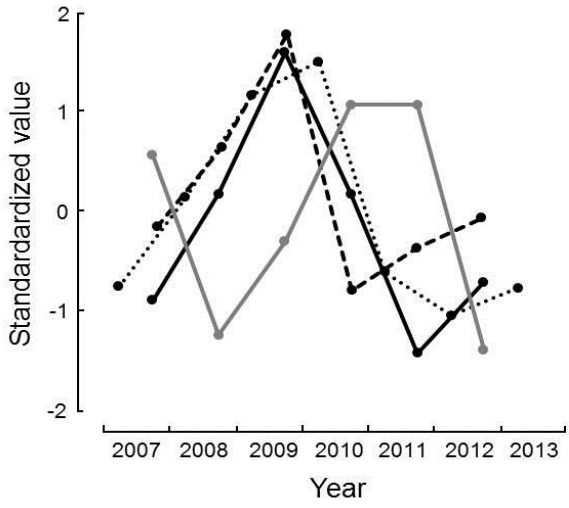


Figure I.3 *Annual variation in spleen mass (log-transformed; solid black line), body condition (dashed black line), and prevalence of coccidians (solid grey line) in juvenile rock ptarmigan (*Lagopus muta*), and rock ptarmigan population density (dotted black line) in northeast Iceland. Spleen, parasite, and body condition data were obtained each October 2007−2012. Ptarmigan density numbers were obtained each May 2007−2013. Values are standardized to (x−μ)/s.*

Discussion

In juvenile ptarmigan, we found that spleen mass was positively associated with parasite species richness and parasite abundance and was particularly positively associated with endoparasite abundance, the presence of coccidians, and the mite M. islandicus. Bursa mass was negatively associated with ectoparasite abundance, in particular with the presence of chewing lice (Table I.3). In other words, spleen mass increased and bursa mass decreased with increased parasite abundance, but changes in the two organs were associated with different parasite groups, and masses were not significantly correlated. Most studies have reported an increase in size of the spleen (splenomegaly: see John 1994, Møller and Erritzøe 1996, Sturkie and Whittow 1999, Møller et al. 1998a, Morand and Poulin 2000, Powers 2000a) and bursa (e.g., Glick 1994, Møller and Erritzøe 1996, Møller et al. 1996) if parasites instigate an immune response, but a few studies do observe or suggest spleen size decrease with an increase in parasites (e.g., Møller et al. 1998b, Shutler et al. 1999, Vicente et al. 2007). We are unaware of other studies reporting reduced bursa mass associated with increased parasites.

Spleen, bursa, and parasite measures: age, body condition, sex, and year effects

Splenomegaly in juvenile ptarmigan was significantly positively associated with parasite richness and abundance, with lighter bursae associated with ectoparasite abundance. In contrast, adult ptarmigan did not show any relation between spleen mass and parasite richness and abundance. Furthermore, the spleen and bursa mass of juvenile birds was positively related to body condition, while the spleen mass of adults was negatively related to body condition (Figure I.1). Møller et al. (1998a) found larger spleens in birds of good body condition but also in diseased individuals. These authors concluded that spleen size responds more strongly to changes in body condition than to changes in disease status. They also showed a strong correlation between condition and immune function, suggesting that the main cause of a weak immune response is poor body condition. In our study, the age-related difference in investment in immune function suggests that young birds are more susceptible to parasites and that they need to invest more in immune defense than adult birds. Hence, according to Møller et al. (1998a), the prerequisite of a strong immune response in juvenile birds should be good body condition (Figure I.1). This is similar to findings for Magpies, where first-year birds were found to be more parasitized than adults and where spleen size increased with the condition of the birds (Blanco et al. 2001), just like in juvenile ptarmigan. The adult ptarmigans in our study, however, had fewer parasites, possibly because they acquired immunity over time or because differences in mortality rates may have eliminated susceptible individuals from the population, leaving

predominantly resistant adults. Our findings suggest that adults in bad condition invest more in immune function than adults in good condition (Figure I.1).

Adult female ptarmigans carried more parasites than their male counterparts and, accordingly, the spleen mass of adult females was generally greater than that of adult males. This may reflect differences in sex roles. We collected our birds during the first week of October, approximately 5 weeks after brood break-up (Holder and Montgomerie 1993, Watson and Moss 2008). The female cares for the chicks alone. This is an energy-demanding activity, and brooding should expose adult females to parasites much more than males because the growing chicks become a hot spot for parasites. This effect may be further enhanced when broods mix in late summer. Accordingly, females should invest more in immune defense than males, resulting in greater spleen mass. Similarly, in a variety of bird species, Møller et al. (1998b) found that sex differences in spleen and bursa size were not present among juveniles, but that adult males had consistently smaller spleens than adult females. These authors suggested that sex differences in immune function may evoke sex differences in parasitism, but reasoned that adult females with larger immune defense organs would be healthier and less prone to parasite infections than males. This is contrary to our findings for the ptarmigan. However, in the same study, Møller et al. (1998b) also showed that females have initially larger immune organs than males due, for example, to the suppressive effects of androgens in males. Therefore, we cannot rule out that sex differences in spleen mass are solely due to sex characteristics.

Spleen, bursa, and parasites: effect of particular parasite groups

Different parasite groups together with increased body condition were related to different spleen and bursa mass effects in juvenile birds. For example, juveniles seemed to be particularly prone to coccidian infections, and their spleens were heavier when coccidians were present. These parasites can cause coccidiosis (Powers 2000b) that could stimulate an immune reaction leading to splenomegaly. Coccidian infections occur frequently because juvenile birds have not yet acquired the mature immune function found in adult birds. The annual peaks in coccidian intensity and prevalence for both juvenile and adult birds occur in October, the month ptarmigan were collected during our 6-year study (Þórarinsdóttir et al. 2010). The prevalence and abundance of skin parasites were associated with increased spleen mass. Ectoparasites have been found to be associated with splenomegaly and increased immune function (Blanco et al. 2001, Brown and Brown 2002). *M. islandicus* live in the upper skin layer and feed on the epidermal tissue and body fluids of the ptarmigan. This mite causes mange in ptarmigan and should therefore provoke immune responses.

Bursae were lighter when the lice *Lagopoecus affinis* and *Goniodes lagopi* were present and *G. lagopi* abundant, but the relationship was negative. Both these ischnoceran chewing

lice feed primarily on feathers and dead skin, whereas the more mobile amblyceran *Amyrsidea lagopi* feed on living tissue, such as skin and blood (Price et al. 2003, Clayton et al. 2008). It is hard to conceive that the presence of these ischnoceran chewing lice should elicit an immune response. The relationships we observed could thus be coincidental because *A. lagopi* did not relate to variation in bursa mass. In their study on ischnoceran and amblyceran chewing lice and the immune response of avian hosts, Møller and Rózsa (2004) found no relationship between host immune response and ischnoceran chewing lice, contrary to that found for amblycerans. Other agents, such as bacteria, fungi, or viruses, may be more important factors driving changes in bursa mass. There should in particular be more efficient defenses against lice, such as preening behavior and the use of preen oil from the preen gland (Moyer et al. 2003, Clayton et al. 2010).

Spleen mass: the year effect and ptarmigan density

The spleen mass of juvenile birds varied among years in a cyclic pattern, being low at the start of the study in 2007, increasing to a peak in 2009, and then declining to a minimum in 2011, before increasing again in 2012 (Figure I.2). Adult spleen mass showed the same general annual pattern, albeit not as significantly.

Mean spleen mass of juvenile birds in the autumn was positively correlated with body condition and ptarmigan density the following spring (Figure I.3). Mean bursa mass was only correlated with body condition, but not density. These results suggest that juvenile ptarmigan with large spleens and bursae have a good body condition and are therefore in line with those of other studies (e.g., Møller et al. 1998a, Vicente et al. 2007, Schulte-Hostedde and Elsasser 2011). One parasite group, however, did show an annual pattern similar to that observed for spleen mass, body condition, and ptarmigan population density – but with a time-lag; this was the coccidians in juvenile birds (Figure I.3). We hypothesized that if parasite infections are important in the ptarmigan population cycle, we would expect parasites, immune organ size, and body condition to show a time-lag with respect to ptarmigan numbers. Prime condition should be reached during the „increase phase“ of the ptarmigan cycle, following which it should decline to a low around 2 or 3 years after the peak in ptarmigan numbers, concurrent with a peak in parasite numbers. Also, this cycle should be more pronounced for juvenile birds. However, the mismatch in the annual pattern among coccidian prevalence as well as spleen mass and body condition is contrary to our hypothesis and suggests that other factors may be more important in triggering immune function in the ptarmigan. Møller et al. (1998a) proposed that hypersensitivity reactions could be one alternative explanation for finding large immune defense organs in diseased birds.

Conclusions

Spleen mass in our collected rock ptarmigan was positively associated with parasite species richness and abundance, in particular with endoparasite abundance, presence of coccidians, and a mange-inducing mite – but only in juveniles. Bursa mass was negatively associated with ectoparasite abundance – in particular with the presence of certain chewing lice. The two immune defense organs together with the body condition of the birds were associated with the abundance and prevalence of different parasite groups and species, and changes in size of the organs were not correlated. Changes in the spleen mass of juvenile ptarmigan over the years of the study were approximately synchronous with changes in body condition and population density, but coccidian prevalence lagged behind population change by approximately 2 years. Hence, we conclude that the parasites investigated in our study are not the only trigger for changes in spleen and bursa mass in juvenile ptarmigan and that other factors are possibly more important. There is evidence that microparasites such as bacteria and viruses inflict stronger immune responses. Our study showed that spleen mass was a marker of immune response in the ptarmigan; however, there may be more suitable tools for monitoring immune investment in response to parasite burden, such as immunogenetics. Even so, spleen mass is more suitable than bursa mass because spleen mass is independent of body size, both age groups have spleens, and the spleen shows a significant positive relationship with certain parasite measures.

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Paper II

Feather holes of rock ptarmigan are associated with amblyceran chewing lice

Ute Stenkewitz, Ólafur Karl Nielsen, Karl Skírnisson, Gunnar Stefánsson.
Wildlife Biology: accepted for publication.

Abstract

Feather holes have traditionally been suggested to be feeding traces of chewing lice (mallophagans). There is controversy whether mallophagans are the real source of feather holes. We studied mallophagan infestations and holes in tail feathers of 528 rock ptarmigan (*Lagopus muta*) collected 2007-2012 in Northeast Iceland. Three mallophagans were found, *Amysidea lagopi* (prevalence 13%), *Goniodes lagopi* (72%), and *Lagopoecus affinis* (51%). The prevalence of feather holes was 15% and based on pattern the holes could be separated into two groups termed feather hole swarms (FHS), prevalence 9%, and single holes (SH), prevalence 6%. Holes for FHS were concentrated in the central tail feathers and decreased outwards, but holes for SH did not show any such pattern. There was a significant positive relationship between the number of holes for FHS birds and *A. lagopi* number, and the prevalence was similar. No other combinations of FHS or SH and the mallophagans indicated any relationship. The observed differences between FHS and SH suggest that feather holes have different origin. Our thesis based on known feeding habits of amblycerans like *A. lagopi* is that the holes in FHS are created during the pin feather stage when the lice bite the pin feather to draw blood. The holes in FHS were often in lines parallel to the feather shaft and the distance between adjacent holes was similar to the daily growth band, and where apparent the holes were sitting in the light portion of the band suggesting diurnal rhythm in lice feeding activity. Concluding, feather holes in ptarmigan may have various origins, but there is a clear correlation between the presence and numbers of *A. lagopi* and FHS. This is a novel finding for the grouse family and the genus *Amyrsidea* and should be a valuable contribution to the studies of feather hole formation.

Introduction

Feather holes are found in many different bird species such as the domestic chicken, *Gallus gallus* forma *domestica* (Wilson 1933, Crutchfield and Hixson 1943, Trivedi et al. 1991), the barn swallow *Hirundo rustica*, and some other passerine species (Møller 1991, Vas et al. 2008). Feather holes are thought to have been created by the feeding activities of chewing lice (Mallophaga, Order: Phthiptera). Mallophagans are often site-specific and their morphology correlates with the sites preferred (Bush et al. 2001). There are two main groups of mallophagans, the suborders Ischnocera and Amblycera. Ischnocerans are highly specialized, live in the plumage, and feed primarily on keratin of feather barbules of down parts (e.g., Johnson and Clayton 2003, Møller and Rózsa 2005, Clayton et al. 2008). In contrast, amblycerans tend to occur in contact with host skin and feed on the blood of their hosts by biting the skin or pin feathers, but also by shearing or scraping feathers and skin with their mandibles (e.g., Bishopp and Wood 1917, Crutchfield and Hixson 1943, Ash 1960, Johnson and Clayton 2003, Møller and Rózsa 2005).

Recently, there has been controversy whether mallophagans are the causative agent of feather holes (Vágási et al. 2011, Vágási 2014), and furthermore what species or group of mallophagans are responsible for the holes (Møller 1991, Vas et al. 2008). Feather holes have been used in several influential studies as a proxy for mallophagan load (e.g., Kose et al. 1999, Moreno-Rueda 2010), in order to examine the impact of lice infestations on such traits as flight performance (Barbosa et al. 2002), mate choice (Moreno-Rueda and Hoi 2012), reproductive success (Pap et al. 2005), moult (Moreno-Rueda 2014), or survival (Pap et al. 2005). Vágási (2014) proposed three non-mutually exclusive hypotheses for the creation of feather holes: (a) they are created by chewing lice, (b) they are created by feather-degrading bacteria, and (c) they are one form of fault bars. Fault bars are growth defects and seen as straight, translucent lines perpendicular to feather barbs (Wood 1950, Solomon and Linder 1978).

Feather holes have been found on the rock ptarmigan *Lagopus muta* (hearafter ptarmigan; Nielsen unpubl.). Three species of mallophagans parasitize the ptarmigan, the amblyceran *Amyrsidea lagopi* and the ischnocerans *Goniodes lagopi* and *Lagopoecus affinis*. Most common is *G. lagopi* (prevalence, adult hosts 47%, juvenile hosts 86%), followed by *L. affinis* (adults 25%, juveniles 65%), and *A. lagopi* (adults 3%, juveniles 18%). All 3 species show significant host age related differences, with higher prevalences in juvenile hosts (Stenkewitz et al. unpubl.). *A. lagopi* has an elongated body and its head is bell-bottomed, but not bulky (Figure Ⅱ.1A). This species is agile and runs quickly across skin and feathers (Johnson and Clayton 2003). *G. lagopi* (Figure Ⅱ.1B) and *L. affinis* (Figure Ⅱ.1C) have a rather short but elongated body form with a rounded head which characterizes sluggish body lice that occupy lush feathers of the body and escape preening by burrowing in the downy basal regions of feathers (Johnson and Clayton 2003, Clayton et al. 2008).

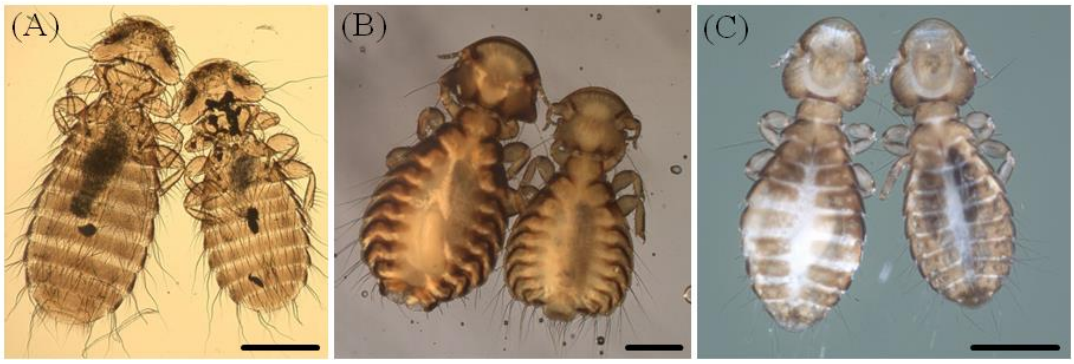

Figure II.1 *Chewing lice (mallophagans) infesting the Icelandic rock ptarmigan (A)* Amyrsidea lagopi*; (B)* Goniodes lagopi*; (C)* Lagopoecus affinis*. Females (shown on the left) are larger than males. Bar lengths: 0.5 mm.*

Infestation of the three mallopagan species and ptarmigan body condition are not significantly associated (Stenkewitz et al. unpubl.). There is though a negative relationship between preen gland mass and prevalence of all three mallophagan species (González 2014), and also between the mass of the bursa of Fabricius – an organ of immune function in young birds – and the prevalence of *G. lagopi* and *L. affinis* (Stenkewitz et al. 2015). Both of these observations imply that there are physiological costs associated with mallophagan infestations in ptarmigan.

In 2006, we began studying the relationship between ptarmigan health and population change (Nielsen and Skírnisson 2009). Soon we noted that some of the birds sampled had a peculiar pattern of holes in tail feathers and we called those "feather hole swarms" (Figure II.2). We wanted to examine this further and propose that this pathological character is created by mallophagan feeding activities. *A priori* we do not know if any one particular mallophagan species is responsible, but we expect a relationship between prevalence and abundance of the mallophagan accountable and feather holes in the combined sample and also individual years 2006-2012.

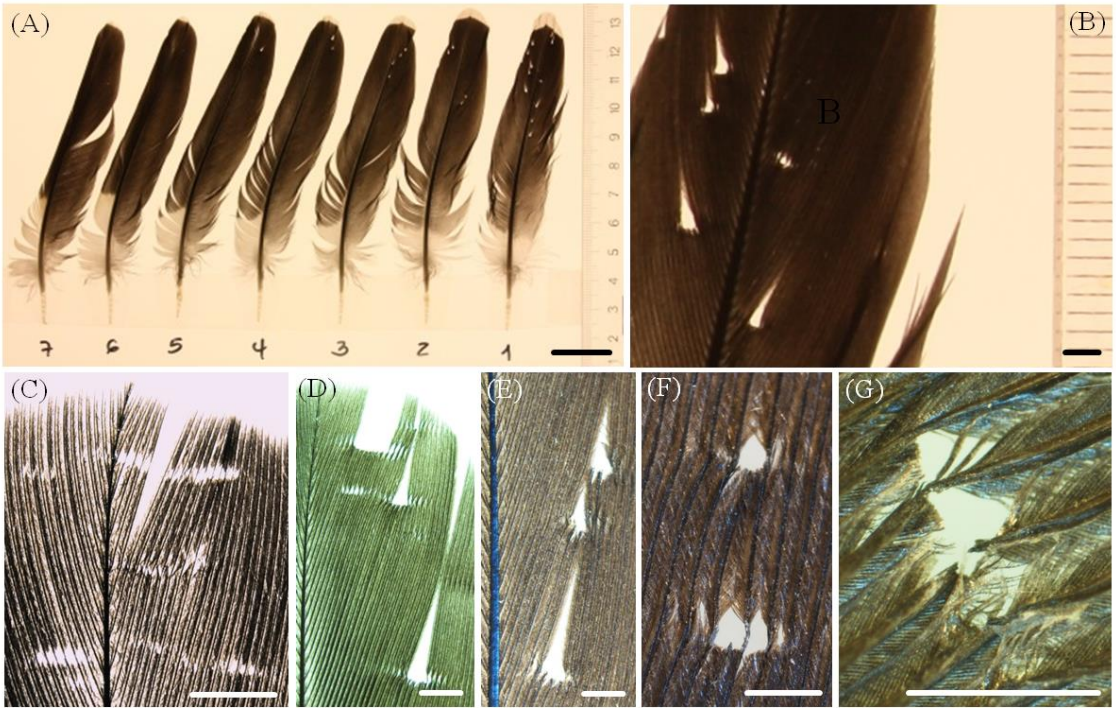

Figure II.2 *Feather holes and fault bars in tail feathers of Icelandic rock ptarmigan. (A) Right tail side with feather hole swarms (FHS). Feather holes on five of the seven feathers are showed. (B) Five feather holes. (C) Four fault bars at the tip of a tail feather seen as transluscent lines. (D) Feather breakage at fault bar. (E) – (G) Closeups of feather holes. Bar lengths: (A) 2 cm. (B) 2 mm. (C) 2 mm. (D) 2 mm. (E) 1 mm. (F) 1 mm. (G) 1 mm.*

Methods

Birds used for this analysis were collected specifically for a long-term study on the relation between ptarmigan population change and ptarmigan's health related parameters (i.e., Skirnisson et al. 2012, Stenkewitz et al. 2015). To do all the sampling and analysis required for the study at large it was necessary to sacrifice birds. But it should be noted that the ptarmigan is very common in Iceland and a popular game bird and since 1995 between 40 and 160 thousand birds have been shot every year (http://www.ust.is).

The ptarmigan were collected (shot) from moorlands, lava fields and alpine areas west, east, and north of Lake Mývatn in northeast Iceland (65°37' N, 17°00' W). The birds were collected in the first week of October 2007–2012 outside the hunting season authorised by the Icelandic Institute of Natural History. Each bird was tagged immediately after collection. To avoid cross-contamination, each bird was wrapped in absorbent paper and placed in a paper bag, then sealed by interfolding and stapling. Birds were cooled to 4°C and processed within 3 days of collection.The first week of October was chosen as reference point to control for seasonal changes in parasite and feather hole prevalence and abundance. The annual number of juvenile birds analysed for the health study is 60 (equal sex ratio). The number of adults has varied between 18 and 41 birds. The average proportion of juveniles in autumn on the study area is 80% (Nielsen et al. 2004) so each year juveniles were collected in excess and individuals for analysis were selected at random from this catch. All adults caught were analysed, but as adult females are partly migratory (Garðarsson 1988), males dominated the adult catch (Table Ⅱ.1).

Table II.1 *Annual sample of rock ptarmigan for feather hole studies in northeast Iceland, early October 2007–2012.*

	Adult		**Juvenile**		
	Males	Females	Males	Females	Total
2007	13	5	29	29	76
2008	12	13	28	27	80
2009	11	7	30	28	76
2010	27	12	30	30	99
2011	24	16	30	30	100
2012	31	9	29	28	97
Total	118	63	176	172	528

During dissection, the tail was removed, kept frozen, and later checked for feather holes. Mallophagans were collected according to Skirnisson et al. (2012) using a hand-held vacuum cleaner (Princess, Turbo tiger, Type 2755). The plumage of the intact bird was vacuum-cleaned for about two minutes; within this time the whole bird can be vacuumed systematically and thoroughly. The vacuum cleaner was modified for this purpose. The

nozzle (4×1.5 cm) was connected to an external collection chamber fitted with a circular sack-like filter (92 cm², diameter of pores 2–30 µm). The filter was kept frozen until analysis when its contents were transferred to a 400 ml glass jar using the beam of a water-filled washbottle. Seven drops of the surfactant TritonH X-100 were added to the jar to reduce adhesive forces and to promote particle settling. The jar was fitted with a lid and shaken vigorously by hand and allowed to settle overnight. Mallophagans were collected under a stereoscope and embedded on a slide in Hoyer's medium (Anderson 1954) for later identification (Timmermann 1950, Scharf and Price 1983) and quantification.

An intact ptarmigan tail has 14 rectrices. The plucked tail feathers were mounted on a transparent plastic film in a right order, numbered, and photographed with illumination from below (Figure Ⅱ.2A). A feather hole generally looks triangular, cone-shaped, or drop-like and is 0.5–1.5 mm wide at the base where barbs are missing and sharp towards the top where the surrounding barbs close the created gap (Figure Ⅱ.2B, E, F). Occasionally, particularly when the barbs are damaged or deformed but not broken, the gap consists of missing barbules only (Figure Ⅱ.2F, G). We documented feather hole swarms (FHS) and single holes (SH) in tail feathers. Feather hole swarms always consisted of holes that were exhibited in a single line parallel to the feather shaft; sometimes there was more than one line. The distance between adjacent holes in FHS was frequently 2–4 mm, though there were exceptions, and on feathers where the growth band could be seen the holes were located in the light portion of the band. For analysis, feather holes from every feather from each tail were counted using the images. Only tails containing 7 or more feathers were used to study the relationship between the number of feather holes and mallophagans. In case of missing feathers (255 out of 7392 or 3.5 %), we used the same number of holes as on the equal feather from the other side of the tail to calculate total number of holes for that individual. This is justified by the low number of missing feathers involved and similar mean number of holes on equivalent feathers (Figure Ⅱ.3). We only had access to dissected tails to study feather holes. We did not have access to other feathers except for wings of 26 birds that had *A. lagopi*, but no holes in the tail feathers.

We performed statistical analyses using the software package R (R Core Team 2014, version 3.1.0). Prevalence was defined as the proportion of birds with feather holes or mallophagans (Bush et al. 1997). To test if the prevalence of FHS, SH and mallophagans differed, we applied a Fisher's exact test. To test if the number of holes for birds with FHS and SH differed, we applied a Mann-Whitney U test. To test if the number of feather holes and mallophagans were related over the years, we applied generalized linear models, fitting quasipoisson family. To account for the individual years, we included factor year as interaction term and considered a fixed factor in each model. The model with the combined sample was corrected for type Ⅲ error using drop1 function in R. For the model with the interaction term, the summary function was used to be able to present each year as well as the kind of relationship (positive or negative expressed in the t-value). We did not include

age in the model as we are mainly interested in the relationship between the number of holes and mallophagas, and also because of sample size. To test for birds with feather holes, whether the frequency of feather holes or the mean number of feather holes was associated with the position of a feather within the tail, we used χ^2 tests with Yates' correction as well as non-parametric Friedman ANOVA tests, respectively. All tests were two-tailed and statistical significance deemed when $p \leq 0.05$.

Results

Five-hundred and twenty eight ptarmigan were examined for feather holes and louse abundance. Sixty-nine (13%) had *A. lagopi*, 378 (72%) *G. lagopi*, 271 (51%) *L. affinis*, and 79 (15%) had holes in tail feathers. From the latter, 49 birds (9%) had FHS and 30 (6%) SH in their tail feathers, this difference in prevalence was significant (Fisher's exact test p = 0.035). The mean number of holes for intact tails with FHS was 43.5 (n = 40, range 7–79, SE = 3.26) and with SH was 3.3 (n = 28, range 1–9, SE = 0.43). The difference in hole number between FHS and SH was highly significant (Mann-Whitney U = 2.00, n_{FHS} = 40, n_{SH} = 28, $p < 0.001$).

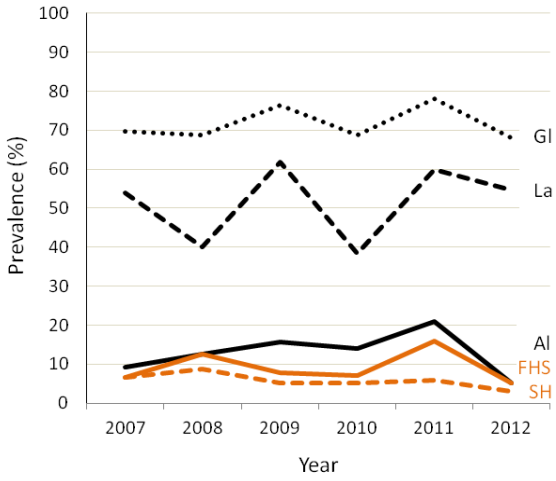

Figure II.3 *Prevalence of feather hole swarms (FHS), single holes (SH), and mallophagans in Icelandic rock ptarmigan 2007–2012 (n = 528).* Al = Amyrsidea lagopi; Gl = Goniodes lagopi; La = Lagopoecus affinis.

Location of holes within tail

For FHS, there was a significant difference with respect to the position of the tail feather and both the proportion of feathers affected (Yates' chi-square = 54.2, df = 6, $p < 0.001$) and the number of holes in affected feathers (Friedman ANOVA chi-square = 136.0, df = 6, $p < 0.001$). Both the frequency and the number of holes were highest in feathers in the mid part of the tail and decreased outwards (Figure II.4). Most holes were located on the

distal half of each tail feather, and holes located on the proximal half were right below the center line and only found on the two innermost tail feathers on either side (Figure II.2A). For SH, there was no difference with either the proportion of tail feathers affected (Yates' chi-square = 9.582, df = 5, p = 0.088) or the number of holes in affected feathers (Friedman ANOVA chi-square = 11.4, df = 6, p = 0.077) and the position of the feather within the tail.

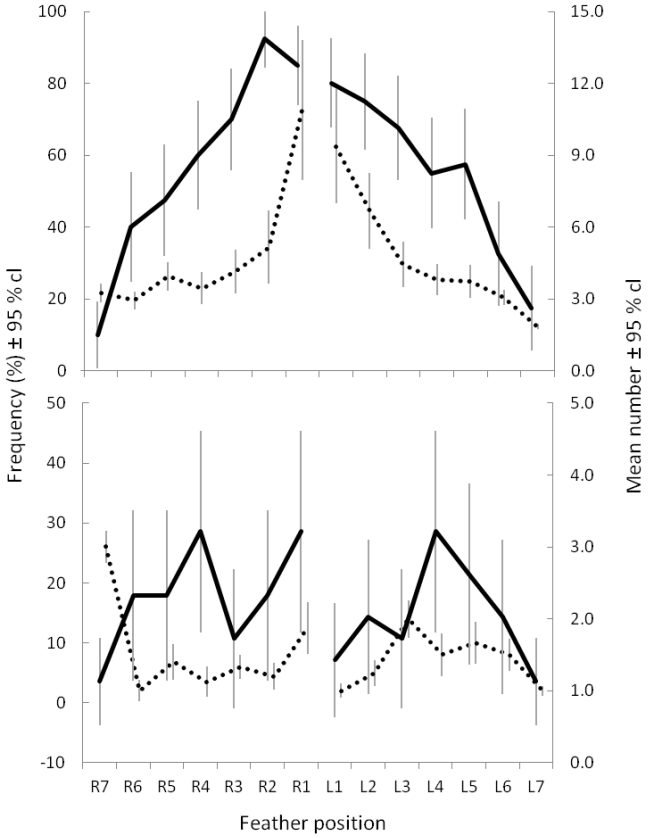

Figure II.4 *Frequency (continuous line; ± 95% confidence intervals) and mean number (dotted line; ± 95% confidence intervals) of feather holes for feather hole swarms (FHS; top) and single holes (SH; bottom) in tail feathers of Icelandic rock ptarmigan 2007–2012. The calculations are based on birds with intact tails only (FHS: n = 40, SH: n = 28).*

FHS and mallophagans

Prevalence of FHS (9%) and the amblyceran *A. lagopi* (13%) in the total sample did not significantly differ (Fisher's exact test p = 0.063). In two years the prevalence of FHS was significantly lower than the prevalence of *A. lagopi* (Figure II.2A, Table II.2). Out of 75 birds with FHS and *A. lagopi*, 43 (57%) had both FHS and *A. lagopi*, 6 (8%) had only FHS, and 26 (35%) had only *A. lagopi*. Of the 26 birds that had no FHS in their tails, 8 (32%) had holes in secondary feathers. Also, two of the 26 birds had what we termed as SH in the tail feathers.

FHS and *A. lagopi* showed a significant positive relationship ($t = 6.5$, $df = 74$, $p < 0.001$). With respect to the individual years, four years showed a significantly positive relationship between the numbers of FHS and *A. lagopi*, and for two years significance was just above the rejection limit (Table II.3).

Prevalence of FHS (9 %) and the ischnocerans *G. lagopi* (72 %, Fisher's exact test $p < 0.001$) and *L. affinis* (51%, Fisher's exact test $p < 0.001$) differed significantly, the ischnocerans were much more prevalent in all years (Figure II.3, Table II.2). Further, numbers of FHS and *G. lagopi* ($t = -0.7$, $df = 382$, $p = 0.467$) or *L. affinis* ($t = -1.1$, $df = 283$, $p = 0.277$) did not show any relationship, neither in the combined sample nor the individual years (Figure II.5, Table II.3).

Out of 383 birds with FHS and *G. lagopi*, holes and *G. lagopi* co-occurred in 44 (11 %), 5 (1%) had only holes, and 334 (87%) had *G. lagopi* only. Out of 284 birds with FHS and *L. affinis*, holes and *L. affinis* co-occurred in 36 (13%), 14 (5%) had only holes, and 235 (83%) birds had only *L. affinis*.

SH and mallophagans

The prevalence of SH (6%) was significantly lower than the prevalence of any of the three mallophagan species (Fisher's exact test $p < 0.001$ for each). Also there was no relationship

Table II.2 *Results from Fisher's exact tests for the prevalence of feather hole swarms (FHS) and mallophagans for Icelandic rock ptarmigan 2007–2012. Significant values ($p \leq 0.05$) indicate differences in prevalence.*

Feather holes	Year	n	p
Amyrsidea lagopi	2007	7	0.569
	2008	10	1.000
	2009	12	0.014
	2010	12	0.073
	2011	22	0.021
	2012	6	0.596
Goniodes lagopi	2007	48	< 0.001
	2008	52	< 0.001
	2009	57	< 0.001
	2010	66	< 0.001
	2011	73	< 0.001
	2012	65	< 0.001
Lagopoecus affinis	2007	38	< 0.001
	2008	31	< 0.001
	2009	45	< 0.001
	2010	37	< 0.001
	2011	55	< 0.001
	2012	51	< 0.001

Table II.3 *Results from generalized linear models between the number of feather holes for rock ptarmigan with feather hole swarms (FHS), and mallophagan numbers, northeast Iceland, early October 2007–2012. Significant values ($p \leq 0.05$) indicate a relationship between mallophaga numbers and the number of feather holes.*

Feather holes	Year	n	t	p
Amyrsidea lagopi	2007	8	1.7	0.092
	2008	12	3.3	0.002
	2009	12	3.8	< 0.001
	2010	14	1.8	0.073
	2011	22	5.6	< 0.001
	2012	7	2.0	0.050
Goniodes lagopi	2007	54	-1.6	0.108
	2008	57	-0.9	0.372
	2009	58	-0.8	0.419
	2010	69	-1.7	0.084
	2011	78	-0.4	0.676
	2012	67	-1.8	0.069
Lagopoecus affinis	2007	43	-0.9	0.379
	2008	36	-0.9	0.346
	2009	49	-1.3	0.209
	2010	43	-1.3	0.194
	2011	60	-0.3	0.783
	2012	53	-1.3	0.206

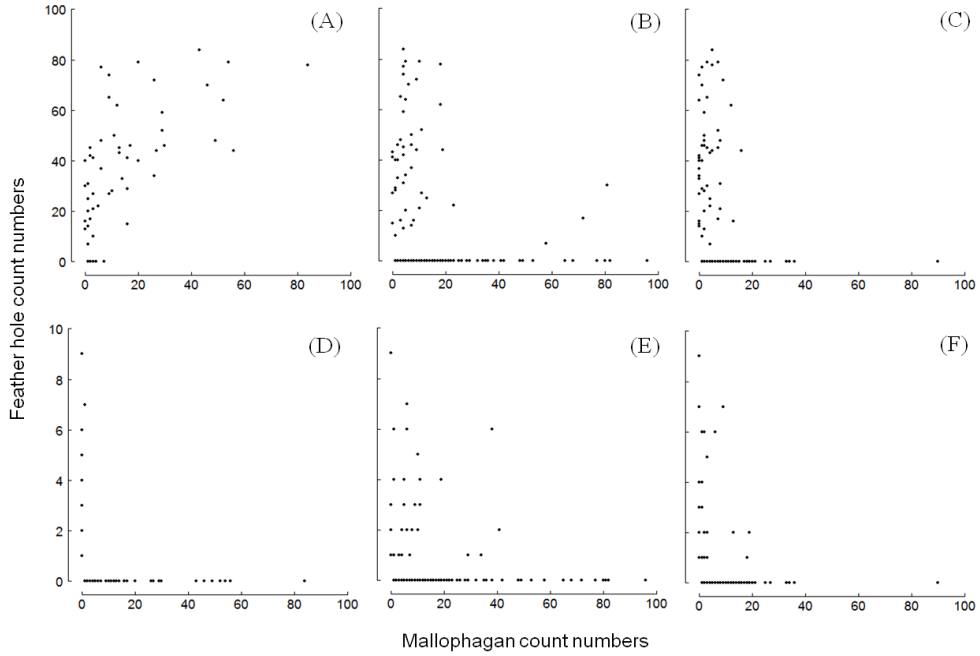

Figure II.5 *Associations between the number of feather holes and mallophagans for Icelandic rock ptarmigan 2007–2012. Birds with feather hole swarms (FHS) are depicted in (A)–(C) and single holes (SH) in (D)–(F). (A) and (D)* Amyrsidea lagopi*; (B) and (E)* Goniodes lagopi*; (C) and (F)* Lagopoecus affinis*.*

between the number of any of the three mallophagans and the number of holes (*A. lagopi*: F = 6.0, p = 0.063 after Holm-Bonferroni correction, *G. lagopi*: F = 0.1, p = 0.816, *L. affinis*: F = 0.4, p = 0.527; Figure II.5). For *A. lagopi* and SH there was very little overlap in occurrence, and out of 97 birds with either or/and, 2 birds (2%) had both SH and *A. lagopi*, 28 (29%) only SH, and 67 (45%) only *A. lagopi*.

Discussion

Different origins of feather holes

Our studies showed that 15% of ptarmigan had holes in their tail feathers. We classified the holes into two groups based on their patterns: FHS and SH. FHS were more prevalent then SH (9% versus 6%) and affected tails with FHS had more holes than SH (mean number 43.5 versus 3.3 holes). How the holes were distributed within the tail for the two groups also differed clearly. Hole frequency of occurrence and mean number of holes per feather for birds with FHS showed the highest values for the innermost tail feathers and decreased outwards. Holes for birds with SH did not form any such pattern and looked randomly distributed. This difference justified treating the two groups separately in the analysis of a relationship with the mallophagans.

The only significant relationship between feather holes and mallophagans was between abundance of FHS and the amblyceran *A. lagopi*. Numbers of feather holes in tails with FHS were related with numbers of *A. lagopi* in the combined sample and all the individual years showed a *positive* relationship between the two variables. Also the prevalence of FHS and *A. lagopi* was similar. No relationship was observed between the two ischnocerans, *G. lagopi* and *L. affinis*, and FHS nor between SH and any of the three mallophagans. These observations further strengthen our view that the two types of feather holes have different origin and that only holes in FHS are created by mallophagans and in our case the amblyceran *A. lagopi*. The only other attempt to correlate the number of feather holes and mallophagans, to our knowledge, is by Møller (1991) who found a significant relationship between the number of feather holes and mallophagans on barn swallows. This study was however based on a small sample (n = 20 birds) and the mallophagans found were not identified to species level.

We do not have any explanation for the SH pattern. Also, some of the FHS holes could be breakage at a fault bar. At least 4% of 452 feathers with holes had some holes that were clearly associated with fault bars. That is, a fault bar touched or ran through the feather hole, most often at the base of the hole, but also at any level. Also, ptarmigan in our study population are known to harbour feather degrading bacteria (Sveinsdóttir et al. 2015), but no attempt has been made to associate them with feather holes.

How does *Amyrsidea lagopi* create holes?

We find it unlikely that *A. lagopi* bites the holes while eating keratin in full grown feathers. The amblycerans to which the *A. lagopi* belongs are known to feed on living tissue rather than keratin (e.g., Crutchfield and Hixson 1943, Johnson and Clayton 2003), and also the diameter of a ptarmigan tail feather barb is at least 2–4 times greater than the mouth aperture of a fully grown *A. lagopi*. This suggests that biting damage by *A. lagopi* is done during the pin feather stage. Pin feathers are developing feathers that have a blood supply flowing through them (Lucas and Stettenheim 1972). Amblycerans are known to feed on pin feathers (Bishopp and Wood 1917, Crutchfield and Hixson 1943). Wilson (1933) observed the amblyceran poultry body louse *Menacanthus stramineus* (= *Menopon stramineum*) sucking blood from pin feathers, and also recorded old bite marks on pin feathers. Stockdale (1964) observed that most *M. stramineus* were feeding on the liquid portion (lymph and blood) of wounds and freshly plucked pin feathers. Also, Agarwal et al. (1983) demonstrated that up to 88% of *Menacanthus eurysternus* infesting the common myna *Acridotheres tristis* fed exclusively on host blood obtained from pin feathers. All mentioned amblycerans as well as *A. lagopi* from our study belong to the family Menoponidae. Our thesis is that the damage rendering feather holes in FHS is done when the amblyceran gnaws through the corneal sheath of the pin feather to draw blood and thereby damaging the developing barb.

The match between birds with FHS and *A. lagopi* was not perfect, six birds had only FHS and no *A. lagopi*, and 26 birds had only *A. lagopi*. Regarding the first group then we assume that feather holes are created during growth of the tail feathers and that takes place in July and early August, so there is a two months gap between creation of holes and the collection of mallophagans. Accordingly, extinction of *A. lagopi* could be part of the explanation for this mismatch or that we simply missed them during collecting of mallophagans. Additionally, amblycerans like *A. lagopi* are more mobile than ischnocerans and more likely to leave the host when handled or dying (Ash 1960, Bush et al. 2001, Clayton et al. 2008). The fact that we find *A. lagopi* but no FHS in tail feathers could be due to the mallophagan utilizing habitat other than the tail. Supporting this claim are feather holes found in the secondary wing feathers in 8 of these 26 birds in this category. Also, the distinction of FHS and SH is based on the pattern formed by the holes and there could be ambiguity involved and 2 of the 26 birds with *A. lagopi* but no FSH were defined to have SH. Another possible explanation would be for *A. lagopi* feeding on other live tissues than pin feathers.

Location of feather holes for FHS

The innermost tail feathers were clearly preferred, seen in both frequency of occurrence and number of feather holes. Possible explanations for this symmetrical pattern could have to do with security for *A. lagopi* by avoiding host preening and getting lost during take-off

and landing, or it reflects structural differences of feathers (outer tail feathers are more stiff) affecting access to blood, but in general the causes for this pattern remain unclear.

Feather holes were almost exclusively found on the distal part of the feathers. This suggests that *A. lagopi* feed on the pin feathers during the first phase in their growth. Growth bars (Wood 1950) in tail feathers of juvenile ptarmigan are 2 to 4 mm wide and between 3 and 6 mm in adults (Stenkewitz unpubl.). Similar feather growth rates have been reported for blue grouse (*Dendragapus obscurus*; Bendell 1955). The maximum length of an affected distal part of a tail feather is 70 mm. Assuming a feather growth of c. 3 mm/day for juveniles and 4 mm/day for adults suggests that the time window available for the mallophagans to inflict their damage is approximately 3 weeks long. As the pin feather grows longer, the feather tip unfolds while blood supply is maintained in the lower part. At this stage in the development of the feather, according to our thesis, conditions are such that the mallophagans cannot draw blood from it anymore.

Why do the holes align themselves up in lines? This could be the result of repeated bites from the same louse either clinging to the pin feather or approaching it from the same angle for each feeding event. The distance between adjacent holes was frequently similar to the width of the daily growth band, 2–4 mm. Further, on feathers where growth bands were apparent the holes were associated with the light portion of the band, the part produced during the night (e.g., Wood 1950). This suggests a diurnal feeding rhythm of the lice.

Conclusions

Based on the observed relationship, we conclude that feather holes in ptarmigan have multiple origins with the feeding activity of the amblyceran *A. lagopi* during the pin feather stage is very likely one of those factors. The latter finding is supported by the diameter of fully grown barbs, the morphology of *A. lagopi* mouth parts, the known feeding habits of amblycerans, the relationship between the number of *A. lagopi* and feather holes, and similar prevalence of the two. To our knowledge this is the first time anyone has shown a quantitative relationship between a specific mallophagan species and feather holes. These findings are novel for the grouse family and the genus *Amyrsidea* and should be an important contribution to future studies of feather hole formations. Because feather holes in tails can be easily detected on live and dead birds, their presence can serve as a proxy for *A. lagopi* presence and hole numbers as one indicator of the health status of the bird.

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Paper III

Host-parasite interactions and population dynamics of rock ptarmigan

Ute Stenkewitz, Ólafur Karl Nielsen, Karl Skírnisson, Gunnar Stefánsson.
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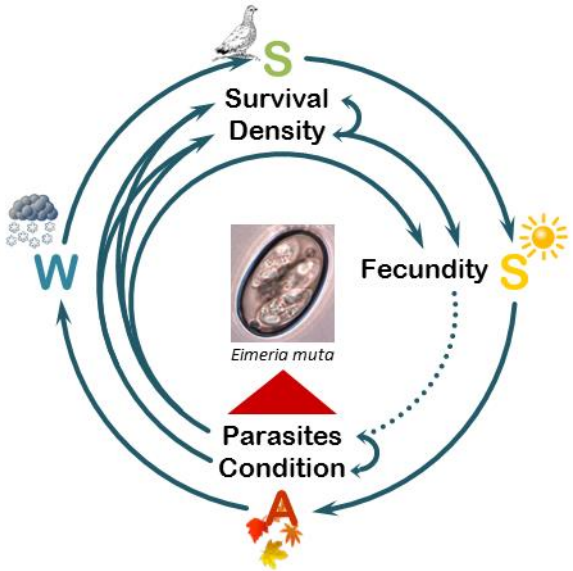

Abstract

Populations of rock ptarmigan (*Lagopus muta*) in Iceland fluctuate in multiannual cycles with peak numbers c. every 10 years. We studied the ptarmigan-parasite community and how parasites relate to ptarmigan age, body condition, and population density. We collected 632 ptarmigan in northeast Iceland in early October from 2006 to 2012; 630 (99.7 %) were infected with at least one parasite species, 616 (98 %) with ectoparasites, and 536 (85 %) with endoparasites. We analysed indices for the combined parasite community (16 species) and known pathogenic parasites, two coccidian protozoans *Eimeria muta* and *Eimeria rjupa*, two nematodes *Capillaria caudinflata* and *Trichostrongylus tenuis*, one chewing louse *Amyrsidea lagopi*, and one skin mite *Metamicrolichus islandicus*. Juveniles overall had more ectoparasites than adults, but endoparasite levels were similar in both groups. Ptarmigan population density was associated with endoparasites, and in particular prevalence of the coccidian parasite *Eimeria muta*. Annual aggregation level of this eimerid fluctuated inversely with prevalence, with lows at prevalence peak and vice versa. Both prevalence and aggregation of *E. muta* tracked ptarmigan population density with a 1.5 year time lag. The time lag could be explained by the host specificity of this eimerid, host density dependent shedding of oocysts, and their persistence in the environment from one year to the next. Ptarmigan body condition was negatively associated with *E. muta* prevalence, an indication of their pathogenicity, and this eimerid was also positively associated with ptarmigan mortality and marginally inversely with fecundity. There were also significant associations between fecundity and chewing louse *Amyrsidea lagopi* prevalence (negative), excess juvenile mortality and nematode *Capillaria caudinflata* prevalence (positive), and adult mortality and skin mite *Metamicrolichus islandicus* prevalence (negative). Though this study is correlational, it provides strong evidence that *E. muta* through time-lag in prevalence with respect to host population size and by showing significant relations with host body condition, mortality, and fecundity could destabilize ptarmigan population dynamics in Iceland.

Introduction

Parasite communities of wildlife species have rarely been studied over an extended time period (Esch et al. 1997). Detailed studies can provide insight into many aspects of parasite ecology, the relationships between host and parasites, and adaptations resulting from this intimate network (Esch et al. 1997, Kennedy and Harnett 1997, Atkinson et al. 2008). Parasites can influence population dynamics by affecting host body condition, fecundity, and survival, and host-parasite interactions are known to be one of the driving forces of multiannual cycles in animal populations (e.g., May and Anderson 1978, Anderson and

May 1981, Grenfell and Chappell 1995, Hudson et al. 2001, Bush et al. 2001, Berryman 2002). Cycles have been reported in a variety of herbivorous species in northern latitudes including moths, hares, lemmings, voles, and grouse (Keith 1963, Berryman 2002), and are well documented for species in the genus *Lagopus*. The parasitic nematode *Trichostrongylus tenuis* is thought to be one of the agents driving the red grouse *Lagopus lagopus scoticus* cycle in Scotland (Hudson et al. 1998). Parasites of willow ptarmigan (*L. l. lagopus*) in Norway, have been reported to affect demographic parameters including body condition and breeding success of the host, and were negatively associated with changes in numbers of the ptarmigan population (Holmstad et al. 2005a,b).

Some rock ptarmigan (*Lagopus muta*) populations show multiannual cycles (Holmstad et al. 2005b, Weeden 1965, Nielsen and Pétursson 1995, Moss and Watson 2001). Traditionally, the ptarmigan population in Iceland has cycled with a 10–12 year period (Nielsen and Pétursson 1995), but recently this has changed and the periods have become shorter (Sturludóttir 2015). The gyrfalcon (*Falco rusticolus*) and the rock ptarmigan in Iceland have a coupled predator-prey cycle and the falcon is thought to be an agent driving the ptarmigan cycle (Nielsen 1999, 2011). However, other researchers have demonstrated the importance of studying the effects of several different factors on the cyclic behaviour of a population (e.g., Watson et al. 1998, Krebs et al. 2001, Redapth et al. 2006). Parasites have the potential to effect host survival by making birds more prone to predation, weakening body condition, or changing host behaviour (Hudson et al. 1992, Holmstad et al. 2005a, Hughes et al. 2012).

The parasite fauna of rock ptarmigan in Iceland has been described and 17 species have been reported (Skirnisson et al. 2012, 2016). In this paper, we want to examine the potential role of the parasites on the population dynamics of rock ptarmigan. We do this by investigating the relationship between ptarmigan density, body condition, mortality, fecundity, and measures of parasite abundance and aggregation over a period of 7 years (2006–2012). We look at the combined parasite community and focus on six known pathogenic parasite species, namely *Eimeria muta* and *Eimeria rjupa*, intestinal microparasites that can cause coccidiosis (Rommel et al. 2000), *Capillaria caudinflata*, a helminth known to cause capillariasis in Icelandic ptarmigan (Kloster 1923), *Trichostrongylus tenuis*, a helminth known to cause trichostrongylosis in grouse (also known as grouse disease) (Atkinson et al. 2008, Hudson 1986), *Metamicrolichus islandicus*, a skin mite that can cause mange (pers. obs.), and *Amyrsidea lagopi*, an amblyceran chewing louse that can cause feather damage (Stenkewitz et al. in press). The Anderson and May model (Anderson and May 1978, May and Anderson 1978) suggests that time delays in parasite abundance in relation to host population size, reduced aggregation of parasites during periods of high abundance, and the influence of parasites on host mortality and fecundity are the three destabilizing qualities of parasite-host dynamics. So, if the parasite community or any of the parasites of the rock ptarmigan are

of importance, we expect the prevalence of a species to track host density, but with a time-lag, be least aggregated during the parasite's peak of prevalence, and show a direct relation with the host's body condition, fecundity, and/or mortality.

Methods

Study Area

The study area is in northeast Iceland centred on Lake Mývatn (65°40' N 17°00' W). The general topography is flat with rolling hills rising from the coast to 400–500 m above sea level at the southern border, 70 km inland. This relief is broken by isolated mountains, the highest being Bláfjall, 1222 m above sea level. Two major glacial rivers border the study area, Skjálfandafljót in the west and Jökulsá á Fjöllum in the east. Heath vegetation characterizes the xeric uplands. Important heath plants include dwarf shrubs such as *Betula nana* and *Salix phylicifolia*, and many species belonging to the heather family (Ericaceae) including *Empetrum nigrum*. Also important are various species of grasses (Poaceae), sedges (Carex), mosses, and lichens. In summer the ptarmigan is common on heath and grassland habitats. Winter habitats include alpine areas, rough lava fields and *Betula pubescens* shrubs.

Ptarmigan Body Condition and Parasites

Ptarmigan for Parasite Analyses

Birds used for this analysis were collected specifically for a long-term study on the relation between ptarmigan population change and ptarmigan's health related parameters (i.e., Skirnisson et al. 2012, Stenkewitz et al. 2015) that has been authorised by the Icelandic Institute of Natural History under law 64/1994, chapter 4, article 7 (http://www.althingi.is/lagas/140a/1994064.html). To do all the sampling and analysis required for the study at large it was necessary to sacrifice birds. But it should be noted that the ptarmigan is very common in Iceland and a popular game bird and since 1995 between 40 and 160 thousand birds have been shot every year (http://www.ust.is).

The birds were collected by experienced hunters using shotguns in moorlands, lava fields and alpine areas west, east, and north of Lake Mývatn in the 1st week of October, 2006–2012. We chose the first week of October as the reference point to: (a) account for seasonal changes in parasite measures and size of anatomical and physiological features of ptarmigan (Atkinson et al. 2008, Bicudo et al. 2010, Thórarinsdóttir et al. 2010); and (b) sample the ptarmigan population at the start of winter as winter survival defines population change (Garðarsson 1988, Magnússon et al. 2004). Ptarmigan are free-flying wild birds and hunters could not select individuals at random. Birds were collected by conventional walk-up hunting where they were shot sitting or flying when encountered. Hunters tagged

each bird immediately after collection, and to avoid cross-contamination it was wrapped in absorbent paper and placed in a paper bag. Each bag was sealed by interfolding and stapling. Birds were cooled to 4°C and dissected within 3 days of collection.

The annual goal was to sample 100 birds, 40 adults and 60 juveniles. This was achieved in most years for juveniles (2006 60, 2007 60, 2008 57, 2009 59, 2010 60, 2011 60, 2012 60), but not adults (2006 31, 2007 20, 2008 25, 2009 19, 2010 40, 2011 41, 2012 40). We analyzed all adults caught each year, but juveniles were shot in excess and we selected individuals from those at random, but kept the sex ratio equal.

Age Identification

We assigned the age of each bird based on pigmentation of the primaries (Weeden and Watson 1967) and in the laboratory this was confirmed during necropsy by inspecting for presence (juvenile) or absence (adult) of the bursa of Fabricius. We recognized two age classes: juveniles (about 3 months of age) and adults (about 15 months or older).

Body Condition

We calculated a body condition index by regressing body mass on body size and using the residuals as the index. For body size, we took six external and internal morphometric measurements for each bird: (a) wing length, measured with a ruler from the carpal joint to the tip of the flattened and straightened wing to the nearest mm; (b) head + bill length, measured with calipers from the hindmost point of the head to the tip of the bill to the nearest 0.1 mm; (c) tarsus length, measured with calipers from the joint between tarsus and toes to the intertarsal joint to the nearest 0.1 mm; (d) tarsus and mid-toe length, measured with a ruler from the joint to the base of the central claw to the nearest mm; (e) sternum length, measured with calipers from the tip of the *Spina externa* along the center line to the *Margo caudalis* to the nearest 0.1 mm; and (f) sternum-coracoid length, measured with calipers from the center line of the *Margo caudalis* to the cranial end of the *Coracoideum* to the nearest 0.1 mm (anatomical terms follow (Baumel 1979). These six body measures (a–f) were highly correlated with each other. Factor 1 from a principle component analysis (PCA) was used as an index of body size. This Factor explained 61.4% of the variance in the original variables and was highly related to them (loadings: wing = 0.831; head + bill = 0.833; tarsus = 0.528; tarsus + mid-toe = 0.647; sternum = 0.891; and sternum-coracoid = 0.899).

Collection and Quantification of Ectoparasites

We collected and quantified species of one hippoboscid (*Ornithomya chloropus*), three mallophagans (*Goniodes lagopi*, *Lagopoecus affinis*, *Amyrsidea lagopi*), one flea (*Ceratophyllus garei*), four astigmatan (*Tetraolichus lagopi*, *Strelkoviacarus holoaspis*, *Metamicrolichus islandicus*, *Myialges borealis*) and one prostigmatan (*Mironovia lagopus*) mite/s using procedures described by (Skirnisson et al. 2012). Mallophagans and

mites were embedded in Hoyer's medium (Anderson 1954) for later identification based on (Timmermann 1950) (*G. lagopi*, *L. affinis*), (Scharf and Price 1983) (*A. lagopi*), (Mironov et al. 2010) (Astigmata), and (Bochkov and Skirnisson 2011) (*M. lagopus*). *O. chloropus* was identified following (Theodor and Olroyd 1964).

Scoring was used to quantify the abundance of the quill mite *M. lagopus*. We examined quills of seven feathers – the upper-wing primary coverts 4 and 5 and secondary flight feathers 3–7 (numbered distal to proximal). Each feather was scored: 0 = no mites, 1 ≤ 10 mites present, and 2 > 10 mites present. Scores were summed to derive a value for each individual.

Collection and Quantification of Endoparasites

We removed the lower gastrointestinal tract. The small intestine and large intestine were separated from the ceca, placed in a zip lock plastic bag, and stored at -20°C. Fecal material (1–2 g) was taken from the large intestine prior to freezing, or, if the large intestine was empty, the posterior part of the small intestine. The modified McMaster procedure described in (Skirnisson et al. 2012) was applied to obtain quantitative values of oocysts of *Eimeria muta* and *E. rjupa*, and their identification was based on (Skirnisson and Thorarinsdottir 2007). *Blastocystis* sp. were found, but not quantified.

The small intestine and ceca were examined for the presence of helminths (*Capillaria caudinflata*, *T. tenuis*, *Passerilepis serpentulus*) following (Skirnisson et al. 2012), and identified following (Madsen 1945, Wehr 1971, McDonald 1974) for the nematodes *C. caudinflata* and *T. tenuis*, and Alexander Galkin at the Russian Academy of Sciences, St. Petersburg for the cestode *P. serpentulus*.

Parasite Measures

We examined the parasite community (i.e., all parasite species known for the Icelandic rock ptarmigan except *Blastocystis* sp. and *Mesocestoides canislagopodis*) for adult and juvenile hosts in all years of the study. For this, we used a comparative value for each bird consisting of the ranked parasite data where 1 was allotted to the lowest positive finding and midranks were used for ties (Holmstad et al. 2005a). The ranked values of each parasite species were summed depicting the abundance for endoparasites, ectoparasites, and all parasites for each bird. We further used parasite richness, the mean of the total number of parasite species of an individual host in each age group (Bush et al. 1997).

For the individual parasite species we used parasite prevalence and aggregation. Parasite prevalence was defined as the proportion of birds infected by a particular parasite species (Bush et al. 1997). Parasite aggregation was illustrated by a measure that applies to the right skewed parasite distributions, the Discrepancy index *D* (Poulin 1993). This is a

dimensionless index that ranges between 0 and 1; the distribution becomes more aggregated as the value approaches 1.

Ptarmigan Population and Demographics

We collected three sets of population data: (1) spring densities of territorial males, (2) age ratios in spring, and (3) age ratios in late summer. From those, measures of fecundity and mortality were derived.

Ptarmigan Spring Densities

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). The locations of territorial males as well as ptarmigan kills were plotted on a map. A "kill" was the remains of a ptarmigan killed and eaten after arrival on the census plot in spring. The main cause of death was predation by gyrfalcon (84 %) (Nielsen 1986). The "freshness" of the kill was based on the state of the feathers. The total number of males in spring is composed of the sum of the number of territorial males censused and killed. Not all kills could be sexed, so to estimate the proportion of males we used the sex ratio of ptarmigan killed by gyrfalcons in spring on the study area (73 % males) (Nielsen 1996, Nielsen et al. 2004) provides a detailed description of the census plots and methods. The ptarmigan population abundance index used was the annual mean density of males on these six plots and covers the years 2004–2013.

Age Ratios in Spring

Fully grown ptarmigan were aged based on pigmentation of the primaries (Weeden and Watson 1967). Two age classes were recognized, first year birds (juveniles = juv) and older birds (adults = ad). Spring samples for aging were birds found dead (mostly killed by gyrfalcons), birds trapped for banding or birds photographed while flying using high speed cameras.

Age Ratios in Late Summer (Fecundity)

In the last week of July and the first week of August we searched actively on foot for ptarmigan. We distinguished between adults (males and females) and chicks according to size, color, and sound. The age ratio was calculated using total number of females observed and assuming that half of the chicks were females. This ratio was used as a measure of fecundity.

Mortality Rates

Mortality rates were calculated according to (Magnússon et al. 2004). For these calculations, a year is defined starting on 1st May and ending 30th April. Two mortality rates are recognized: (1) Z_2 or apparent adult mortality rate; (2) $Z_{X,W}$ or juvenile excess mortality (mortality that juveniles suffer in excess to adults).

The population abundance index and spring age ratios were used to estimate the Z_2 mortality rate, assuming that spring abundance was proportional to the total number of birds in the study area. It was assumed that any bird alive at the end of winter was either in its second-year or older at the end of the following winter, provided it survived. So, adult mortality from spring to spring was calculated as:

$$\hat{Z}_2^t = \ln(Y^{t-1}) - \ln(Y^t) - \ln(\hat{p}_2^t)$$

where

Y^t = spring abundance index year t
Y^{t-1} = spring abundance index year $t-1$
$\hat{p}_2^t$ = fraction of adult birds in spring year t

The $Z_{X,W}$ mortality rate describes mortality that first year birds suffer from 1 August to 30 April in excess to adult mortality. The age ratios in late summer and at the end of the following winter were used to estimate excess juvenile mortality as:

$$\hat{Z}_{X,W}^t = ln\left(\frac{\hat{p}_1^{t,s}}{\hat{p}_2^{t,s}}\right) - ln\left(\frac{\hat{p}_1^t}{\hat{p}_2^t}\right)$$

where

$\hat{p}_1^{t,s}$ = fraction of juvenile birds late summer
$\hat{p}_1^t$ = fraction of juvenile birds at end of winter
$\hat{p}_2^{t,s}$ = fraction of adult birds late summer
$\hat{p}_2^t$ = fraction of adult birds at end of winter

Juveniles share Z_2 with the adults or at least a rate that shows the same trend (Nielsen et al. 2004). Accordingly, the total mortality rate of juveniles was approximated as the sum of the Z_2 and the $Z_{X,W}$ rates.

Statistical Analysis

We calculated annual prevalence and confidence intervals and discrepancy indices for each parasite species using the software QP web (Reiczigel and Rózsa 2013). All other statistical analyses were performed using the software package R (R Core Team 2014). Tests were two-tailed and statistical significance was set at $p \leq 0.05$.

We used generalized linear models (GLMs) to assess the relationship between body condition (response variables) and parasite measures (explanatory variables) of individual birds. Gaussian family with identity link was specified to examine parasite richness and abundance of all parasites, ectoparasites, and endoparasites. Binomial family with logit link was specified to examine prevalence of the individual parasite species. Alpha levels ($p \leq 0.05$) were adjusted using Holm–Bonferroni corrections.

We used linear regression models to test whether and how trajectories of ptarmigan mortality, fecundity, and population density (response variables) are related with parasite measures (explanatory variables). For density, parasite measures were related with current year ptarmigan densities. The time lag was estimated by fitting regressions with different time lags. The degrees of freedom, n-3, were calculated taking into account the estimation of the time lag in addition to the slope and the intercept. Because ptarmigan density measures are from spring and parasite measures from autumn, there is a 0.5 year time difference between current year parasite numbers and ptarmigan densities, a 1.5 year difference with densities 1 calendar year ago, and a 2.5 year difference with densities 2 calendar years ago. For all models, each age group was examined individually.

Results

Ptarmigan Demographics

Population Density

There were peaks in ptarmigan numbers in 2005 (8.1 cocks/ km²) and 2010 (7.9 cocks/ km²), and lows in 2007 (4.0 cocks/ km²) and 2012 (3.5 cocks/ km²) (Figure Ⅲ.1). During the tenure of our parasite study, the ptarmigan population increased for 4 years and decreased for 3 years (Figure Ⅲ.1).

Body condition

Adults were in a better condition than juveniles, but the trajectories showed the same pattern, rising to a peak in 2009, falling sharply in 2010, and improving slightly in 2011 and 2012 (Figure Ⅲ.1).

Mortality Rates

The Z_2 mortality rate changed in a regular fashion; it was high at the start of the study in 2005/2006, decreased to 2007/2008, increased to a peak in 2009/2010, and decreased again (Table III.1). The $Z_{X,W}$ mortality rate fluctuated in an irregular fashion over the course of the study (Table III.1).

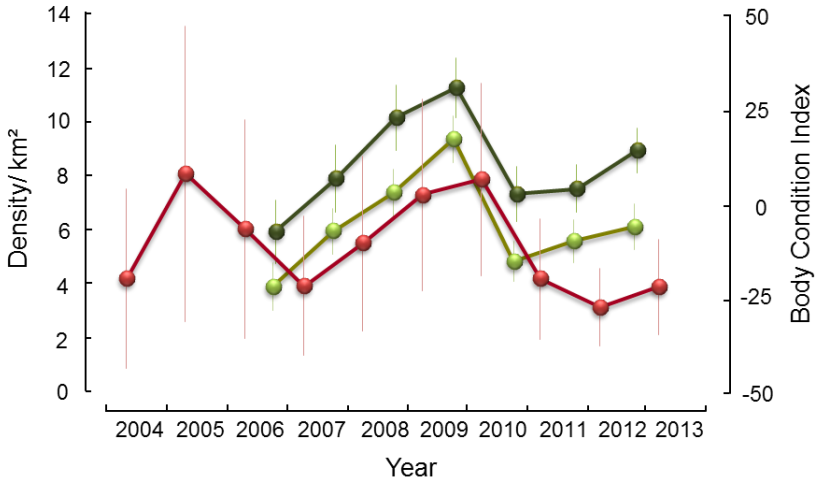

Figure III.1 *Red line: Mean population densities (± 95 % confidence intervals) of male rock ptarmigan on 6 census plots from spring 2004–2013 in northeast Iceland. Green lines: Body condition indices (± 95 % confidence intervals) of juvenile (lighter green) and adult (darker green) ptarmigan from autumn 2006–2012 in northeast Iceland.*

Table III.1 *Mortality rates of rock ptarmigan in northeast Iceland, 2006–2012. Z_2 = Annual mortality rate of adults; $Z_{X,W}$ = Juvenile excess winter mortality; $Z_2 + Z_{X,W}$ = Annual mortality rate of juveniles*

Year	Mortality rates		
	Z_2	$Z_{X,W}$	$Z_2 + Z_{X,W}$
2006/2007	1.29	0.87	2.16
2007/2008	0.77	0.61	1.38
2008/2009	0.47	1.11	1.58
2009/2010	1.08	0.44	1.52
2010/2011	1.40	1.00	2.40
2011/2012	0.92	0.89	1.81
2012/2013	0.84	0.84	1.68

Fecundity

Fecundity was high all years except in 2011 (Figure III.2B, Table III.2).

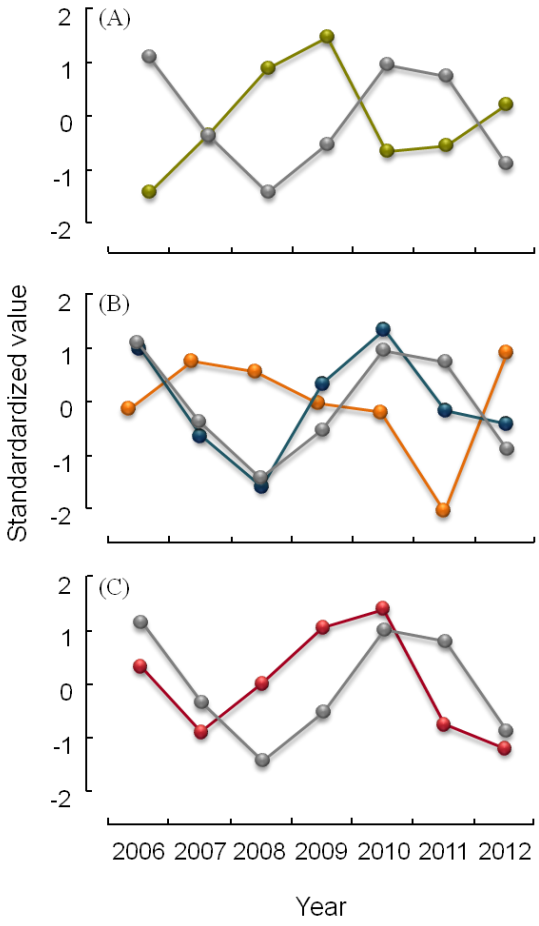

Figure III.2 *Trajectories of* Eimeria muta *prevalence (grey line) and (A) body condition (green line) of adult rock ptarmigan, (B) adult mortality rate Z_2 (blue line) and fecundity (orange line), and (C) ptarmigan population density (red line) in northeast Iceland, 2006–2012. Values are standardized to (X-μ)/σ.*

Table III.2 *Age ratios of rock ptarmigan in northeast Iceland, 2006–2013. Late summer age ratio is equivalent to fecundity.*

Year	**Age ratios**	
	Spring (n)	Late summer (n)
2006		0.77 (367)
2007	0.57 (163)	0.79 (318)
2008	0.67 (162)	0.79 (511)
2009	0.55 (155)	0.77 (631)
2010	0.68 (262)	0.76 (550)
2011	0.54 (275)	0.71 (246)
2012	0.49 (292)	0.80 (366)
2013	0.63 (251)	

Parasites

We examined 631 ptarmigan – 416 juveniles and 215 adults of which 630 (99.7%) had at least one parasite species. The two parasite-free birds were adult males. There were 616 birds (98 %) infested with ectoparasites and 536 (85 %) infected with endoparasites. Of those, 572 birds (91 %) carried mites, 509 (81 %) mallophagans, 505 (80 %) coccidians, 245 (39 %) hippoboscids, 201 (32 %) helminths, and 2 (0.3 %) fleas. From the six chosen pathogenic parasite species, *E. muta* was most prevalent (78 %), followed by *C. caudinflata* (29 %), *M. islandicus* (23 %), *E. rjupa* (15 %), *A. lagopi* (13 %), and *T. tenuis* (4 %).

Combined parasite community

Juveniles carried more parasite species and ectoparasites than adults, but endoparasite numbers were overall similar in both age groups (Figure Ⅲ.3A). Parasite trajectories fluctuated over the years of this study, but were particularly distinct for endoparasites with peaks in 2010 and descents from 2006 to 2008/2009 and from 2010 to 2012 in both age groups (Figure Ⅲ.3A).

Individual parasite species

More juveniles than adults carried *E. muta*, *E. rjupa*, *M. islandicus*, and *A. lagopi*, but *C. caudinflata* and *T. tenuis* tended to be more prevalent in adults (Figure Ⅲ.3B). *E. muta* and *E. rjupa* trajectories fluctuated similarly, with peaks in 2010/11 and lows in 2007/08 for both age groups (Figure Ⅲ.3B). Prevalence of *M. islandicus* in juveniles decreased from 2006 to 2012 interspersed with a peak year in 2007 and a bottom year in 2009 in adults (Figure Ⅲ.3B). Prevalences of *C. caudinflata* and *A. lagopi* went up and down in every year of this study (Figure Ⅲ.3B).

The parasite species were highly aggregated, and the aggregation index for the different parasite species except for *E. muta* changed little over the years of this study (Figure Ⅲ.3C). The aggregation index of *E. muta* in juveniles peaked in 2007, reached a low in 2010, and then increased again (Figure Ⅲ.3C).

Parasites and Ptarmigan Demographics

Population Density

Endoparasites and in particular *E. muta* prevalence showed a significant positive relationship with ptarmigan population density in both age groups. *E. muta* aggregation in juveniles showed a significant inverse relationship with density. The best fit provided the model considering a time lag of 1 year (Table Ⅲ.3). That is, endoparasite abundance and *E. muta* prevalence peaked and *E. muta* aggregation was lowest 1.5 years after the peak in

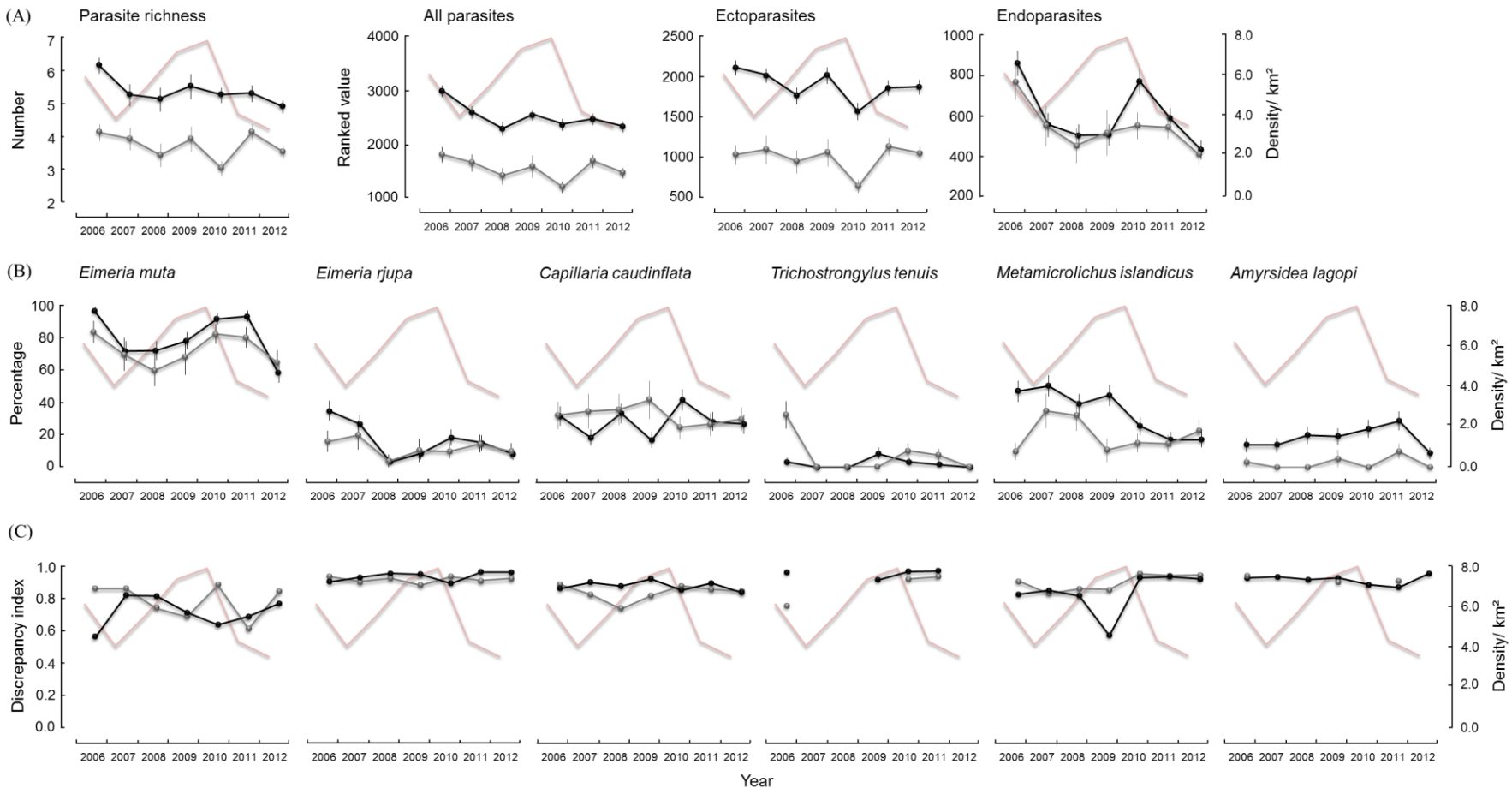

Figure III.3 *(A) Parasite species richness (± SE) and ranks (± SE) for all parasites, ectoparasites, and endoparasites, (B) prevalence (± SE) and (C) aggregation of selected pathogenic parasite species of juvenile (black line) and adult (grey line) rock ptarmigan in northeast Iceland, 2006–2012. Rosy line in background represents ptarmigan population density.*

ptarmigan numbers (Figure Ⅱ.2, Ⅲ.3A). Surprisingly, *T. tenuis* prevalence in juveniles showed a significant negative relationship with ptarmigan population density, a 2 year time lag fitted best, but prevalence for this species was very low (Table Ⅲ.3).

Body Condition

Body condition of adults was significantly negatively related with parasite richness, parasite abundance, and prevalence of *E. muta* and *T. tenuis*, but positively with *C. caudinflata* prevalence (Table Ⅲ.4). Body condition of juveniles was significantly related with parasite richness, parasite abundance, and all selected pathogenic parasite species except *T. tenuis* (Table Ⅲ.5).

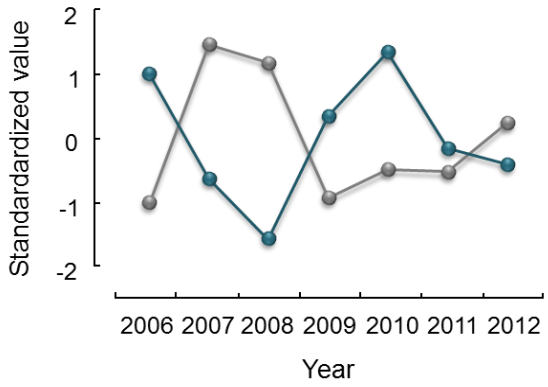

Figure III.4 *Trajectories of mortality Z_2 (blue line) and* Metamicrolichus islandicus *prevalence (grey line) of adult rock ptarmigan in northeast Iceland, 2006–2012. Values are standardized to (X-μ)/σ.*

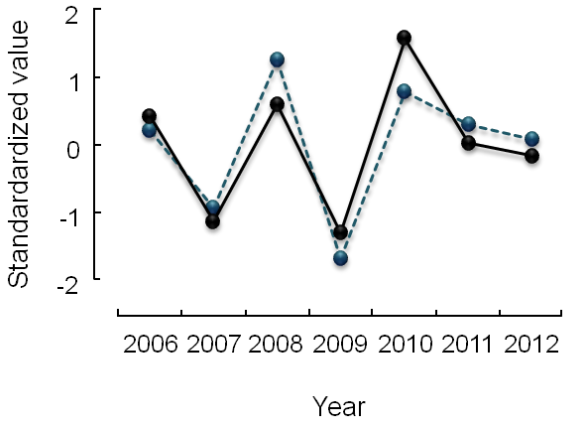

Figure III.5 *Trajectories of excess winter mortality $Z_{X,W}$ (blue dashed line) and* Capillaria caudinflata *prevalence (black continuous line) of juvenile rock ptarmigan in northeast Iceland, 2006–2012. Values are standardized to (X-μ)/σ.*

Mortality Rates

Annual adult mortality was significantly positively related with prevalence of *E. muta* and negatively with *M. islandicus* (Figure Ⅲ.4, Table Ⅲ.4). Annual juvenile mortality was significantly positively related with endoparasites and *C. caudinflata* prevalence, and marginally with *E. muta* prevalence (Table Ⅲ.5). Excess juvenile winter mortality was significantly positively related with *C. caudinflata* prevalence (Figure Ⅲ.5, Table Ⅲ.5).

Fecundity

Fecundity was significantly positively related with prevalence of *A. lagopi* in both age groups and marginally with *E. muta* prevalence in juvenile birds (Figure Ⅲ.6, Table Ⅲ.4, Ⅲ.5).

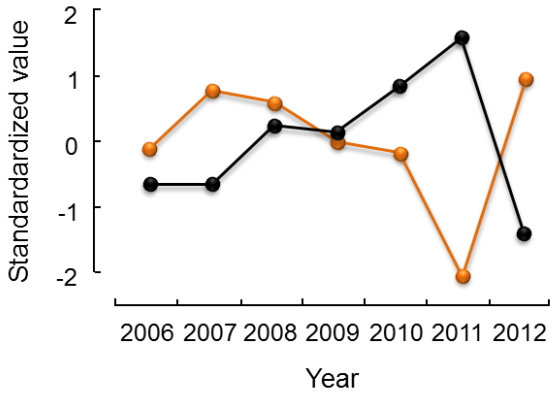

Figure III.6 *Trajectories of fecundity (orange line) and* Amyrsidea lagopi *prevalence (black line) of juvenile rock ptarmigan in northeast Iceland, 2006–2012. Values are standardized to (X-μ)/σ.*

Discussion

The Anderson and May model (Anderson and May 1978, May and Anderson 1978) identified low aggregation of parasites within the host population, parasite-induced host mortality and reduction in host reproductive potential, respectively, as well as time delays in parasite reproduction and transmission as the major regulating or destabilizing qualities that parasites can have on host population dynamics. Our results indicate that the eimerid *E. muta* parasitizing rock ptarmigan in Iceland fulfils all of these conditions. Aggregation levels of *E. muta* fluctuate inversely with its prevalence, with low aggregation at peak prevalence and vice versa, and both prevalence and aggregation track ptarmigan density with a 1.5 year time lag, respectively. Further, *E. muta* is associated with poorer body condition, increased mortality, and reduced fecundity (Figure Ⅲ.2). For red grouse in Scotland, coupled parasite-host cycles have been described and tested experimentally

Table III.3 *Results from linear regression models between spring densities (2004–2012) and selected pathogenic parasites (2006–2012) of adult and juvenile rock ptarmigan in northeast Iceland. Density and parasite trajectories were regressed without (t) and with time lag, shifting the parasite trajectories 1 (t-1) and 2 (t-2) years back in time. Best fits are shown.*

Measure	**Parasite species**	**Adult ptarmigan**					**Juvenile ptarmigan**				
		Time lag	Intercept	Slope	R^2	p	Time lag	Intercept	Slope	R^2	p
Parasite richness		t-1	0.54	1.53	0.38	0.415	t-2	22.28	-3.01	-0.71	0.086
All parasites		t	10.43	-3.2×10^{-3}	-0.38	0.411	t-1	-4.47	4.3×10^{-3}	0.62	0.154
Ectoparasites		t	12.43	-6.9×10^{-3}	-0.68	0.109	t	10.51	-2.6×10^{-3}	-0.28	0.545
Endoparasites		t-1	-0.14	1.1×10^{-2}	0.80	**0.041**	t-1	0.94	8.7×10^{-3}	0.81	**0.036**
Prevalence	*Eimeria muta*	t-1	-6.43	0.17	0.97	**0.001**	t-1	-2.46	0.11	0.91	**0.007**
	Eimeria rjupa	t-1	3.83	0.19	0.60	0.165	t-1	4.38	0.11	0.74	0.070
	Capillaria caudinflata	t-1	10.59	-0.14	-0.47	0.295	t	3.55	7.1×10^{-2}	0.36	0.434
	Trichostrongylus tenuis	t-1	5.48	0.10	0.72	0.079	t-2	7.25	-0.44	-0.81	**0.038**
	Metamicrolichus islandicus	t-2	4.00	0.11	0.68	0.109	t-2	7.88	-4.9×10^{-2}	-0.42	0.358
	Amyrsidea lagopi	t-1	5.60	0.23	0.52	0.245	t-1	4.21	0.11	0.45	0.319
Aggregation	*Eimeria muta*	t	4.48	1.34	8.3×10^{-2}	0.862	t-1	16.43	-14.12	-0.79	**0.043**

Table III.4 *Results from linear regression models between trajectories of parasite measures of pathogenic species and body condition indices, annual adult mortality (Z_2), and brood size of adult rock ptarmigan in northeast Iceland, 2006–2012. * adjusted using Holm-Bonferroni corrections*

Parasite measure	**Body Condition Index**		**Annual Mortality (Z_2)**				**Fecundity**			
	t value	p	Intercept	Slope	R^2	p	Intercept	Slope	R^2	p
Parasite richness	3.00	< **0.001***	1.10	3.6×10^{-2}	2.1×10^{-3}	0.922	0.87	-2.8×10^{-2}	1.5×10^{-2}	0.397
All parasites	2.82	< **0.001***	0.00	-3.6×10^{-5}	5.3×10^{-4}	0.961	0.83	-4.0×10^{-5}	7.0×10^{-2}	0.567
Ectoparasites	2.71	< **0.001***	1.84	-8.8×10^{-4}	0.21	0.306	0.79	-2.2×10^{-5}	1.4×10^{-2}	0.797
Endoparasites	-2.36	< **0.001***	0.04	1.7×10^{-3}	0.38	0.141	0.81	-7.8×10^{-5}	8.6×10^{-2}	0.523
Parasite species										
Eimeria muta	-2.90	< **0.001***	-1.08	2.8×10^{-2}	0.68	**0.022**	0.92	-2.0×10^{-3}	0.40	0.129
Eimeria rjupa	-1.09	0.293	0.76	1.7×10^{-2}	8.1×10^{-2}	0.537	0.78	-1.1×10^{-3}	3.4×10^{-2}	0.693
Capillaria caudinflata	1.54	**0.024***	1.58	-1.9×10^{-2}	0.12	0.447	0.70	2.1×10^{-3}	0.17	0.361
Trichostrongylus tenuis	-1.91	**0.024***	0.85	1.7×10^{-2}	0.40	0.125	0.77	-7.2×10^{-4}	7.8×10^{-2}	0.543
Metamicrolichus islandicus	1.03	0.368	1.46	-2.5×10^{-2}	0.64	**0.032**	0.74	1.7×10^{-3}	0.31	0.196
Amyrsidea lagopi	1.14	0.267	0.93	1.4×10^{-2}	2.6×10^{-2}	0.730	0.79	-7.1×10^{-3}	0.79	**0.008**

Table III.5 *Results from linear regression models between trajectories of parasite measures of pathogenic species and body condition indices, annual juvenile mortality ($Z_2 + Z_{X,W}$), juvenile excess winter mortality ($Z_{X,W}$), and brood size of juvenile rock ptarmigan in northeast Iceland, 2006–2012.*

	Body Condition Index		**Mortality ($Z_2 + Z_{X,W}$)**			
Parasite measure	t value	p	Intercept	Slope	R^2	p
Parasite richness	-3.84	< **0.001***	-7.1×10^{-2}	0.35	0.14	0.405
All parasites	-3.68	< **0.001***	0.98	3.3×10^{-4}	4.6×10^{-2}	0.645
Ectoparasites	3.63	< **0.001***	3.40	-8.5×10^{-4}	0.18	0.342
Endoparasites	-3.19	< **0.001***	0.62	1.9×10^{-3}	0.68	**0.022**
Parasite species						
Eimeria muta	-3.88	< **0.001***	0.35	1.8×10^{-2}	0.48	0.084
Eimeria rjupa	-1.70	**0.015***	1.58	1.3×10^{-2}	0.15	0.392
Capillaria caudinflata	-1.93	< **0.001***	0.80	3.5×10^{-2}	0.68	**0.022**
Trichostrongylus tenuis	-1.34	0.125	1.75	2.1×10^{-2}	1.7×10^{-2}	0.758
Metamicrolichus islandicus	2.07	< **0.001***	2.05	-7.8×10^{-3}	9.1×10^{-2}	0.510
Amyrsidea lagopi	2.41	< **0.001***	1.51	1.6×10^{-2}	8.2×10^{-2}	0.534

	Excess Winter Mortality ($Z_{X,W}$)				**Fecundity**			
Parasite measure	Intercept	Slope	R^2	p	Intercept	Slope	R^2	p
Parasite richness	1.36	-0.10	3.0×10^{-2}	0.709	0.87	-2.0×10^{-2}	6.4×10^{-2}	0.583
All parasites	1.55	-2.9×10^{-4}	0.10	0.499	0.81	-1.6×10^{-5}	1.6×10^{-2}	0.788
Ectoparasites	2.32	-7.9×10^{-4}	0.40	0.125	0.74	1.5×10^{-5}	8.5×10^{-3}	0.844
Endoparasites	0.59	3.9×10^{-4}	7.0×10^{-2}	0.565	0.80	-5.9×10^{-5}	9.1×10^{-2}	0.510
Parasite species								
E. muta	0.58	3.0×10^{-3}	3.4×10^{-2}	0.691	0.90	-1.6×10^{-3}	0.54	0.059
E. rjupa	0.86	-2.5×10^{-3}	1.5×10^{-2}	0.792	0.77	-2.7×10^{-4}	9.9×10^{-3}	0.832
C. caudinflata	0.17	2.3×10^{-2}	0.78	**0.009**	0.79	6.1×10^{-4}	3.0×10^{-2}	0.712
T. tenuis	0.92	-4.2×10^{-2}	0.33	0.181	0.77	-2.4×10^{-3}	5.8×10^{-2}	0.603
M. islandicus	1.06	-6.8×10^{-3}	0.19	0.335	0.74	8.4×10^{-4}	0.16	0.380
A. lagopi	0.67	8.7×10^{-3}	6.6×10^{-2}	0.577	0.83	-3.7×10^{-3}	0.68	**0.023**

(Dobson and Hudson 1992, Martínez-Padilla et al. 2014). In this grouse population exhibiting 4–8 year cycles, *Trichostrongylus tenuis* reduced fecundity and survival and there was a density dependent relationship between grouse numbers in one year and worm burdens in the subsequent year (Dobson and Hudson 1992). The fairly low levels of parasite aggregation observed in this system increased the tendency of the system to oscillate (Dobson and Hudson 1992). Alternatively, ptarmigan body condition after the peak in abundance nosedives for other reasons than parasites making the birds more susceptible to parasitism. Here, the chicken versus the egg question arises: are ptarmigan in poor body condition more susceptible to *Eimeria* or does the parasite cause ptarmigan to be in poor body condition? The Anderson-May model suggests for parasites to have a regulating effect on host numbers, it needs the parasite to affect the host which is what our data implies for *E. muta*. However, our study is correlational and so we do not know if *E. muta* is sufficiently virulent in itself or if it becomes virulent only or increasingly when the system is already enfeebled due to other factors, or possibly due to the combined parasite community. Parasite richness, the overall parasite community, and majority of chosen pathogenic parasites were all correlated with ptarmigan condition directly (Table Ⅲ.4, Ⅲ.5).

Whatever the initial trigger may be, our data implies that there is a strong relation between ptarmigan condition, population density, and particularly the eimerid *E. muta*.

Ptarmigan eimerids have a direct life cycle with oocysts shed in feces, sporulation in the environment, and infection through ingestion. The oocysts are present in the feces year round, but prevalence of *E. muta* peak between October and January (Thórarinsdóttir et al. 2010). Eimerids generally are host specific (Pellérdy 1974) and we assume *E. muta* (and also *Eimeria rjupa*) will not persist in species other than rock ptarmigan. We know the prepatent period of *Eimeria* varies between 4 and 6 days with a peak in oocyst shedding within 10 days (Herrick and Ott 1936, Rommel et al. 2000). Thus, oocysts shed by ptarmigan in the first week of October are caused by infections occurring by mid September when the ptarmigan are moving to autumn habitats in alpine areas. Host density-dependent shedding of oocysts and their subsequent persistence in the environment from one year to the next could be the reason for the observed time-lag between ptarmigan numbers and *E. muta* prevalence. Ptarmigan hatched in the two years succeeding the peak in their numbers should be exposed to the maximum number of infective oocysts in the environment. Environmental persistence is well known for *Eimeria*, infective oocysts of some species can survive up to 602 days in soil (Fahr and Wehr 1949), stand repeated freeze and thaw cycles Landers (1953), and this life history characteristic is sufficient to maintain eimerid populations (Fuller et al. 2012). Life history characteristics of parasites including the time needed for helminth larval stages to grow to maturity after infection and arrested development of the helminth larvae, have been given as explanations for time lags between host and parasite populations in similar systems (Dobson and Hudson 1992, Newey et al. 2005).

In addition to the severalfold relationship between population parameters and *E. muta*, we found a close relationship between juvenile excess winter mortality and annual juvenile mortality (a measure that partly consists of excess winter mortality) as well as *C. caudinflata* prevalence (Figure Ⅲ.5). *Capillaria* species are known to cause severe symptoms such as diarrhoea, weakness, weight loss, and a drop in egg production (capillariasis) (Atkinson et al. 2008). *C. caudinflata* has an indirect life-cycle with earthworms as intermediate host (Morehouse 1942). Ptarmigan chicks have a mixed diet of plants and invertebrates such as earthworms, but adult birds eat mainly plants (Garðarsson 1971). It is of interest that adult birds in our sample show *C. caudinflata* infections. The life span of *C. caudinflata* is c. 10 months (Olsen 1974). This suggests that some of the adults could be carrying infections acquired as juveniles, but high prevalence among adults suggests that also members of this cohort get infected. In Icelandic ptarmigan, prevalence of *C. caudinflata* eggs in feces peaks in October and January (Thórarinsdóttir et al. 2010), suggesting peaks of intestinal worm burden and/or worm reproduction during these times of the year. There is an approximate four-month time difference between ptarmigan hatch and the first peak in *C. caudinflata* egg shedding in October. The data suggest that

juveniles suffer more from *C. caudinflata* infections than adults, i.e. the relationship with the mortality rates; *C. caudinflata* infections seem to be one of the drivers of the $Z_{X,W}$ rate (mortality in August through April). That juveniles suffer more from *C. caudinflata* infections than adults may have to do with varying levels of immune function to resist or treat infections (Stenkewitz et al. 2015).

The reverse relation between fecundity and the amblyceran chewing louse *Amyrsidea lagopi* prevalence is of interest (Figure III.6). It is well known that feather lice can be severely damaging to their host (summaries of various studies in Clayton et al. 2015), including by reducing fecundity (DeVaney 1976, Clayton 1990, Moreno-Rueda and Hoi 2012). The amblyceran mallophagan *Menacanthus stramineus* in high intensity, for instance, was related with reduced egg production (Watson 1965) . Contrary in other studies, controlled experiments did not show any effects of lice on reproductive success of swifts *Apus apus* and rock doves *Columba livia* (Clayton and Tompkins 1995, Tompkins et al. 1996). In Icelandic ptarmigan, *A. lagopi* is strongly associated with the creation of feather holes (Stenkewitz et al. Forthcoming). If this association happens through trade-offs between host reproduction and self-maintenance or for other reasons needs to be tested experimentally. A study on collared flycatchers *Ficedula albicollis* showed that feather wear of parents are traded-off by parental activity, and that the degree of feather wear was associated with survival of the flycatchers (Merilä and Hemborg 2000).

The reverse relation between adult mortality and prevalence of *Metamicrolichus islandicus* is peculiar. When mortality is high, then fewer birds in the population are infested with this parasite that can cause mange. We do not have an explanation for this.

The helminth *Trichostrongylus tenuis* is a pathogenic nematode that was associated with reduced body condition in willow ptarmigan in Norway (Holmstad et al. 2005a) and has been shown to be the determinant of the red grouse cycle (Martínez-Padilla et al. 2014). In our study, this nematode occurred in such low numbers ($\leq$ 28 worms) that it seems improbable that this parasite could have caused serious harm (Hudson 1986). Yet, this parasite did show an inverse relation with body condition in adult ptarmigan and the 1.5 year time lag is near significant for both age groups.

The combined parasite community correlated with ptarmigan condition, but only endoparasites were also positively correlated with annual mortality in juveniles, probably mostly attributable to *E. muta*. Comparatively, though none of the parasites in Norwegian willow ptarmigan had a significant impact on their own, the parasite community was negatively related with host fitness, and this in turn was suggested to promote effects on host body mass and breeding mortality (Holmstad et al. 2005).

Population size of the main resident predator, the gyrfalcon, changes also in a delayed density dependent manner with the ptarmigan population which has been suggested to be the main driver of the ptarmigan population cycles (Nielsen 1999). So, parasitism in the

ptarmigan population may act directly and/or sublethal parasitism may act synergistically with predation by acting upon different population parameters (Morehouse 1942) or by making the ptarmigan more prone to gyrfalcon predation (Keymer and Read 1991, Thomas et al. 2010, Hughes et al. 2012).

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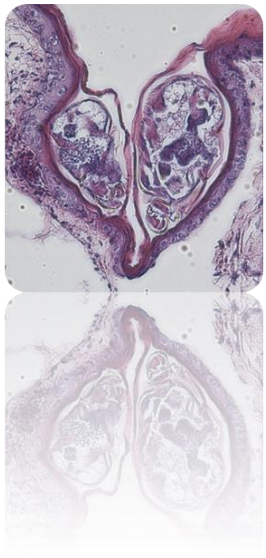
Paper IV

The parasite community of rock ptarmigan *Lagopus muta* in Iceland: Community structure and co-occurrence within the host population

Ute Stenkewitz. Manuscript.



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Introduction

Vertebrate hosts are home to multiple parasite species forming a parasite community. Parasite communities of vertebrate species have rarely been studied, and even less over extended time periods (Esch et al. 1997). Parasite assemblies can give insight into many aspects of parasite ecology such as the relationship between parasite species, host and parasites, and adaptations resulting from these intimate networks (Esch et al. 1997, Kennedy et al. 1997, Atkinson et al. 2008). In fact, one bird housing a parasite community can be envisioned as an entire ecosystem of its own. Species in a parasite community co-evolved and -adapted, and are thus prone to interrelate in some way directly or indirectly, positively or negatively with each other (Holmstad and Skorping 1998, Forbes et al. 1999, Behnke et al. 2005, Holmstad et al. 2008, Morrill et al. 2013). For instance, the presence of one parasite taxon might influence the presence and intensity of infection by another (Holmstad and Skorping 1998 in Morrill et al. 2013). That is, if one parasite species occurs in high intensity, another species may be suppressed on cost of the former (Behnke et al. 2001). Or opposite, different taxa may enhance each other‘s growth by co-occurring, with one parasite species modifying the host environment in such a way so the next species can benefit (Behnke et al. 2001). Whatever the case, while one parasite species may or may not exert any influence on its host, together they may exert a variety of influences on the individual host or on demographic parameters of a host population. Further, to secure their own survival – and through this excerting influence on whole population dynamics – parasite occurence on hosts differs according to host age and sex. For instance, ectoparasites may particularly proliferate or accumulate on incubating hens (Hudson 1986, Nordling et al. 1998, Knowles et al. 2008). Or, they build up on chicks and young birds that are most susceptible because their immune system and preening efficacy are still poorly developed (Moss and Watson 2001, Cole and Friend 1999).

Parasites of Icelandic rock ptarmigan (hereafter ptarmigan) were described (Skirnisson et al. 2012, 2016a, b) and their influence on ptarmigan population cycles investigated as part of the Ptarmigan Health Project (Stenkewitz et al. 2016) – a research program on the relationship between health related parameters of ptarmigan and population change running since 2006 (Nielsen and Skírnisson 2009). Seventeen parasite species are now known to Icelandic rock ptarmigan whereas 40 have been listed for the entire range of rock ptarmigan (Skirnisson et al. 2012). The Icelandic parasite community consists of 10 ectoparasites (five mites, three lice, one hippoboscid fly, one flea) and 7 endoparasites (one heterocontophyt, two coccidians, four helminths) (see Synopsis Table 4.1 and 4.2). Tetrathyridia of the tapeworm *Mesocestoides canislogopodis* are occasionally detected in the ptarmigan body cavity, the final host in the life cycle is the Arctic fox *Vulpes lagopus*, ptarmigan serves as second intermediate host (Skírnisson et al. 1993, 2016b). The heterocontophyt *Blastocystis* sp. is commonly found in ptarmigan, but it cannot yet be quantified with certainty. Blood parasites are lacking in

Icelandic ptarmigan (Skirnisson et al. 2012). The habitat of coccidians and helminths (other than tetrathyridia of *M. canislogopodis*) is the gastrointestinal tract; mites, lice, flies and fleas occur on/ in the skin and feathers (see Synopsis Figure 4.1 and 4.2). In the course of the present study, it has become evident that parasites are distributed unevenly between juvenile and adult, also between adult male and female hosts. Furthermore, preliminary data suggest that some mites seem to act mutually, symbiotically, or possibly even beneficiary (Proctor 2003) to ptarmigan rather than parasitic.

The purpose of this study is to (1) extend the current knowledge of the ptarmigan parasite fauna and illustrate in detail how each parasite and the parasite community is distributed in and on ptarmigan over a period of seven years, (2) investigate if and how the parameters age, sex, and year ignite variation in each parasite species and the parasite community as a whole, and (3) examine if and which parasites are associated.

Methods

Study area and ptarmigan collecting

The study area is in northeast Iceland centred on Lake Mývatn (65°40’ N 17°00’ W); flat with rolling hills rising from the coast to 400–500 m above sea level at the southern border (70 km inland). This relief is interspersed by isolated mountains, the highest being Bláfjall, 1222 m above sea level. Two major glacial rivers border the study area, Skjálfandafljót in the west and Jökulsá á Fjöllum in the east. The xeric uplands are characterized by heath vegetation. Important heath plants include dwarf shrubs such as *Betula nana* and *Salix phylicifolia*, and many species belonging to the heather family (Ericaceae) including *Empetrum nigrum*. Also important are various species of grasses (Poaceae), sedges (*Carex*), mosses, and lichens. In summer, the ptarmigan is common in heath and grassland habitats. Winter habitats include alpine areas, rough lava fields and *Betula pubescens* shrubs.

In the 1st week of October 2006 – 2012, each year c. 100 ptarmigan were collected in moorlands, lava fields and alpine areas west, east, and north of the lake. Ptarmigan used for these analyses were collected specifically for a long-term study on the relationship between ptarmigan population change and health related parameters (Skirnisson et al. 2012, Stenkewitz et al. 2015, 2016). Ptarmigan were collected outside the hunting season by a license issued by the Icelandic Institute of Natural History. Individuals were collected by conventional walk-up hunting where the birds were shot sitting or flying when encountered in areas where they gathered. Each bird collected was sealed in a paper bag to avoid cross-contamination, kept cool at 4°C, and dissected within 3 days of collection. The first week of October was chosen as reference point, amongst others, to account for seasonal changes in parasite measures (Atkinson et al. 2008, Thórarinsdóttir et al. 2010).

Ptarmigan ageing and sexing

Each bird was aged based on pigmentation of the primaries (Weeden and Watson 1967; http://utgafa.ni.is/vefur/rjupan/index.html) and sexed using both the loral stripe and the size and color of the combs (Montgomerie and Holder 2008). During necropsy, age and sex were confirmed by inspecting the gonads and presence or absence of the bursa of Fabricius. Two age classes were distinguished: adults (about 15 months or older) and juveniles (about 3 months old). Ptarmigan become mature as 1 year old (Holder and Montgomerie 1993).

Parasite collecting and quantifying

Hippoboscid flies were collected by the hunter from the fresh bird if seen and fixed in 70 % ethanol. Each bird was wrapped in absorbent paper and placed in a paper bag immediately after collection to avoid cross-contamination; the bag sealed by interfolding and stapling. Birds were cooled to 4°C and dissected within 3 days of collection. In the laboratory, each ptarmigan carcass was inspected for hippoboscids and mallophagans. Further collection and quantification of hippoboscids, mallophagans, fleas and astigmatan mites were done following procedures specified in Skirnisson et al. (2012). Mallophagans and mites were embedded in Hoyer's medium for later identification (Anderson 1954, Gaud and Atyeo 1996). The hippoboscid fly *Ornithomya chloropus* was identified based on Theodor and Oldroyd (1964), the mallophagans *Goniodes lagopi* and *Lagopoecus affinis* based on Timmermann (1950), and *Amyrsidea lagopi* based on Scharf and Price (1983), the astigmatan mites based on Mironov et al. (2010), and the prostigmatan mite *Mironovia lagopus* based on Bochkov and Skirnisson (2011).

Scoring was used to quantify the abundance of the quill mite *M. lagopus*. Quills of seven feathers, the upper-wing primary coverts 4 and 5 and secondary flight feathers 3–7 (numbered distal to proximal) were examined. Each feather was scored: 0 = no mites, 1 ≤ 10 mites present, and 2 > 10 mites present. The scores were summed to derive a value for each individual.

The lower gastrointestinal tract was removed. Small and large intestines and ceca were separately packed and stored at -20°C to later be able to quantify parasitic worms (helminths). Fecal material (1–2 g) was taken from the rectum or, if the rectum was empty, from the posterior part of the small intestines. The modified McMaster procedure described in Skirnisson et al. (2012) was used to quantify oocysts of *Eimeria muta* and *E. rjupa*; their identification based on Skirnisson and Thorarinsdottir (2007). *Blastocystis* sp. were found, but not quantified.

Small and large intestines and ceca were examined for the presence of helminths applying procedures specified in Skirnisson et al. (2012). Identifications of the nematodes *Capillaria caudinflata* and *Trichostrongylus tenuis* were based on Madsen (1945), Wehr (1971), and

McDonald (1974). Alexander Galkin at the Russian Academy of Sciences, St. Petersburg identified the cestode *Passerilepis serpentulus*. Identification of *Mesocestoides canislagopodis* tetrathyridia was based on Skirnisson et al. (2016b).

Parasite species and measures

I examined the parasite community (i.e., all 17 parasite species known for the Icelandic rock ptarmigan except *Blastocystis* sp. and the rarely occurring *Mesocestoides canislagopodis* tetrathyridia (Skirnisson et al. 2016b) of adult and juvenile male and female hosts in all years of the study. The parasite community was composed of five endoparasite and 10 ectoparasite species. The endoparasites were two coccidians (*E. muta, E. rjupa)* and three helminths (two nematodes *C. caudinflata, T. tenuis,* and the cestode *Passerilepis serpentulus*; see Synopsis Table 4.1 and 4.2). The ectoparasites were five mites (four astigmatan *Tetraolichus lagopi, Strelkoviacarus holoaspis, Metamicrolichus islandicus, Myialges borealis,* and the prostigmatan *M. lagopus*), three lice (two ischnocerans *G. lagopi, L. affinis,* and the amblyceran *A. lagopi*), one hippoboscid fly (*O. chloropus*), and one flea (*Ceratophyllus garei*; see Synopsis Table 4.1).

I used a comparative value for each bird consisting of the ranked parasite data where 1 was allotted to the lowest positive finding and midranks were used for ties (Holmstad et al. 2005). The ranked values of each parasite species were summed depicting the abundance for endoparasites, ectoparasites, and all parasites for each bird. I used parasite richness, the mean of the total number of parasite species of an individual bird in each age and sex group (Bush et al. 1997). For the individual parasite species, I utilized parasite prevalence, intensity, and aggregation. Parasite prevalence was defined as the proportion of birds infected by a particular parasite species (Bush et al. 1997). Parasite intensity was defined as the average number of a particular parasite species among infected birds (Bush et al. 1997). Parasite aggregation was illustrated by a measure that applies to the right skewed parasite distributions, the Discrepancy index *D* (Poulin 1993). This is a dimensionless index that ranges between 0 and 1; the distribution becomes more aggregated as the value approaches 1.

Statistical analysis

Annual prevalence and confidence intervals and discrepancy indices for each parasite species were obtained using the software QP web (Reiczigel J et al 2016). All other statistical analyses were performed using the software packages Minitab 17 (Minitab 2016) and R (R Core Team 2016). Tests were two-tailed and statistical significance at level $p \leq 0.05$.

Descriptive statistics of parasite richness, all parasites (ranked), endoparasites (ranked), ectoparasites (ranked), and each parasite species were calculated; for every ptarmigan age and sex group combined and per year. To assess factors influencing the joined parasite measures, generalized linear models (GLMs) were used. Gaussian family with identity link was specified for parasite richness, all parasites, and ectoparasites. Quasipoisson family with log link was

specified for endoparasites. Binomial family with logit link was specified to examine endoparasite prevalence. For individual parasite species, a two-part ('hurdle') model was applied (e. g., Zeileis et al. 2008, Kelehear et al. 2012, Chipeta et al. 2013). Hurdle models ('pscl' package in R) are multiple regression models that contain two-parts; one part of the model uses logistic regression to model presence-absence of parasites and the other part uses generalized linear regression to assess the factors affecting parasite intensity (hosts without parasites are excluded here). A negative binomial distribution of the individual parasite species was assumed (dist="negbin") in each model. Because intensity is applicable to hosts with parasites present only, hosts without parasites are excluded from the second segment of the model. For the GLM as well as for both segments of the hurdle model, explanatory factors age, sex, and year were included. Factors that were non-significant were removed and analyses on the reduced models re-ran. Each year was also considered individually and thus inserted as a categorical variable in each model. To obtain a single p-value for all years, a full model with and a reduced model without year were compared using Anova (for GLMs) or lrtest (for hurdle models; lmtest package in R) (Zeileis et al. 2008).

To test for association of parasites, I first performed Spearman's rank correlation that measures the association between two quantities (counts) of parasites. I visualized these pairwise correlations by creating correlograms. I then applied Principal Component Analyses (PCA); the procedure identifies a smaller number of uncorrelated variables, called principal components, from a large set of data to explain the maximum amount of variance with the fewest number of principal components. Prior to analyses I log-transformed the data. Interpretation of the principal components is based on factor loadings and understanding of the data. Loadings range from -1 to 1. The closer the loadings are to -1 or 1, the stronger the effect of the variable. Loadings close to zero indicate that the factor has a weak effect on the variable. The number of principal components was determined using Kaiser method (Kaiser 1960) and scree test, but also the percentage of variation was examined.

Results

Ptarmigan parasite community in Iceland, Sweden, and Norway

Comparisons among Icelandic rock ptarmigan, Norwegian willow and rock ptarmigan, and Swedish willow ptarmigan regarding parasite prevalence and intensity revealed that those parasites shared generally tended to be more common (both more prevalent and intense) in mainland birds (Table Ⅳ.1).

Distribution of parasites within the host population

All parasite distributions were highly positively (right) skewed (Figure Ⅳ.1); there were many birds with few parasites whereas few birds with many parasites. Parasite richness was

Table IV.1 *Comparison of prevalence and intensity of parasites occurring in both rock and willow ptarmigan in Iceland, Norway, and Sweden.*

		Icelandic rock ptarmigan[1]	Norwegian rock ptarmigan[2,3]	Norwegian willow ptarmigan[4, 5]	Swedish willow ptarmigan[6]
	Sampling month Sampling year	early October 2006–2012	mid-end September 1992	mid-end September 1992–2002, 2001[5]	late August-early September 1989–2002
Prevalence	*Eimeria muta*	92 %			
	Eimeria rjupa	71 %			
	Eimeria spp.		91 %	62 %	76 %
	Capillaria caudinflata	29 %	10 %	6 %	3 %
	Trichostrongylus tenuis	4 %	18 %[3]	47 %	<1 %
	Goniodes lagopi	73 %		97 %[5]	
	Lagopus affinis	51 %		93 %[5]	
	Ornithomya chloropus	38 %		64 %[5]	
	Ceratophyllus garei	0.3 %		3 %[5]	
Mean intensities	*Capillaria caudinflata*	15.1		3.1	< 10
	Trichostrongylus tenuis	3.4	20	67.8	<1
	Goniodes lagopi	10.2		12.8[5]	
	Lagopoecus affinis	4.7		9.9[5]	
	Ceratophyllus garei	0.3		1.0[5]	

[1] present study; [2] Holmstad 2004; [3] Holmstad et al. 2004; [4] Holmstad et al. 2005a; [5] Holmstad et al. 2008; [6] Daehlen 2003

normally distributed (Figure IV.1). The measures of parasites combined showed slight positive skewness, becoming particularly present with endoparasites; but caution these measures are transformed (ranked) values in combination (Figure IV.1).

A total of 632 ptarmigan – 207 (32.8 %) juvenile females, 209 (33.1 %) juvenile males, 76 (12.0 %) adult females, and 140 (22.2 %) adult males – were examined (Table IV.2). Out of those, 630 (99.7 %) carried at least one parasite species. The two parasite-free birds were both adult males. Six-hundred-sixteen (97 %) birds were infested with ectoparasites (Table IV.3).

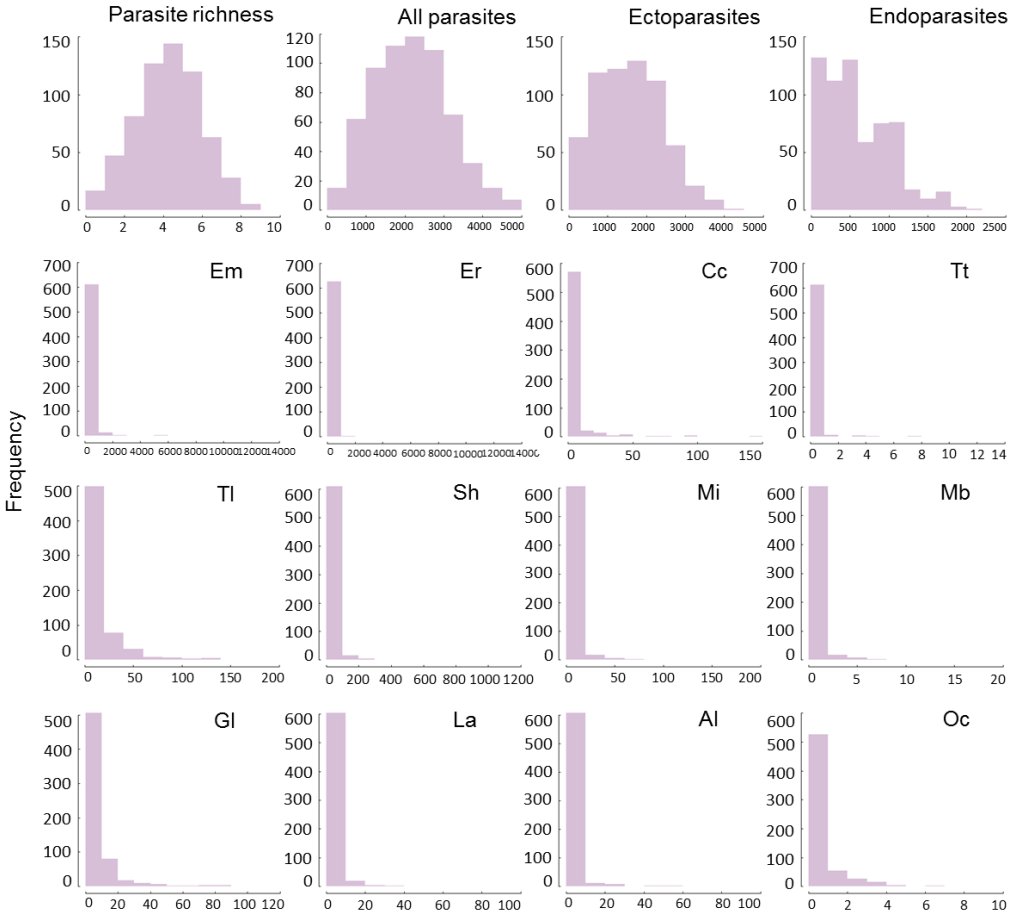


Figure IV.1 *Frequency distributions of parasite species of Icelandic rock ptarmigan (n = 631 birds) in northeast Iceland, early October 2006–2012.*

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Cg = Ceratophyllus garei, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Ml = Mironovia lagopus, Oc = Ornithomya chloropus, Ps = Passerilepis serpentulus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi, Tt = Trichostrongylus tenuis

Table IV.2 *Annual sample of juvenile and adult, male and female rock ptarmigan from northeast Iceland, early October 2006–2012.*

Year	Adults		Both	Juveniles		Both	Total
	Females	Males		Females	Males		
2006	13	18	31	30	30	60	91
2007	5	15	20	30	30	60	80
2008	13	12	25	28	29	57	82
2009	7	12	19	29	30	59	78
2010	13	27	40	30	30	60	100
2011	16	25	41	30	30	60	101
2012	9	31	40	30	30	60	100
Total	76	140	216	207	209	416	632

With regard to age, significantly more juvenile than adult birds carried ectoparasites – including mites and lice ($Z = -5.1$, $p < 0.001$; Figure IV.2, Table IV.3 and IV.4). With regard to host age and sex, ectoparasite infestations were most common in juveniles (100 %), followed by adult females (97 %) and adult males (90 %; Table IV.3); the differences were not significant. Five-hundred-thirty-six (85 %) birds were infected with endoparasites (Table IV.4). With regard to host age, there was no difference for endoparasite prevalence between age groups – including coccidians and helminths – ($Z = -1.2$, $p = 0.226$; Figure IV.2, Table IV.3 and IV.4). With regard to host age and sex, endoparasite infections were most common in juvenile females (88 %) and adult females (86 %), followed by juvenile males (84 %) and adult males (81 %; Table IV.4); the difference for juveniles was significant ($t = 2.6$, $df = 356$, $p = 0.009$) (Figure IV.2).

In the different parasite groups, 566 (90 %) birds carried mites (Table IV.5), 509 (81 %) mallophagans (Table IV.6), 505 (80 %) coccidians (Table IV.7), 245 (39 %) hippoboscids, 210 (33 %) helminths (Table IV.8), and 2 (0.3 %) fleas. The most common parasite was the mite *T. lagopi* (87 %), followed by the coccidian *E. muta* (78 %) and the mallophagan *G. lagopi* (73 %; Figure IV.4, Appendix A).

The greatest mean intensities among mites were found in *T. lagopi* and *S. holoaspis*, among lice *G. lagopi*, among coccidians in *E. muta*, and among helminths in *C. caudinflata* (Figure IV.4, Appendix A). Mean intensity is usually based on a few heavily infected/ infested individuals; median intensity in comparison does not incorporate the heavily infected/ infested individuals (Figure IV.6).

Variation in parasite levels due to age, sex, and year

Parasite community

Parasite richness, and total parasite and ectoparasite levels (ranked) significantly varied with age, sex, year (parasite richness and ectoparasites) and the interaction terms age:sex and age:year (Table IV.9A). That is, juvenile birds (mean parasite richness 5.3 / mean parasite number 2492) carried more parasites than adults (mean parasite richness 3.7; $t = 13.2$, $df = 630$, $p < 0.001$ / mean parasite number 1532; $t = 13.9$, $df = 630$, $p < 0.001$), and adult females (mean parasite richness 4.4 / mean parasite number 1916) more than adult males (mean parasite richness 3.3; $t = 5.4$, $df = 212$, $p < 0.001$ / mean parasite number 1319; $t = 6.2$, $df = 212$, $p < 0.001$) (Figure IV.2, Appendix A). Parasite richness and total parasite level overall decreased from 2006 to 2012 whereas ectoparasite level increased, but there were distinct fluctuations over the years with similar patterns for juveniles and adults (Figure IV.3, Appendix B). Endoparasite levels (ranked) significantly varied with year and the interaction term age:year (Table IV.9A). That is, endoparasite level decreased from 2006 to 2008, increased to 2010, and decreased again to 2012, and this was the case for both adults and juveniles (Figure IV.3, Appendix B).

Parasite groups

Mite and louse prevalence varied significantly with age and sex (Table IV.9B). That is, more juveniles (mites 95 % / lice 94 %) than adults (mites 78 %; $Z = 5.5$, $p < 0.001$/ lice 56 %; $Z = 9.8$, $p < 0.001$), and more females (mites 92 % / lice 84 %) than males (mites 85 % / lice 70 %) carried mites and lice (mites $Z = 2.7$, $p = 0.007$/ lice $Z = 4.1$, $p < 0.001$; Table IV.5). Mite prevalence significantly varied also with year (Table IV.9B); mite prevalence overall increased over the years of this study. *T. lagopi* prevalence varied significantly with age, sex, and year (Table IV.9C).

Coccidian and helminth prevalence varied significantly among years, and for coccidians the interaction of age:year (Table IV.9C). For instance, coccidian prevalence in both juveniles and adults decreased from 2006 to 2008, increased to 2010/2011 and decreased again. In helminths, significantly more males than females were infected (Table IV.9C).

Parasite species

Prevalence

All mite species varied significantly with age (Table IV.9B, C), with more juveniles carrying mites than adults, except for *M. lagopus* where more adults were infested than juveniles (Figure IV.4). *T. lagopi* and *M. islandicus* prevalence varied significantly also with sex and

Table IV.3 *Number (prevalence) of juvenile and adult, male and female rock ptarmigan infested with ectoparasites in northeast Iceland, early October 2006–2012.*

Year	Adults		Both	Juveniles		Both	Total
	Females	Males		Females	Males		
2006	12 (92 %)	17 (94 %)	29 (94 %)	30 (100 %)	30 (100 %)	60 (100 %)	89 (98 %)
2007	5 (100 %)	15 (100 %)	20 (100 %)	30 (100 %)	30 (100 %)	60 (100 %)	80 (100 %)
2008	13 (100 %)	10 (83 %)	23 (92 %)	28 (100 %)	29 (100 %)	57 (100 %)	80 (98 %)
2009	7 (100 %)	12 (100 %)	19 (100 %)	29 (100 %)	30 (100 %)	59 (100 %)	78 (100 %)
2010	12 (92 %)	20 (74 %)	32 (80 %)	30 (100 %)	30 (100 %)	60 (100 %)	92 (92 %)
2011	16 (100 %)	23 (92 %)	39 (95 %)	30 (100 %)	30 (100 %)	60 (100 %)	99 (98 %)
2012	9 (100 %)	30 (97 %)	39 (98 %)	30 (100 %)	29 (97 %)	59 (98 %)	98 (98 %)
Total	74 (97 %)	127 (90 %)	201 (93 %)	207 (100 %)	208 (100 %)	415 (100 %)	616 (97 %)

Table IV.4 *Number (prevalence) of juvenile and adult, male and female rock ptarmigan infected with endo-parasites in northeast Iceland, early October 2006–2012.*

Year	Adults		Both	Juveniles		Both	Total
	Females	Males		Females	Males		
2006	13 (100 %)	15 (83 %)	28 (90 %)	30 (100 %)	29 (97 %)	59 (98 %)	87 (96 %)
2007	3 (60 %)	12 (80 %)	15 (75 %)	23 (77 %)	26 (87 %)	49 (82 %)	64 (80 %)
2008	8 (62 %)	8 (67 %)	16 (64 %)	24 (86 %)	19 (66 %)	43 (75 %)	59 (72 %)
2009	6 (86 %)	9 (75 %)	15 (79 %)	24 (83 %)	25 (83 %)	49 (83 %)	64 (82 %)
2010	12 (92 %)	21 (78 %)	33 (83 %)	28 (93 %)	28 (93 %)	56 (93 %)	89 (89 %)
2011	16 (100 %)	22 (88 %)	38 (93 %)	30 (100 %)	27 (90 %)	57 (95 %)	95 (94 %)
2012	7 (78 %)	26 (84 %)	33 (83 %)	23 (77 %)	22 (73 %)	45 (75 %)	78 (78 %)
Total	65 (86 %)	113 (81 %)	178 (82 %)	182 (88 %)	176 (84 %)	358 (86 %)	536 (85 %)

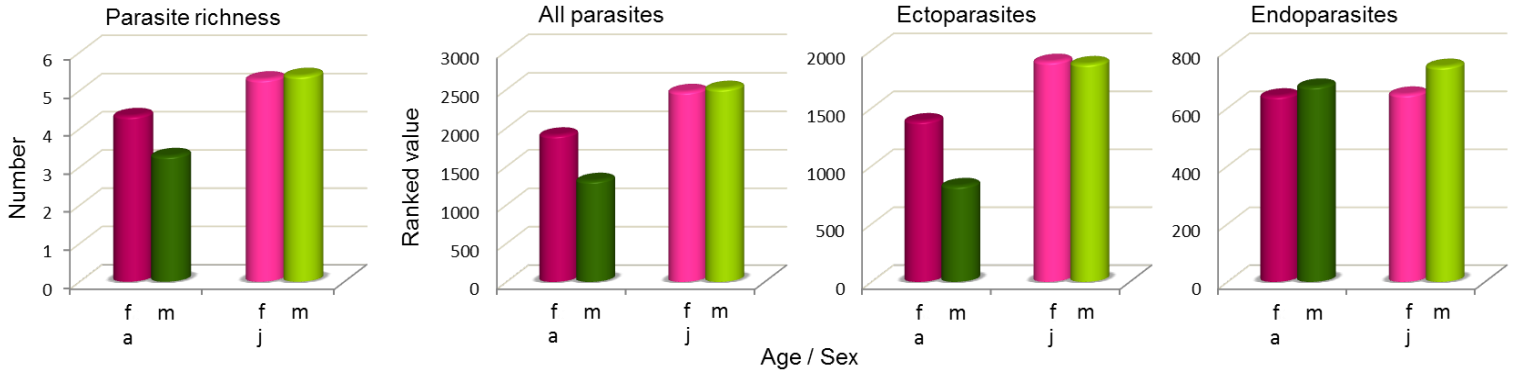


Figure IV.2 *Parasite measures of adult female (af), adult male (am), juvenile female (jf), and juvenile male (jm) rock ptarmigan in northeast Iceland, early October 2006–2012.*

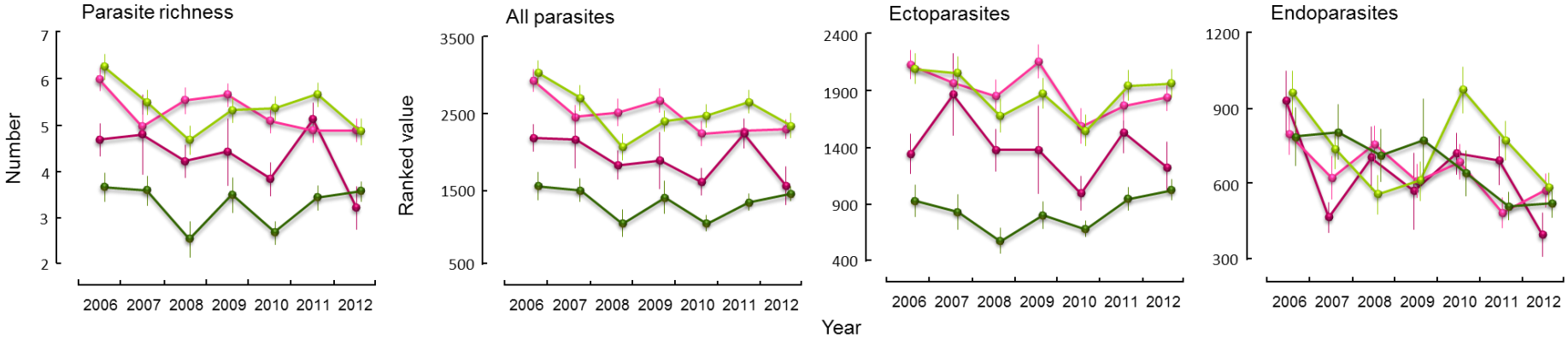


Figure IV.3 *Annual mean parasite measures ± SE of adult female (dark pink), adult male (dark green), juvenile female (light pink), and juvenile male (light green) rock ptarmigan in northeast Iceland, early October 2006–2012.*

Table IV.5 *Number (prevalence) of juvenile and adult, male and female rock ptarmigan infested with mites in northeast Iceland, early October 2006–2012.*

Year	Adults		Both	Juveniles		Both	Total
	Females	Males		Females	Males		
2006	12 (92 %)	14 (78 %)	26 (84 %)	30 (100 %)	29 (97 %)	59 (98 %)	85 (93 %)
2007	5 (100 %)	14 (93 %)	19 (95 %)	30 (100 %)	30 (100 %)	60 (100 %)	79 (99 %)
2008	12 (92 %)	6 (50 %)	18 (72 %)	27 (96 %)	27 (93 %)	54 (95 %)	72 (88 %)
2009	6 (86 %)	11 (97 %)	17 (89 %)	29 (100 %)	30 (100 %)	59 (100 %)	76 (97 %)
2010	10 (77 %)	10 (37 %)	20 (50 %)	27 (90 %)	29 (97 %)	56 (93 %)	76 (76 %)
2011	13 (81 %)	17 (68 %)	30 (73 %)	23 (77 %)	27 (90 %)	50 (83 %)	80 (79 %)
2012	9 (100 %)	30 (97 %)	39 (98 %)	30 (100 %)	29 (97 %)	59 (98 %)	98 (98 %)
Total	67 (88 %)	102 (73 %)	169 (78 %)	196 (95 %)	201 (96 %)	397 (95 %)	566 (90 %)

Table IV.6 *Number (prevalence) of juvenile and adult, male and female rock ptarmigan infested with lice in northeast Iceland, early October 2006–2012.*

Year	Adults		Both	Juveniles		Both	Total
	Females	Males		Females	Males		
2006	9 (69 %)	7 (39 %)	16 (52 %)	30 (100 %)	29 (97 %)	59 (98 %)	75 (82 %)
2007	4 (80 %)	5 (33 %)	9 (45 %)	26 (87 %)	29 (97 %)	55 (92 %)	64 (80 %)
2008	9 (69 %)	3 (25 %)	12 (48 %)	27 (96 %)	27 (93 %)	54 (95 %)	66 (80 %)
2009	7 (100 %)	6 (50 %)	13 (68 %)	26 (90 %)	27 (90 %)	53 (90 %)	66 (85 %)
2010	8 (62 %)	12 (44 %)	20 (50 %)	29 (97 %)	25 (83 %)	54 (90 %)	74 (74 %)
2011	16 (100 %)	13 (52 %)	29 (71 %)	27 (90 %)	29 (97 %)	56 (93 %)	85 (84 %)
2012	3 (33 %)	18 (58 %)	21 (53 %)	30 (100 %)	28 (93 %)	58 (97 %)	79 (79 %)
Total	56 (74 %)	64 (46 %)	120 (56 %)	195 (94 %)	176 (84 %)	358 (86 %)	509 (81 %)

Table IV.7 *Number (prevalence) of juvenile and adult, male and female rock ptarmigan infected with coccidians in northeast Iceland, early October 2006–2012.*

Year	Adults		Both	Juveniles		Both	Total
	Females	Males		Females	Males		
2006	12 (92 %)	14 (78 %)	26 (84 %)	30 (100 %)	29 (97 %)	59 (98 %)	85 (93 %)
2007	3 (60 %)	11 (73 %)	14 (70 %)	21 (70 %)	24 (80 %)	45 (75 %)	59 (74 %)
2008	8 (62 %)	8 (67 %)	16 (64 %)	23 (82 %)	18 (62 %)	41 (72 %)	57 (70 %)
2009	5 (71 %)	8 (67 %)	13 (68 %)	23 (79 %)	25 (83 %)	46 (78 %)	59 (76 %)
2010	12 (92 %)	21 (78 %)	33 (83 %)	28 (93 %)	27 (90 %)	55 (92 %)	88 (88 %)
2011	15 (94 %)	20 (80 %)	35 (85 %)	30 (100 %)	26 (87 %)	56 (93 %)	91 (90 %)
2012	7 (78 %)	23 (74 %)	29 (73 %)	20 (67 %)	17 (57 %)	37 (62 %)	66 (66 %)
Total	62 (82 %)	105 (75 %)	166 (83 %)	175 (85 %)	166 (79 %)	339 (81 %)	505 (80 %)

Table IV.8 *Number (prevalence) of juvenile and adult, male and female rock ptarmigan infected with helminths in northeast Iceland, early October 2006–2012.*

Year	Adults		Both	Juveniles		Both	Total
	Females	Males		Females	Males		
2006	9 (69 %)	9 (18 %)	18 (58 %)	8 (27 %)	15 (50 %)	23 (38 %)	41 (45 %)
2007	0 (0 %)	7 (47 %)	7 (35 %)	7 (23 %)	4 (13 %)	11 (18 %)	18 (23 %)
2008	4 (31 %)	5 (42 %)	9 (36 %)	13 (46 %)	6 (21 %)	19 (33 %)	28 (34 %)
2009	3 (43 %)	5 (42 %)	8 (42 %)	6 (21 %)	8 (27 %)	14 (24 %)	22 (28 %)
2010	6 (46 %)	8 (30 %)	14 (35 %)	10 (33 %)	17 (57 %)	27 (45 %)	41 (41 %)
2011	8 (50 %)	5 (20 %)	13 (32 %)	6 (20 %)	12 (40 %)	18 (30 %)	31 (31 %)
2012	2 (22 %)	10 (32 %)	12 (30 %)	7 (23 %)	10 (33 %)	17 (28 %)	29 (29 %)
Total	32 (42 %)	49 (35 %)	81 (38 %)	57 (28 %)	72 (34 %)	129 (36 %)	210 (33 %)

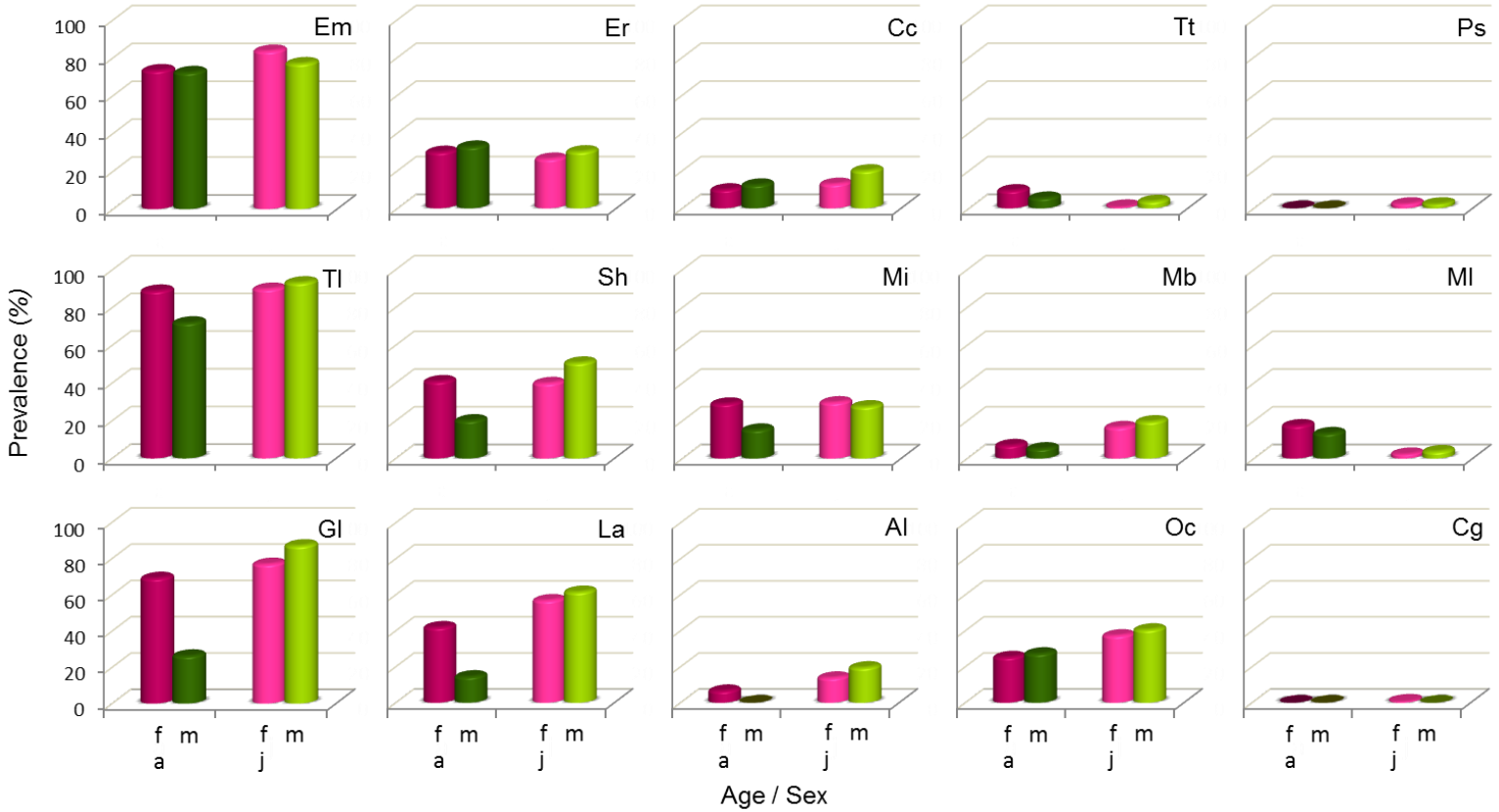


Figure IV.4 *Parasite prevalences of adult female (af), adult male (am), juvenile female (jf), and juvenile male (jm) rock ptarmigan in northeast Iceland, early October 2006–2012.*

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Cg = Ceratophyllus garei, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Ml = Mironovia lagopus, Oc = Ornithomya chloropus, Ps = Passerilepis serpentulus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi, Tt = Trichostrongylus tenuis

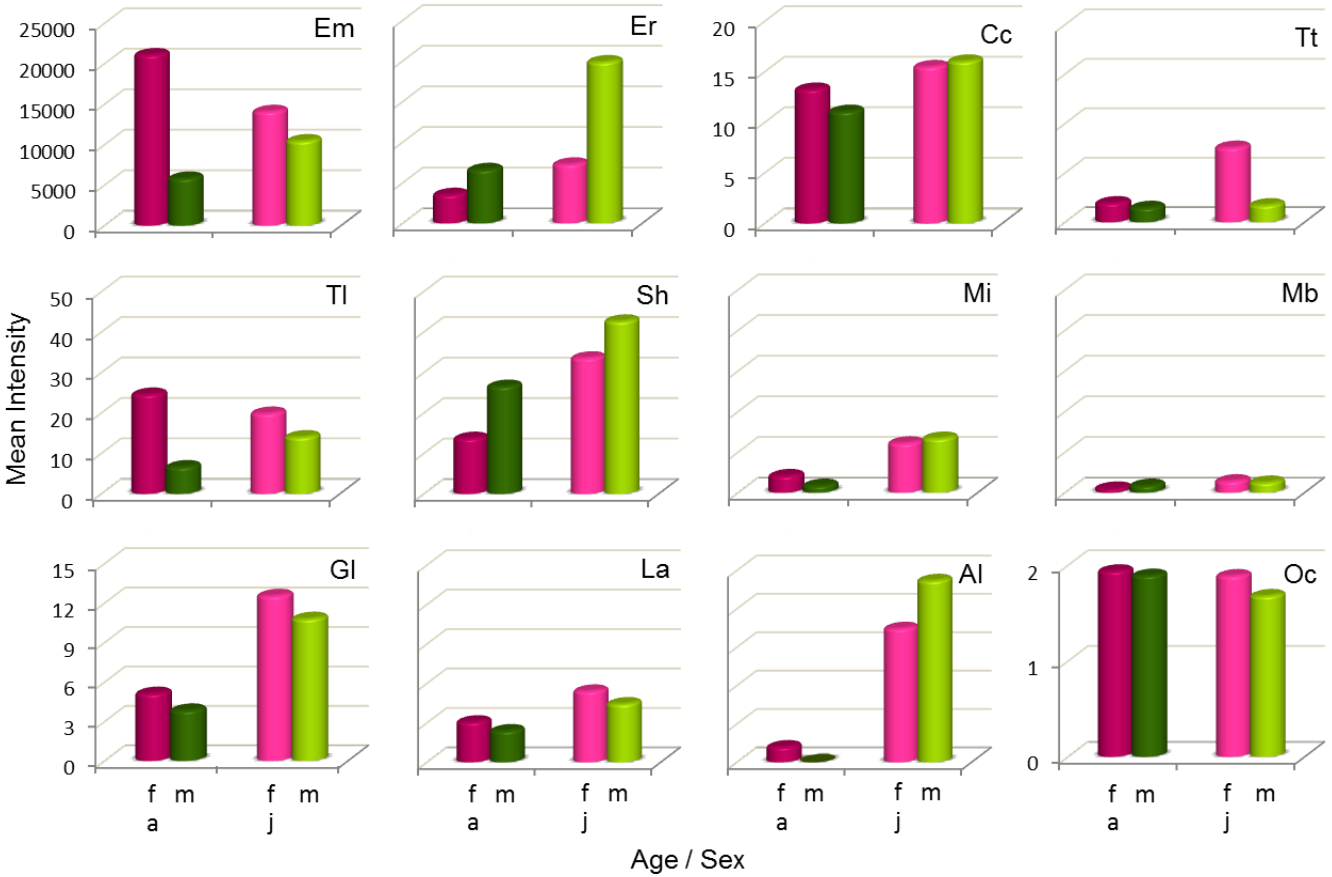


Figure IV.5 *Parasite mean intensities of adult female (af), adult male (am), juvenile female (jf), and juvenile male (jm) rock ptarmigan in northeast Iceland, early October 2006–2012.*

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Oc = Ornithomya chloropus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi, Tt = Trichostrongylus tenuis

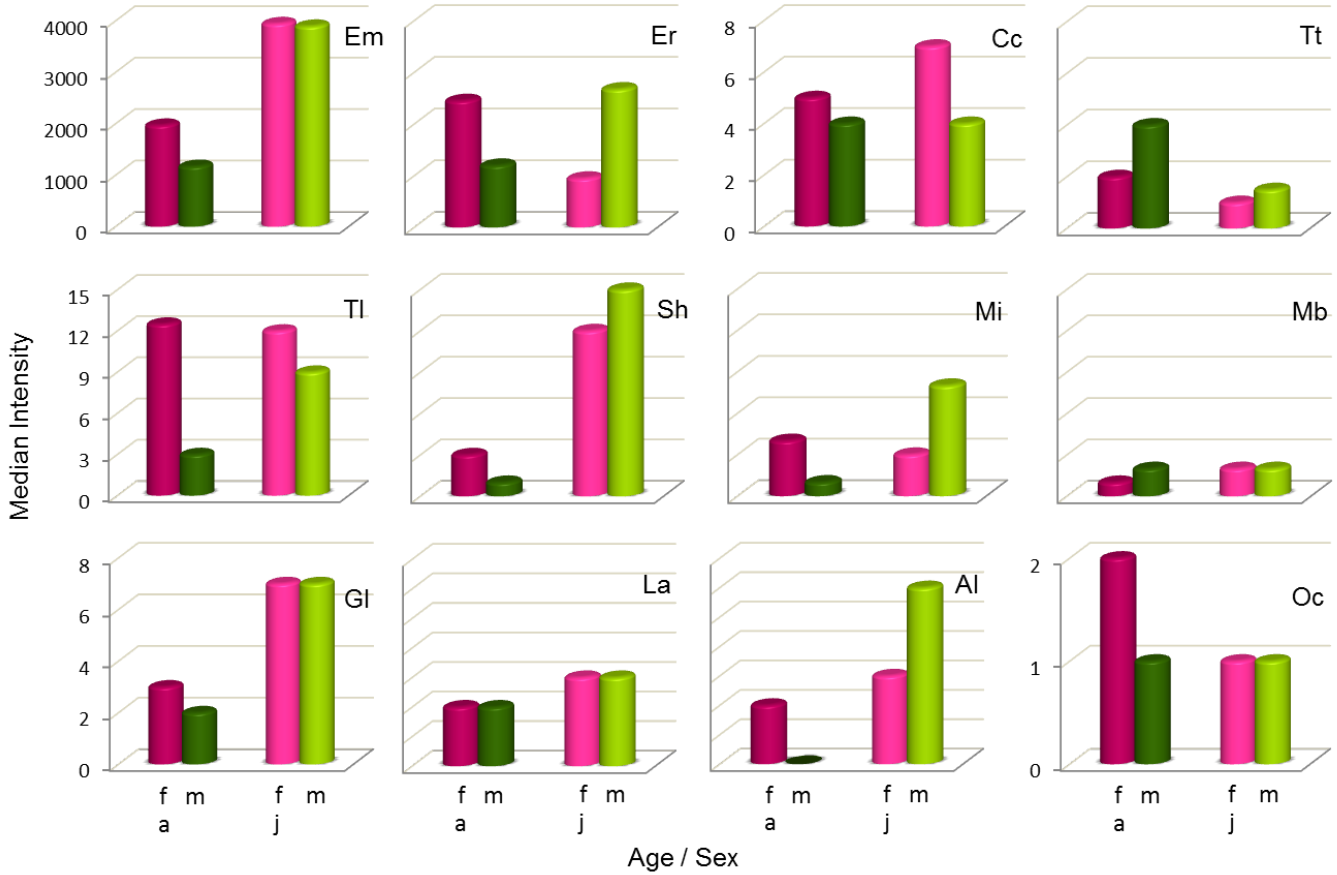


Figure IV.6 *Parasite median intensities of adult female (af), adult male (am), juvenile female (jf), and juvenile male (jm) rock ptarmigan in northeast Iceland, early October 2006–2012.*

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Oc = Ornithomya chloropus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi, Tt = Trichostrongylus tenuis

year (Table IV.9B, C); more females were infested than males. Prevalence for both mite species overall decreased over the course of this study, but for *T. islandicus* it increased again to 2012 (Figure IV.7, Appendix B).

G. lagopi and *L. affinis* prevalence varied significantly with age, sex, and the interactions of age:sex and age:year (only *G. lagopi*) (Table IV.9B). That is, more juveniles than adults, and more adult females than adult males carried *G. lagopi* ($Z = 4.6$, $p < 0.001$) and *L. affinis* ($Z = 4.1$, $p < 0.001$) (Figure IV.4). For adults, *G. lagopi* prevalence increased during the years of this study, but for juveniles it slightly decreased (Figure IV.7, Appendix B). For *A. lagopi*, prevalence varied significantly with age (Table IV.9B), with more adults being infested than juveniles; but also more adult females than males carried *A. lagopi* ($Z = 3.4$, $p = 0.001$) (Figure IV.4).

E. muta and *E. rjupa* prevalence varied significantly with age (only *E. muta*), year, and the interaction term age:year (Table IV.9C). That is, more juveniles than adults carried *E. muta* (Figure IV.4), and prevalence in both juveniles and adults decreased from 2006 to 2008, increased to 2010/2011 and decreased again (Figure IV.7, Appendix B). *E. rjupa* prevalence overall decreased in the course of this study in both adults and juveniles (Appendix B). *T. tenuis* prevalence varied significantly with age (Table IV.9C); more adults than juveniles carried worms. *C. caudinflata* prevalence did not show any source of variation.

Intensity

T. lagopi and *S. holoaspis* intensities varied significantly with age, sex (only *T. lagopi*), year, and age:sex and age:year (only *T. lagopi*) (Table IV.9B). That is, infestation intensities were higher in juveniles than adults (Figure IV.5). For *T. lagopi*, intensity was higher in adult females than males ($t = 4.0$, $df = 163$, $p < 0.001$), but for *S. holoaspis* intensity was slightly higher in males than females in both age groups; though a t-test for the latter showed no significance (Figure IV.5). Intensities slightly decreased from 2006 to 2011 and then sharply increased to 2012 (Figure IV.8, Appendix B). *M. islandicus* intensity varied significantly with age with higher intensity in juveniles than adults (Figure IV.5, Table IV.9B). *M. borealis* intensity did not show any source of variation.

G. lagopi, *L affinis*, and *A. lagopi* intensities varied significantly with age and year, and for *G. lagopi* the interactions of age:sex and age:year (Table IV.9B). That is, intensities were higher in juveniles than adults, and for *G. lagopi* higher in females than males; though a t-test for the latter showed no significance (Figure IV.5). *L. affinis* intensity overall increased in the course of this study, for *G. lagopi*, intensity in adults slightly increased in the course of this study whereas in juveniles they went down from 2006 to 2009, increased to 2011, and then decreased again (Figure IV.8, Appendix B). *O. chloropus* varied significantly with year (Table IV.9B), with intensity decreasing from 2006 to 2009, increasing to 2011, and decreasing again in 2012 (Figure IV.8, Appendix B).

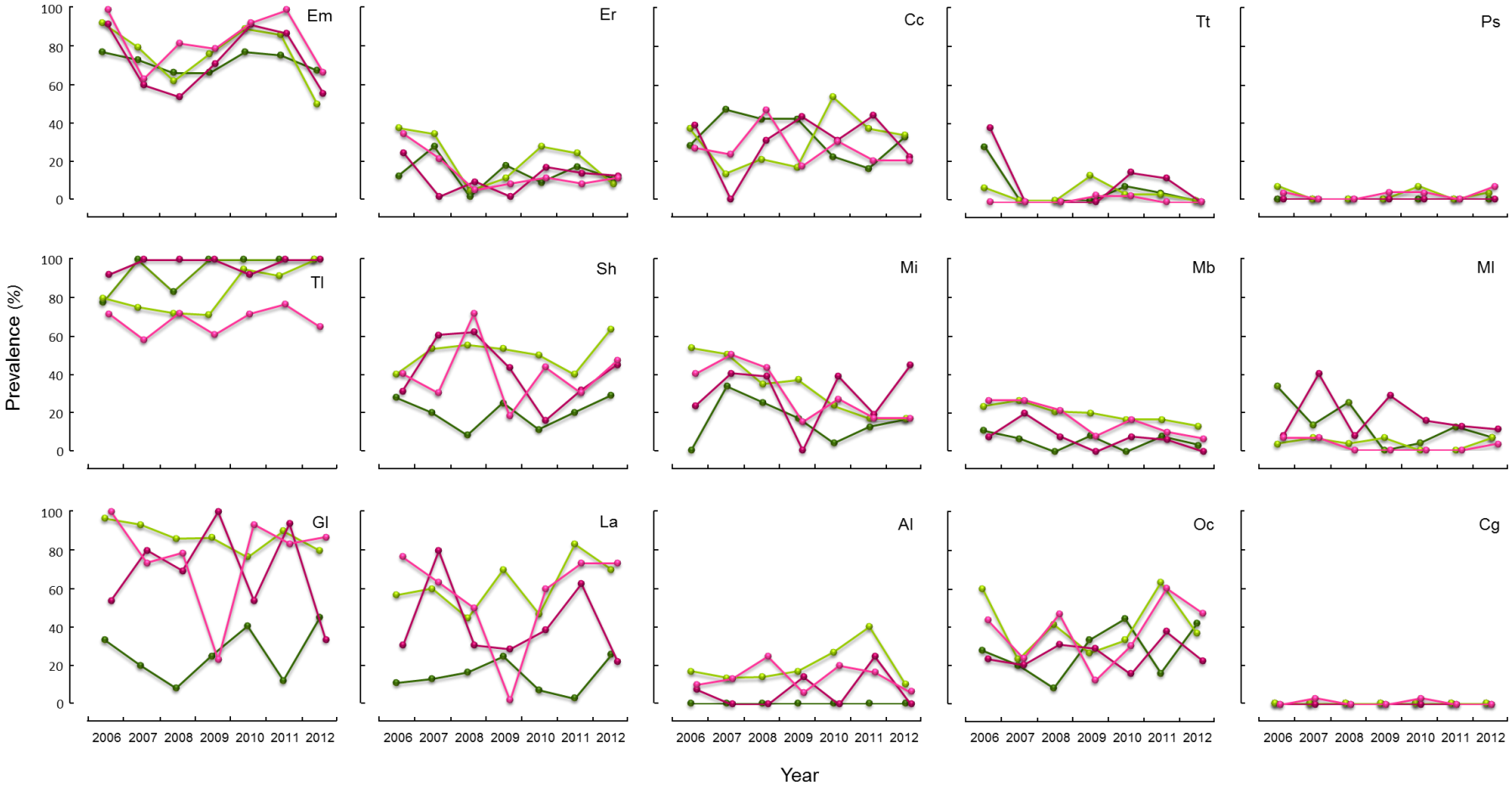


Figure IV.7 *Annual parasite prevalences of adult female (dark pink), adult male (dark green), juvenile female (light pink), and juvenile male (light green) rock ptarmigan in northeast Iceland, early October 2006–2012.*

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Oc = Ornithomya chloropus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi, Tt = Trichostrongylus tenuis

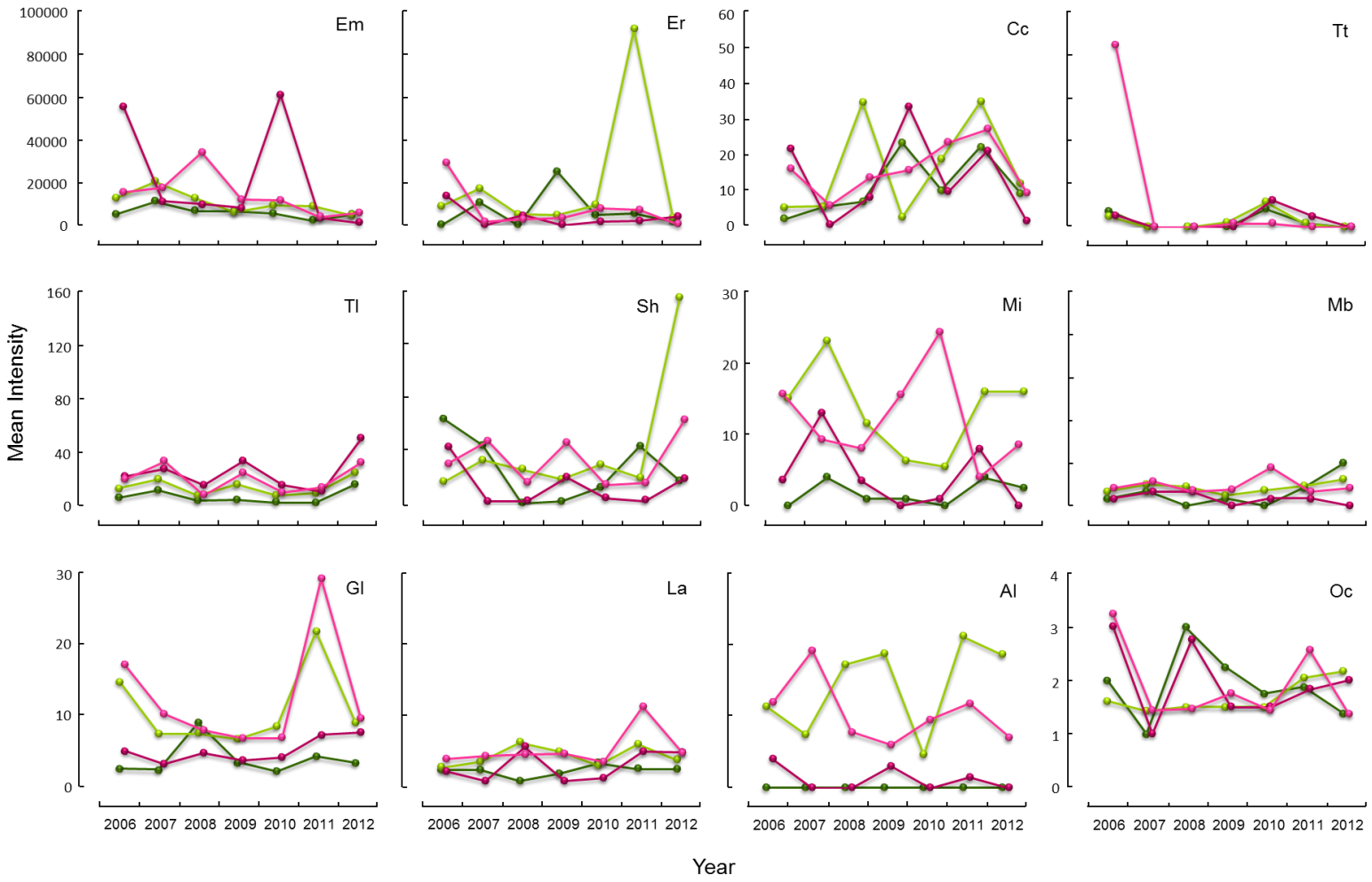


Figure IV.8 *Annual mean parasite intensities of adult female (dark pink), adult male (dark green), juvenile female (light pink), and juvenile male (light green) rock ptarmigan in northeast Iceland, early October 2006–2012.*

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Oc = Ornithomya chloropus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi, Tt = Trichostrongylus tenuis

Table IV.9 *Sources of variation in (A) Parasite measures (ranked values; abundance), (B) Ectoparasite prevalence and mean intensity, (C) and Endoparasite prevalence and mean intensity from hurdle models of rock ptarmigan in northeast Iceland, early October 2006–2012.*

*Summary of results in (A) from GLMs, and (B) and (C) from hurdle models applying the stepwise backward procedure. * Results from likelihood ratio tests to identify whether factor year and/ or interactions terms are significant contributions to the model; negative relationships indicated in brackets.*

(A)

Source of variation	**Parasite richness**		**All parasites**		**Ectoparasites**		**Endoparasites**	
	F value	p	F value	p	F value	p	F value	p
Age	167.37	< 0.001	191.20	< 0.001	206.59	< 0.001		
Sex	5.23 (-)	0.023	7.81 (-)	< 0.001	11.31 (-)	0.001		
Year	5.54 (-)	< 0.001			5.47 (-)	< 0.001	7.54 (-)	< 0.001
Age:sex	10.15 (-)	< 0.001	11.74 (-)	< 0.001	26.79 (-)	< 0.001		
Age:year	3.87 (-)	< 0.001	4.03 (-)	< 0.001	3.21 (-)	< 0.001	5.21	< 0.001

(B) Prevalence

Source of variation	Mites		*Tetraolichus lagopi*		*Strelkoviacarus holoaspis*		*Metamicrolichus islandicus*		*Myialges borealis*		*Mironovia lagopus*	
	z	p	z	p	z	p	z	p	z	p	z	p
Age	5.62	< 0.001	4.80	< 0.001	5.26	< 0.001	5.08	< 0.001	4.39	< 0.001	-4.41	< 0.001
Sex	-2.18	0.030	-2.12	0.034			-2.62	0.009				
Year	53.89*	< 0.001	62.17*	< 0.001			52.33*	< 0.001				

Source of variation	Lice		*Goniodes lagopi*		*Lagopoecus affinis*		*Amyrsidea lagopi*		*Ornithomya chloropus*	
	z	p	z	p	z	p	z	p	z	p
Age	9.66	< 0.001	9.49	< 0.001	8.73	< 0.001	4.50	< 0.001		
Sex	-3.34	< 0.001	-2.79	0.005	-3.17	0.002				
Age:sex			22.53* (-)	< 0.001	17.76* (-)	< 0.001				
Age:year			22.47* (-)	0.033						

Mean Intensities

Source of variation	Mites		*Tetraolichus lagopi*		*Strelkoviacarus holoaspis*		*Metamicrolichus islandicus*	
	z	p	z	p	z	p	z	p
Age	6.06	< 0.001	2.96	0.003	3.95	< 0.001	3.53	< 0.001
Sex			-6.68	< 0.001				
Year	63.43*	< 0.001	82.74*	< 0.001	20.49*	0.002		
Age:sex	13.64* (-)	0.001	74.98* (-)	< 0.001	38.51* (-)	< 0.001		
Age:year	84.74* (-)	< 0.001	126.27* (-)	< 0.001				

Source of variation	Lice		*Goniodes lagopi*		*Lagopoecus affinis*		*Amyrsidea lagopi*		*Ornithomya chloropus*	
	z	p	z	p	z	p	z	p	z	p
Age	11.58	< 0.001	9.12	< 0.001	3.60	< 0.001	3.13	0.002		
Year	74.78*	< 0.001	72.78*	< 0.001	25.28*	< 0.001			20.02*	0.003
Age:sex	16.97* (-)	< 0.001	8.00* (-)	0.018						
Age:year	80.31* (-)	< 0.001	80.08* (-)	< 0.001						

(C) Prevalence

Source of variation	Coccidians		*Eimeria muta*		*Eimeria rjupa*		Helminths	
	z	p	z	p	z	p	z	p
Age			1.90	< 0.001				
Sex							2.07	0.039
Year	36.94* (-)	< 0.001	44.07* (-)	< 0.001	20.33* (-)	0.002	17.04*	0.009
Age:year	117.25* (-)	< 0.001	57.39* (-)	< 0.001	36.71* (-)	< 0.001		

Mean Intensities

Source of variation	Coccidians		*Eimeria muta*		*Eimeria rjupa*		Helminths		*Trichostrongylus tenuis*	
	z	p	z	p	z	p	z	p	z	p
Age									-1.99	0.047
Sex			-4.70	< 0.001						
Year	35.46*	< 0.001								
Age:sex	6.41* (-)	0.011	12.78* (-)	0.002						
Age:year			49.94* (-)	< 0.001						
Sex:year	62.68* (-)	< 0.001					23.06*	0.027		

E. muta intensity varied significantly with sex, and the interaction terms of age:sex and age:year (Table IV.9C). That is, adult females carried more *E. muta* than adult males (t = 2.0, df = 158, p = 0.048) and intensity in both age groups decreased over the years of this study (Figure IV.8, Appendix B). For juveniles, the changes among years were marked, with intensity decreasing from 2006 to 2008, increasing to 2010, and decreasing again to 2012 (Figure IV.8). For adults, the changes among years were smooth; intensity increased from 2006 to 2007 and then decreased softly to 2012 (Figure IV.8). *T. tenuis* intensity varied significantly with age (Table IV.9C), with higher intensity in adults than juveniles (Figure IV.5). *E. rjupa* and *C. caudinflata* intensities did not show any source of variation with respect to age, sex, and year.

Aggregation of parasites within the host population

Most parasites were highly aggregated in the ptarmigan population (Figure IV.9, Appendix A); that is, on a scale from 0 to 1, discrepancy indices tended to be larger than 0.5. The most highly aggregated (between 0.8 and 1) parasites in the juvenile population were *E. rjupa*, *T. tenuis*, *C. caudinflata*, *M. borealis*, *S. holoaspis*, and *M. islandicus* (Figure IV.9, Appendix A). The less aggregated or more evenly distributed parasites (between 0.6 and 0.8) in the juvenile population were *E. muta*, *O. chloropus*, *L. affinis*, *T. lagopi*, and *G. lagopi* (Figure IV.9, Appendix A). Parasites were overall more aggregated in the adult ptarmigan population, but *E. rjupa*, *T. tenuis*, *C. caudinflata*, and *T. lagopi* were more aggregated in the juvenile population (Figure IV.9, Appendix A).

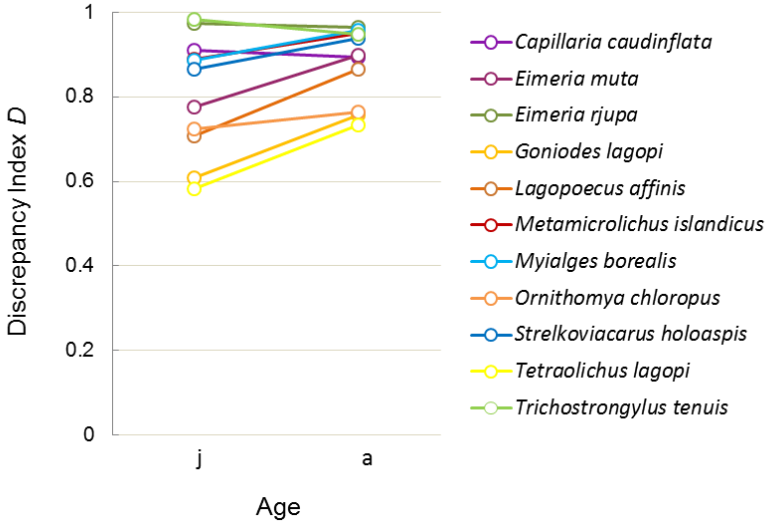


Figure IV.9 *Parasite aggregation in adult and juvenile rock ptarmigan in northeast Iceland, early October 2006–2012.*

Association of parasites

Spearman's rank correlations identified several pairs of associations between endoparasites–endoparasites, endo– and ectoparasites, and ectoparasites–ectoparasites as significantly correlated in all years combined (Table IV.10). Those that were significant also in most individual years were six ectoparasite combinations: *M. islandicus – M. borealis*, *G. lagopi – L. affinis*, *T. lagopi – S. holoaspis*, *T. lagopi – M. islandicus*, *T. lagopi – L. affinis*, and *T. lagopi – G. lagopi* (Appendix C).

Table IV.10 *Spearman's rank correlation pyramids of parasite associations of rock ptarmigan in northeast Iceland, early October 2006–2012.*

Top value: Spearman rho. Bottom value: p-value. Those combinations that were also significant in most individual years have significant p-values highlighted in red.

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Oc = Ornithomya chloropus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi

(A)

	Em	Er	Cc	Tl	Sh	Mi	Mb	Gl	La	Al
Er	0.090									
	0.023									
Cc	0.103	0.025								
	0.009	0.537								
Tl	-0.056	0.018	0.022							
	0.159	0.656	0.587							
Sh	-0.095	-0.072	0.059	0.274						
	0.017	0.072	0.142	**0.000**						
Mi	0.096	0.016	0.006	0.267	0.087					
	0.016	0.685	0.873	**0.000**	**0.030**					
Mb	0.055	-0.011	0.044	0.186	0.072	0.581				
	0.166	0.788	0.268	**0.000**	0.070	**0.000**				
Gl	0.055	0.020	0.056	0.272	0.114	0.007	0.048			
	0.166	0.610	0.160	**0.000**	**0.004**	0.860	0.233			
La	-0.016	0.009	0.036	0.269	0.224	0.027	0.035	0.426		
	0.690	0.827	0.363	**0.000**	**0.000**	0.501	0.374	**0.000**		
Al	0.067	0.010	0.045	0.054	0.052	-0.050	0.036	0.169	0.200	
	0.095	0.807	0.260	0.177	0.188	0.214	0.371	**0.000**	**0.000**	
Oc	0.029	-0.061	0.034	-0.021	0.022	-0.194	-0.086	0.059	0.054	-0.046
	0.465	0.126	0.393	0.600	0.578	**0.000**	**0.031**	0.137	0.175	0.246

In the PCA, there were four principal components (PCs) of interest (i.e., eigenvalues greater than 1; Table IV.11A). PC 1 had eigenvalue (variance) 1.92 and accounted for 17.5 % of the data variability, PC 2 had eigenvalue 1.59 and accounted for 14.5 % of the data variability, etc. PC 1 was mainly defined by age (Figure IV.10A); high positive scores for *T. lagopi*, *M. islandicus*, *M. borealis*, *G. lagopi*, and *L. affinis* indicated greater prevalence in juveniles (Table IV.11B). All these parasites grouped in the same region of PC 1 and groupings of *M. islandicus* and *M. borealis* as well as *G. lagopi* and *L. affinis* indicated a close association between these parasites (Table IV.11B). PC 2 was defined mainly by time (i.e., years of this study) and also age; high scores for *M. islandicus*, *M. borealis*, *G. lagopi*, and *L. affini* indicated spread of scores according to years and the age effect showed in that the two skin mites and two mallophagans stayed together (Figure IV.10A). Also in PC 2, there were groupings of *M. islandicus* and *M. borealis* as well as *G. lagopi* and *L. affinis* indicating a close association between these parasites (Table IV.11B), well visible also in the loadings plot (Figure IV.10B). The hippoboscid fly *O. chloropus*, a parasite parasitized by leastwise *M. borealis*, was found in the opposite spectrum farthest away from the skin mites in each loading plot (Figure IV.10B). The association between the skin mites and to *O. chloropus* remained distinct up to PC 4. From PC 3, year remained the main influencer of the underlying structure (Figure IV.10A), but PC 3 was also defined by age; this time high positive scores showed for *E. muta* and *A. lagopi* indicating greater prevalence and/ or intensities (Table IV.11B). PC 4 was defined by age and also sex; there was a high negative score for *C. caudinflata* (Table IV.11B).

Table IV.11 *(A) Eigenvalues (greater than 1) and (B) principal components from Principal Component Analyses to examine association of parasites of rock ptarmigan in northeast Iceland, early October 2006–2012.*

High loading scores marked in red.

(A)

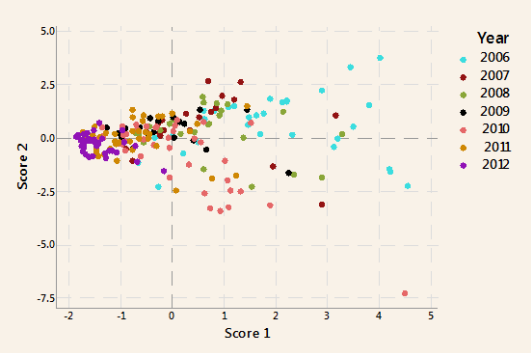
Eigenvalue	1.9235	1.5925	1.2499	1.0165
Proportion	0.175	0.145	0.114	0.092
Cumulative	0.175	0.320	0.433	0.526

(B)

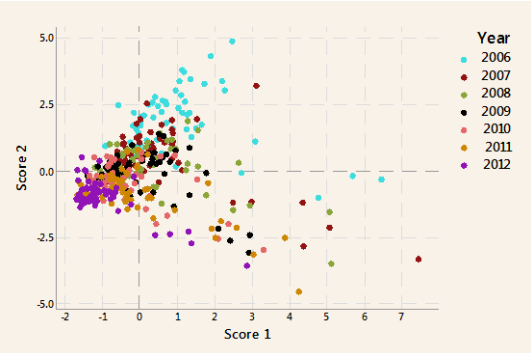
Variable	PC1	PC2	PC3	PC4
Em	0.034	0.156	**0.584**	0.266
Er	0.019	0.059	0.381	0.248
Cc	0.135	-0.039	0.349	**-0.702**
Tl	**0.479**	-0.060	-0.243	0.028
Sh	0.291	-0.274	-0.310	-0.255
Mi	**0.429**	**0.513**	-0.016	0.042
Mb	**0.419**	**0.465**	-0.022	-0.093
Gl	**0.368**	**-0.365**	0.194	0.362
La	**0.407**	**-0.407**	0.107	0.147
Al	0.077	-0.164	**0.432**	-0.382
Oc	-0.017	-0.294	-0.015	0.002

(A)

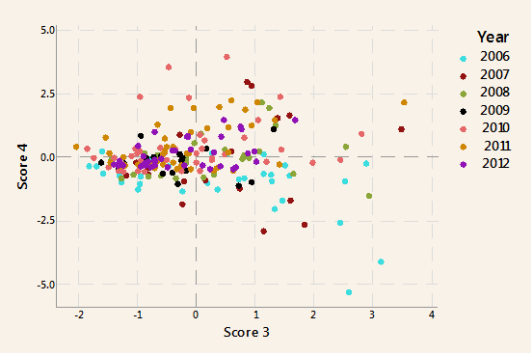
Adults



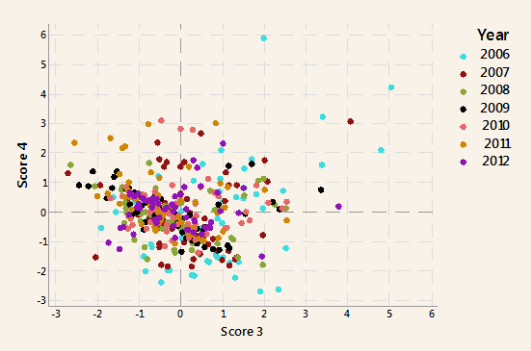
Juveniles



Adults



Juveniles



(B)

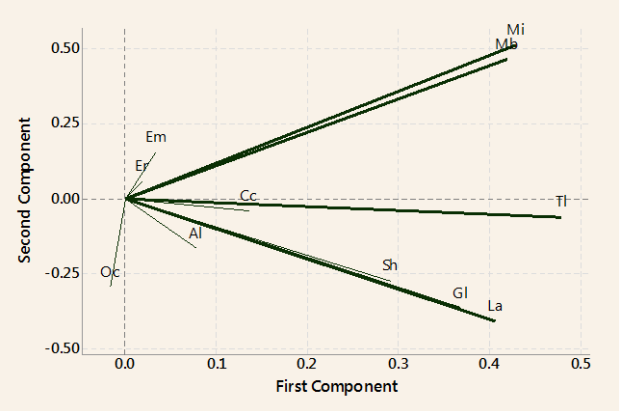


Figure IV.10 *Results from Principal Component Analyses exploring association of parasites of rock ptarmigan in northeast Iceland, early October 2006–2012. (A) Scoreplots of first to fourth principal components grouped by age and year. (B) Loading plot of first and second principal components.*

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Oc = Ornithomya chloropus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi, Tt = Trichostrongylus tenuis

Discussion

Seventeen parasite species are now known to occur in Icelandic rock ptarmigan, one more than reported in Skirnisson et al. (2012). Tetrathyridia of the tapeworm *Mesocestoides canislogopodis* has been added to the list recently (Skirnisson et al. 2016 a). In this study I aim to expand Skirnisson's et al. (2012) first discoveries on the parasite community of ptarmigan and compare the parasite community of Icelandic rock ptarmigan to adjoining populations, present details on the Icelandic parasite community structure with respect to the distribution in adult and juvenile male and female birds over a period of seven years (2006–2012), discuss internal and external factors that would evoke variation and present parasite association.

Ptarmigan parasite community

In comparison with Sweden and Norway

There are only few studies that have addressed the whole or a greater share of the parasite community. With regard to other cycling grouse species, we are aware of one study that addressed both the ecto- and endoparasite community: willow ptarmigan in Norway (Holmstad et al. 2008). Otherwise, mostly endoparasites have been investigated (Babero 1953, Braun and Willers 1967, Watson and Shaw 1991, Hudson et al. 1998, Daehlen 2003, Holmstad 2004, Schei et al. 2005, Cattadori et al. 2005, Isomursu 2014); ectoparasites mostly mentioned in early studies (e.g., Shipley 1909, Bendell 1955, Dick 1981).

Comparisons among Icelandic rock ptarmigan, Norwegian willow and rock ptarmigan, and Swedish willow ptarmigan regarding parasite prevalence and intensity usually revealed clear differences (Table Ⅳ.1); for instance, Icelandic rock ptarmigan carried fewer endoparasite species than Norwegian willow or rock ptarmigan (Holmstad 2014). The endoparasites that these ptarmigan had in common were *Eimeria* spp., *C. caudinflata*, and *T. tenuis* (Table Ⅳ.1). However, measures of *Eimeria* spp. cannot easily be compared because they strongly depend on sampling method, season, and species (differences in pathogenicity; Rommel et al. 2000). Differences in seasonal prevalence and intensity of *E. muta* and *E. rjupa* in Icelandic rock ptarmigan (Thórarinsdóttir et al. 2010) have further underlined the importance of identifying eimerids to species levels, but this was not done in the Scandinavian studies. It remains unknown if one or more eimerid species are involved in infecting rock and willow ptarmigan in Norway and Sweden. Therefore all comparisons regarding eimerid infections are dubious. The most common mallophagan on Icelandic rock ptarmigan was *G. lagopi* compared to *G. lagopi* and *L. affinis* on Norwegian willow ptarmigan; mites were not recorded in the latter (Holmstad et al. 2008), and not found in Daehlen's (2003) study. The other parasite species in common *C. caudinflata*, *T. tenuis*, *O. chloropus*, and *C. garei* showed fairly strong differences in prevalence; in all cases lower in Icelandic rock ptarmigan. Blood parasites have not been detected in Icelandic rock ptarmigan (Skirnisson et al. 2012).

In Iceland

Parasite infections and infestations according to host age in this study showed that ectoparasites were more prevalent in juveniles than adults, but this was not the case for endoparasites. Within each age group, the main patterns of parasite prevalence according to sex were:

Adults

No difference between adult males and females (endoparasites – coccidians, helminths – *E. muta*, *E. rjupa*, *C. caudinflata*, *T. lagopi*, *M. islandicus*, *M. borealis*, *M. lagopus*, *O. chloropus*)

Higher prevalence in adult females than males (parasite richness, all parasites, ectoparasites – mites, lice – *T. tenuis*, *S. holoaspis*, *G. lagopi*, *L. affinis*, *A. lagopi*)

Juveniles

No difference between juvenile males and females (parasite richness, total parasite load, ectoparasites, endoparasites – coccidians, helminths, mites, lice – *E. muta*, *E. rjupa*, *C. caudinflata*, *T. tenuis*, *T. lagopi*, *S. holoaspis*, *M. islandicus*, *M. borealis*, *M. lagopus*, *G. lagopi*, *L. affinis*, *A. lagopi*, *O. chloropus*)

While there were no major differences between juvenile males and females, differences between adult males and females stood out: more adult females carried ectoparasites than adult males. This may have to do with the hens that were busy raising offspring, trade-offs of

energy resources into other than preening activities, and /or the parasites' survival strategy wandering from hen to offspring.

The main patterns of parasite intensity according to sex were:

Adults

No difference between adult males and females (endoparasites* – coccidians*, helminths, mites* – *E. rjupa, C. caudinflata, T. tenuis, S. holoaspis*, M. islandicus, M. borealis, G. lagopi*, L. affinis, A. lagopi, O. chloropus*)

Higher intensity in adult females than males (lice – *E. muta, T. lagopi*)

Juveniles

No difference between juvenile males and females (coccidians*, helminths, mites*, lice* – *E. muta, E. rjupa, C. caudinflata, T. tenuis, T. lagopi*, S. holoaspis*, M. islandicus, M. borealis, G. lagopi*, L. affinis, A. lagopi, O. chloropus*)

Higher intensity prevalence in juvenile males than females (endoparasites)

In the majority of cases there were no differences between sex groups of either age group. However, adult females appeared to be overall more prone to infestations with lice and *T. lagopi*, and to *E. muta* infections. Juvenile males on the other hand appeared to be more prone to endoparasite infections. Those parasite groups and species marked with asterix in the list above showed clear patterns of distribution in connection with sex, but t-tests did not reveal unambiguous significant differences. With regard to prevalence, for all those species marked with asterix – except *M. islandicus* in juveniles –, females showed higher prevalence than males. With regard to intensity, for all those species marked with asterix in adults – except *S. holoaspis* –, females carried more parasites than males, but in juveniles this was equally weighted.

Distinctions in aggregation can be made with respect to age. Parasites were overall more aggregated in the adult ptarmigan population except *E. rjupa, T. tenuis, C. caudinflata*, and *T. lagopi* that were more aggregated in the juvenile population; and this supports earlier findings by Skirnisson et al. (2012).

Factors influencing the distribution of parasites

Host age and sex

The strongest source of variation for the parasite community was host age. Our study showed that juvenile birds were overall more susceptible to parasites than adults; most parasite species were more prevalent and showed higher intensities of infection/ infestation in juveniles than adults; and this phenomenon was showed before (e.g., Clayton and Moore 1997, Møller et al. 1998b, Isomursu et al. 2006, Skirnisson et al. 2012). It was substantiated with the less well developed host defenses (immune system, preen gland activity, and preening behaviour) in

juveniles (Bush et al. 2001, Skirnisson et al. 2012), and the increase of host defenses or selective mortality in adults (Hudson et al. 1992, Clayton and Moore 1997, Hudson et al. 2001, Schei et al. 2005, Skirnisson et al. 2012). That is, as hosts become older, the heavily infected individuals die and overall infection intensity falls; at high age however it is said to rise again (Clayton and Moore 1997). Changes in exposure or individual differences in condition may also contribute (Clayton and Moore 1997). That age was a strong source of variation was supported by the interaction terms that were mostly connected with this factor. For instance, sex or time (year) were often entangled in this interaction term.

Host sex was another source of strong variation. Leastwise all lice and the mite *S. holoaspis* were more prevalent in females, and leastwise lice, the mite *T. lagopi*, and coccidians – particularly *E. muta* – occurred in higher intensities in females than males. The sex phenomenon in Icelandic ptarmigan stands out in that females carried more parasites; in other studies it was predominantly males (e.g., Alexander and Stimson 1988, Zuk 1990, Zuk and McKean 1996, Møller et al. 1998a, Isomursu et al. 2006). The female bias in our study was however subject to adult birds. There were nearly no differences due to sex in juveniles. This was expressed in the interaction term of age and sex. That is, factor age often paired with factor sex, with the difference in parasite prevalence and intensity most often seen in adults where generally females carried more parasites than males; in juveniles these differences were minor (see also chapter above). Male and female biases in different studies may have leastwise to do with differences in sampling times; there are strong seasonal differences in parasite susceptibility throughout the year. Our birds were collected in October, and the females that had raised offsping should have been exposed to parasites much more than males that live solitarily after the breeding season. Parasite exposure of hens and chicks enhances possibly further when broods mix in late summer. This vertical transmission is probably very important for most ptarmigan parasites and at least ectoparasites. Whatsoever, the origin of sex differences in parasitism of vertebrates is yet a speculative subject and a number of different hypotheses have been proposed (e.g., Poulin 1996, Schalk and Forbes 1997, Møller et al. 1998b).

Time

The influence of time, that is the annual changes, on the parasite community was visible in the form of distinct fluctuations in parasite prevalence and intensity. In general, there was strong variation for many parasites among the years. Some species overall decreased in the course of the study whereas others fluctuated in distinct patterns with peak and low phases very similar to those that the ptarmigan population exhibits. Those fluctuations of pathogenic parasites (prevalence, aggregation) that showed relation with ptarmigan population numbers, population parameters, and body condition have been presented and discussed (Stenkewitz et al. 2016). The probably most influential ones showed annual patterns that were similar also in all age and sex groups (e.g., *E. muta* prevalence; Figure IV.7). With respect to the common interaction

term of age and year, then for other parasites annual patterns among age groups varied fairly strongly (e.g., *G.* and *A. lagopi* prevalence; Figure IV.7). Interestingly, with regard to parasite intensity, there were striking intensity peaks of lice, the fly *O. chloropus*, the skin mite *M. islandicus*, the coccidian *E. rjupa*, and the helminth nematode *C. caudinflata* in juvenile birds in 2011, and of *E. muta* in adult females in 2010 (Figure IV.8). For comparison, ptarmigan population densities peaked in spring 2010 and then collapsed. It suggests that some parasite species thrived very well and heavily accumulated on hosts that were still available after the ptarmigan numbers collapsed, like some kind of Noah‘s Ark. This indicates some link between ptarmigan population density, and possibly body condition and/ or population parameters, and the information could for example be incorporated into ptarmigan population models.

Association of parasites

Those pairs of parasite species (abundance) that were correlated in the combined sample as well as most individual years according to Spearman‘s rank correlation were mites, lice, and a combination of the two. These pairwise correlations were exclusively positive and imply that ptarmigan with high abundance of one parasite species are more likely to have high abundance of another species and vice versa. Holmstad and Skorping (1998) suggest this to be the fruit of individual differences in exposure to different parasites, differences in susceptibility, parasite interactions, or samplig artefacts. Results from the individual years indicated that the mentioned parasite associations were more similar than expected by chance.
In comparison, the PCA resulted in two main pairs of potentially co-occurring parasites (*M. islandicus – M. borealis*, *G. lagopi – L. affinis*) that were also detected with Spearman‘s rank correlation, and one more (*E. muta – A. lagopi*). For the association between *E. muta* and *A. lagopi* (PC 3) I have no biological explanation why these two parasites would co-occur and what they could have in common, respectively. Also, this association occurred only from PC 3 and is thus probably less strong than those occurring in PC 1 and PC 2.

M. islandicus is a skin mite (Astigmata) that causes mange in ptarmigan (Skirnisson et al. 2012). *M. borealis* belongs to the Epidermoptida, that is it *is* a skin mite that may also be responsible for the crust on manged ptarmigan (Karl Skírnisson pers. comm.). For *M. borealis* that is so closely associated with *M. islandicus*, yet no larvae, nymphs, and adult males have been found on ptarmigan, but on the abdomen of the hippoboscid fly *O. chloropus* is where its eggs are found. So, *M. borealis* reproduces and changes hosts by using the hippoboscid; the fly serves the mite as final host. Comparatively, *M. islandicus* probably reaches another host by vertical transmission like the other mites (except *M. borealis*) and mallophagans that are found on ptarmigan. Both Spearman’s rank correlation and PCA imply close co-occurrence of these two mites. Interestingly, when examining PCA loading plots, it stands out on each plot that *O. chloropus* is found on the farthest opposite side of the spectrum away from the two skin mites, an indication for it repelling or avoiding *M. borealis*. This could also be the reason

why the skin mites show a curious pattern with regard to ptarmigan condition, survival, and population densities (all positive relationships; Stenkewitz et al. 2016), for the actual distress may not be for the bird but for *O. chloropus*. However, no concurrent evidence exsists and the real mechanism behind is not yet understood. The data for the skin mites further suggest both that infestations, once acquired, persist, indicated by their prevalence in juvenile and adult hosts, and that these two mites might be mutually dependent.

G. lagopi and *L. affinis* are two ischnoceran chewing lice (mallophagans). Mallophagans are known to be site-specific and their morphology correlates with the sites preferred (Bush et al. 2001). They are highly specialized, live in the plumage, and feed primarily on keratin of feather barbules of down parts (e.g., Johnson and Clayton 2003, Møller and Rózsa 2005, Clayton et al. 2008). Ischnoceran mallophagans like *G. lagopi* and *L. affinis* feed primarily on feathers and dead skin (Price et al. 2003, Clayton et al. 2008). Each species can be assigned to informal categories on the basis of overall morphology and how it avoids host grooming (Johnson and Clayton 2003). For instance, *G. lagopi* is a sluggish, tall species with a triangular and bulky head and rather round body. This species avoids preening by dwelling mainly on the head and neck (Johnson and Clayton 2003), or in partridge, *Goniocotes* (syn. *Goniodes*) was found on the flank feather (Ash 1960). *L. affinis* has an elongated body and its head is egg-shaped and rounded down. It is the smallest of all mallophagans occurring in ptarmigan and it appears rather delicate. Its small size should make it easy to hide in the barbs of body feathers. Both mallophagans avoid competition by occupying different habitats on their host. *G. lagopi* likely occurs mainly around the particularly difficult to preen neck and head region of ptarmigan which may be why it is more prevalent and occurs in higher intensity than *L. affinis* that occupies different bodyparts. It stands out how closely the annual prevalence and intensity trajectories match, also in the individual years.

One more association to be mentioned is the one between *T. lagopi* and *S. holoaspis*. These are feather mites that showed positive host-mite relations. These two mites appear to be benign commensals or mutualists – so called paraphrages – benefitting their host through feeding on excess oil gland secret, dirt, bacteria, or harmful fungus; and this was discovered before (Dabert and Mironov 1999, Blanco et al. 2001, Proctor 2003). In mutualist relationships individuals of two different species benefit from one another. In commensal relationships (meaning "eating at the same table") one species benefits from another whereby the latter remains unaffected. The relationship between host and paraphrages are like a win-win situation, very useful to both animal groups. It is a curious phenomenon that these mites co-occur since both these mites are differently adapted, that is occupy different habitat and eat differently; there is no competition for space or food even at high numbers. Thus, this co-occurrence could simply be based on their high numbers.

In summary, the hitherto exploration of parasite associations unfolded exclusively pairwise combinations of species. Spearman‘s rank correlation resulted in six ectoparasite

combinations: mites–mites, mites–lice, and lice–lice. PCA yielded two strong positive associations that were also detected with Spearman‘s rank correlation, one mite-mite (*M. islandicus – M. borealis*) and one louse-louse (*G. lagopi – L. affinis*) combination, and one negative association between the two skin mites and the hippoboscid *O. chloropus*. Though all mentioned associations were correlated also in most of the seven years of this study, the connection between the two skin mites *M. islandicus* and *M. borealis* stands out because it is close and strong all along.

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Appendix A

Parasite levels ± SE of rock ptarmigan in northeast Iceland October 2006–2012.
(A) Combined parasite measures. (B) Parasite prevalence. (C) Parasite intensity (count data, not oocysts per gram, presented) . (D) Parasite aggregation (Discrepancy index D*).*

(A)

Adults

Year	Parasite richness			All parasites ranked			Ectoparasites ranked			Endoparasites ranked		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	4.7±0.35	3.7±0.31	4.1±0.25	2168.1±177.4	1530.4±185.4	1797.5±141.1	1343.0±174.9	930.4±140.3	1100.8±114.2	928.7±121.2	782.3±115.3	850.0±83.2
2007	4.8±0.86	3.6±0.32	3.9±0.33	2147.6±380.3	1474.2±153.5	1642.3±158.4	1866.8±359.0	833.4±154.4	1091.5±174.6	468.3±61.2	801.3±107.9	734.4±93.2
2008	4.2±0.36	2.5±0.39	3.5±0.31	1809.5±192.6	1040.0±174.3	1456.6±151.4	1376.5±187.3	577.8±113.6	1029.0±142.2	703.0±124.9	707.9±104.4	705.7±78.3
2009	4.4±0.72	3.5±0.38	3.8±0.36	1868.9±376.4	1381.2±212.2	1574.8±205.1	1378.1±385.6	805.1±119.0	1058.2±171.1	573.0±150.7	768.3±163.8	664.1±119.8
2010	3.8±0.36	2.7±0.25	3.1±0.22	1585.8±180.4	1040.4±103.9	1222.0±99.5	997.4±151.2	682.3±67.8	800.3±74.5	720.8±81.8	638.5±90.0	668.2±64.1
2011	5.1±0.36	3.4±0.27	4.1±0.25	2226.0±196.1	1317.5±111.2	1671.8±122.7	1532.9±183.6	947.3±100.0	1187.3±105.2	693.3±96.2	507.0±54.8	585.3±52.8
2012	3.2±0.46	3.6±0.21	3.5±0.19	1538.0±254.7	1430.4±97.5	1454.3±93.3	1226.8±220.2	1028.2±93.2	1073.8±87.4	400.3±88.2	519.1±57.9	493.7±49.4
All	4.4±0.17	3.3±0.11	3.7±0.10	1915.8±87.9	1318.9±52.7	1531.7±50.2	1358.5±82.1	866.4±86.1	1051.3±44.1	693.7±46.1	637.1±34.8	655.3±27.9

Juveniles

Year	Parasite richness			All parasites ranked			Ectoparasites ranked			Endoparasites ranked		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	6.0±0.25	6.3±0.27	6.1±0.18	2925.3±145.6	3025.7±160.7	2975.2±107.7	2128.0±127.1	2095.5±134.0	2111.5±91.6	797.4±83.1	962.5±86.9	878.3±60.5
2007	5.0±0.26	5.5±0.27	5.2±0.19	2445.9±154.2	2698.0±168.5	2571.7±114.4	1969.0±117.5	2059.1±137.8	2013.8±90.0	622.2±85.2	737.3±77.6	683.1±57.4
2008	5.5±0.28	4.7±0.31	5.1±0.22	2500.8±178.5	2046.7±170.0	2269.5±125.8	1851.9±143.3	1680.9±145.2	1764.6±101.8	757.3±72.5	558.6±76.7	669.2±54.3
2009	5.7±0.25	5.3±0.26	5.5±0.18	2663.0±156.4	2387.7±133.2	2522.7±103.2	2157.9±146.6	1877.5±133.6	2015.0±99.9	610.7±67.2	612.5±77.1	611.3±50.8
2010	5.1±0.26	5.4±0.26	5.2±0.19	2229.5±163.6	2458.1±149.0	2343.6±110.7	1589.3±155.7	1549.4±139.2	1569.1±103.6	686.2±69.7	974.0±92.1	829.8±60.4
2011	4.9±0.27	5.7±0.26	5.3±0.19	2254.5±144.2	2640.9±152.6	2447.5±107.1	1769.9±135.3	1945.5±133.9	1857.5±95.0	485.0±59.8	772.9±76.2	621.1±51.2
2012	4.9±0.25	4.9±0.28	4.9±0.19	2282.5±126.0	2327.9±161.6	2304.9±101.7	1842.9±121.7	1964.2±121.8	1902.3±85.7	573.6±66.1	585.6±59.8	579.2±44.2
All	5.3±0.10	5.4±0.11	5.3±0.07	2470.4±59.27	2514.4±61.7	2492.3±42.8	1900.5±52.2	1882.3±52.0	1891.1±36.8	648.5±28.1	761.5±32.4	703.8±21.6

(B)

All

Year	*Tetraolichus lagopi*	*Strelkoviacarus holoaspis*	*Metamicrolichus islandicus*	*Myialges borealis*	*Mironovia lagopus*
2006	91.2±2.8	36.3±5.0	34.1±5.0	19.8±4.2	11.0±3.3
2007	98.8±1.2	38.8±5.5	42.5±5.5	22.5±4.7	10.0±3.4
2008	82.9±4.2	54.9±5.5	30.5±5.1	15.9±4.0	6.1±2.6
2009	97.4±1.8	51.3±5.7	34.6±5.4	19.2±4.5	5.1±2.5
2010	74.0±4.4	33.0±4.7	10.0±3.0	11.0±3.1	3.0±1.7
2011	73.3±4.4	30.7±4.6	8.9±2.8	10.9±3.1	5.0±2.2
2012	96.0±2.0	46.0±5.0	12.0±3.3	7.0±2.6	6.0±2.4
All	87.0±1.3	41.0±2.0	23.4±1.7	14.7±1.4	6.5±1.0

Year	*Amyrsidea lagopus*	*Goniodes lagopi*	*Lagopoecus affinis*	*Ornithomya chloropus*	*Ceratophyllus garei*
2006	9.9±3.1	79.1±4.3	50.5±5.2	42.9±5.2	0.0
2007	10.0±3.4	71.2±5.1	53.8±5.6	22.5±4.7	1.2±1.2
2008	13.4±3.8	69.5±5.1	40.2±5.4	36.6±5.3	0.0
2009	15.4±4.1	75.6±4.9	61.5±5.5	33.3±5.3	0.0
2010	14.0±3.5	69.0±4.6	39.0±4.9	33.0±4.7	1.0±1.0
2011	20.8±4.0	78.2±4.1	59.4±4.9	58.4±4.9	0.0
2012	5.0±2.2	67.0±4.7	53.0±5.0	40.0±4.9	0.0
All	12.7±1.3	72.8±1.8	50.9±2.0	38.8±1.9	0.3±0.1

Year	*Eimeria muta*	*Eimeria rjupa*	*Capillaria caudinflata*	*Trichostrongylus tenuis*	*Passerilepis lagopi*
2006	92.3±2.8	28.6±4.7	31.9±4.9	13.2±3.6	3.3±1.9
2007	71.2±5.1	25.0±4.8	22.5±4.7	0.0	0.0
2008	68.3±5.1	3.7±2.1	34.1±5.2	0.0	0.0
2009	75.6±4.9	9.0±3.2	23.1±4.8	6.4±2.8	1.3±1.3
2010	88.0±3.3	15.0±3.6	35.0±4.8	6.0±2.4	3.0±1.7
2011	88.1±3.2	14.9±3.5	27.7±4.5	4.0±2.0	0.0
2012	61.0±4.9	9.0±2.9	28.0±4.5	0.0	3.0±1.7
All	78.2±1.6	15.0±1.4	29.2±1.8	4.3±0.8	1.6±0.5

Adults

Year	*Tetraolichus lagopi*			*Strelkoviacarus holoaspis*			*Metamicrolichus islandicus*			*Myialges borealis*			*Mironovia lagopus*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	66.7±13.1	77.8±9.8	83.9±6.6	30.8±12.8	27.8±10.6	29.0±8.1	23.1±7.7	0.0	9.7±5.3	7.7±7.4	11.1±7.4	9.7±5.3	7.7±7.4	33.3±11.1	22.6±7.5
2007	33.3±21.1	93.3±6.5	95.0±4.9	60.0±21.9	20.0±10.3	30.0±10.2	20.0±7.3	26.7±8.1	25.0±9.7	20.0±17.9	6.7±6.5	10.0±6.7	40.0±8.8	13.3±8.8	20.0±8.9
2008	92.3±7.4	50.0±14.4	72.0±9.0	61.5±13.5	8.3±7.1	36.0±9.6	30.8±8.7	8.3±5.0	20.0±8.0	7.7±7.4	0.0	4.0±3.9	7.7±7.4	25.0±12.5	16.0±7.3
2009	85.7±13.2	91.7±8.0	89.5±7.0	42.9±18.7	25.0±12.5	31.6±10.7	0.0	16.7±6.8	10.5±7.0	0.0	8.3±8.0	5.3±5.1	28.6±17.1	0.0	10.5±7.0
2010	76.9±11.7	37.0±9.3	50.0±7.9	15.4±10.0	11.1±6.0	12.5±5.2	7.7±4.9	0.0	2.5±2.5	7.7±7.4	0.0	2.5±2.5	15.4±10.0	3.7±3.6	7.5±4.2
2011	75.0±10.8	64.0±9.6	68.3±7.3	31.2±11.6	20.0±8.0	24.4±6.7	12.5±6.0	4.0±3.6	7.3±4.1	6.2±6.0	8.0±5.4	7.3±4.1	12.5±8.3	12.0±2.2	12.2±5.1
2012	100.0±0.0	90.3±5.3	92.5±4.2	44.4±16.6	29.0±8.1	32.5±7.4	0.0	6.5±4.5	5.0±3.4	0.0	3.2±3.2	2.5±2.5	11.1±10.5	6.5±4.4	7.5±4.2
All	86.8±3.9	70.7±3.9	76.4±2.9	38.2±5.6	20.7±3.4	26.9±3.0	14.5±4.1	7.1±2.2	9.7±2.0	6.6±2.8	5.0±1.8	5.6±1.6	14.5±4.0	12.1±2.8	13.0±2.3

Year	*Amyrsidea lagopi*			*Goniodes lagopi*			*Lagopoecus affinis*			*Ornithomya chloropus*			*Ceratophyllus garei*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	7.7±7.4	0.0	3.2±3.2	53.8±13.8	33.3±11.1	41.9±8.9	30.8±12.8	11.1±7.4	19.4±7.9	23.1±11.7	27.8±10.6	25.8±7.9	0.0	0.0	0.0
2007	0.0	0.0	0.0	80.0±17.9	20.0±10.3	35.0±10.2	80.0±17.9	13.3±8.8	30.0±8.9	20.0±17.9	20.0±10.3	20.0±8.9	0.0	0.0	0.0
2008	0.0	0.0	0.0	69.2±12.8	8.3±8.0	40.0±8.5	30.8±12.8	16.7±10.8	24.0±8.0	30.8±12.8	8.3±8.0	20.0±8.0	0.0	0.0	0.0
2009	14.3±13.2	0.0	5.3±5.1	100.0±0.0	25.0±12.5	52.6±10.1	28.6±17.1	25.0±12.5	26.3±10.1	28.6±17.1	33.3±13.6	31.6±10.7	0.0	0.0	0.0
2010	0.0	0.0	0.0	53.8±13.8	40.7±9.5	45.0±6.0	38.5±13.5	7.4±5.0	17.5±6.0	15.4±10.0	44.4±9.6	35.0±7.5	0.0	0.0	0.0
2011	25.0±10.8	0.0	9.8±4.6	93.8±6.0	12.0±6.5	65.9±7.3	62.5±11.9	3.0±3.4	31.7±7.3	37.5±12.1	16.0±7.3	53.7±7.8	0.0	0.0	0.0
2012	0.0	0.0	0.0	33.3±15.7	45.2±8.9	42.5±6.8	22.2±13.9	25.8±7.9	25.0±6.8	22.2±13.9	41.9±8.9	37.5±7.7	0.0	0.0	0.0
All	7.9±3.1	0.0	2.8±1.1	68.4±5.3	35.7±4.0	47.2±3.4	40.8±5.6	15.7±3.1	24.5±2.9	26.3±5.1	38.6±4.1	34.3±3.2	0.0	0.0	0.0

Year	*Eimeria muta*			*Eimeria rjupa*			*Capillaria caudinflata*			*Trichostrongylus tenuis*			*Passerilepis lagopi*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	92.3±7.4	77.8±9.8	83.9±6.6	23.1±11.7	11.1±5.7	16.1±6.6	38.5±13.5	27.8±10.6	32.3±14.8	38.5±13.5	27.8±10.6	32.3±8.4	0.0	0.0	0.0
2007	60.0±21.9	73.3±11.4	70.0±10.2	0.0	26.7±8.1	20.0±8.9	0.0	46.7±12.9	18.3±14.6	0.0	0.0	0.0	0.0	0.0	0.0
2008	53.8±13.8	66.7±13.6	60.0±9.8	7.7±7.4	0.0	4.0±3.9	30.8±12.8	41.7±14.2	36.0±16.0	0.0	0.0	0.0	0.0	0.0	0.0
2009	71.4±17.1	66.7±13.6	68.4±10.7	0.0	16.7±6.9	10.5±7.0	42.9±18.7	41.7±14.2	42.1±17.5	0.0	0.0	0.0	0.0	0.0	0.0
2010	92.3±7.4	77.8±8.0	82.5±6.0	15.4±10.0	7.4±4.8	10.0±4.7	30.8±12.8	22.2±8.0	25.0±13.7	15.4±10.0	7.4±5.0	10.0±4.7	0.0	0.0	0.0
2011	87.5±8.3	76.0±8.5	80.5±6.2	12.5±8.3	16.0±6.7	14.6±5.5	43.8±12.4	16.0±7.3	26.8±13.4	12.5±8.3	4.0±3.9	7.3±4.1	0.0	0.0	0.0
2012	55.6±16.6	67.7±8.4	65.0±7.5	11.1±10.5	9.7±5.4	10.0±4.7	22.2±13.9	32.3±8.4	30.0±13.2	0.0	0.0	0.0	0.0	0.0	0.0
All	76.3±4.9	72.9±3.8	74.1±3.0	11.8±3.7	12.1±2.8	12.0±2.2	32.9±5.4	30.0±3.9	31.0±3.1	11.8±3.7	5.7±2.0	7.9±1.8	0.0	0.0	0.0

Juveniles

Year	*Tetraolichus lagopi*			*Strelkoviacarus holoaspis*			*Metamicrolichus islandicus*			*Myialges borealis*			*Mironovia lagopus*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	93.3±4.6	96.7±3.3	95.0±2.8	40.0±8.9	40.0±8.9	40.0±6.3	40.0±8.9	53.3±9.1	46.7±6.4	26.7±8.1	23.3±7.7	25.0±5.6	6.7±4.6	3.3±3.2	5.0±2.8
2007	100.0±0.0	100.0±0.0	100.0±0.0	30.0±8.4	53.3±9.1	41.7±6.4	50.0±9.1	50.0±9.1	50.0±6.5	26.7±8.1	26.7±8.1	26.7±5.7	6.7±4.6	6.7±4.6	6.7±3.2
2008	89.3±5.8	86.2±6.4	87.7±4.4	71.4±8.5	55.2±9.2	63.2±6.4	42.9±9.4	34.5±8.8	38.6±6.4	21.4±7.8	20.7±7.7	21.1±5.4	0.0	3.4±3.4	1.8±1.8
2009	100.0±0.0	100.0±0.0	100.0±0.0	18.0±7.1	53.3±9.1	57.6±6.4	15.0±6.6	36.7±8.8	44.1±6.5	8.0±5.0	20.0±7.4	23.7±5.5	0.0	6.7±4.6	3.4±2.4
2010	86.7±6.2	93.3±4.6	90.0±3.9	43.3±9.0	50.0±9.1	46.7±6.4	26.7±8.1	23.3±7.7	25.0±5.6	16.7±6.8	16.7±6.8	16.7±4.8	0.0	0.0	0.0
2011	73.3±8.1	80.0±7.3	76.7±5.5	30.0±8.4	40.0±8.9	35.0±6.2	16.7±6.8	16.7±6.8	16.7±4.8	10.0±5.5	16.7±6.8	13.3±4.4	0.0	0.0	0.0
2012	100.0±0.0	96.7±3.3	98.3±1.7	46.7±9.1	63.3±8.8	55.0±6.4	16.7±6.8	16.7±6.8	16.7±4.8	6.7±4.6	13.3±6.2	10.0±3.9	3.3±3.3	6.7±4.6	5.0±2.8
All	91.8±1.9	93.3±1.7	92.5±1.3	45.9±3.5	50.7±3.5	48.3±2.5	32.4±3.2	28.7±3.1	30.5±2.3	19.3±2.7	19.6±2.7	19.5±1.9	2.4±1.1	3.8±1.3	3.1±0.8

Year	*Amyrsidea lagopi*			*Goniodes lagopi*			*Lagopoecus affinis*			*Ornithomya chloropus*			*Ceratophyllus garei*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	10.0±5.5	16.7±6.8	13.3±4.4	100.0±0.0	96.7±3.3	98.3±1.7	76.7±7.7	56.7±9.0	66.7±6.1	43.3±9.0	60.0±8.9	51.7±6.5	0.0	0.0	0.0
2007	13.3±6.2	13.3±6.2	13.3±4.4	73.3±8.1	93.3±4.6	83.3±4.8	63.3±8.8	60.0±8.9	61.7±6.3	23.3±7.7	23.3±7.7	23.3±5.5	3.3±3.3	0.0	1.7±1.7
2008	25.0±8.2	25.0±8.0	19.3±5.2	78.6±7.8	86.2±6.4	82.5±5.0	50.0±9.4	44.8±9.2	47.4±6.6	46.4±9.4	41.4±9.1	43.9±6.6	0.0	0.0	0.0
2009	6.0±4.4	6.0±4.3	18.6±5.1	23.0±7.8	86.7±6.2	83.1±4.9	2.0±2.6	70.0±8.4	72.9±5.8	12.0±6.0	26.7±8.1	33.9±6.2	0.0	0.0	0.0
2010	20.0±7.3	20.0±7.3	23.3±5.5	93.3±4.6	76.7±7.7	85.0±4.6	60.0±8.9	46.7±9.1	53.3±6.4	30.0±8.4	33.3±8.6	31.7±6.0	3.3±3.3	0.0	1.7±1.7
2011	16.7±6.8	16.7±6.8	28.3±5.8	83.3±6.8	90.0±5.5	86.7±4.4	73.3±8.1	83.3±6.8	78.3±5.3	60.0±8.9	63.3±8.8	61.7±6.3	0.0	0.0	0.0
2012	6.7±4.6	6.7±4.6	8.3±3.6	86.7±6.2	80.0±7.3	83.3±4.8	73.3±8.1	70.0±8.4	71.7±5.8	46.7±9.1	36.7±8.8	41.7±6.4	0.0	0.0	0.0
All	15.9±2.5	19.6±2.7	17.8±1.9	85.0±2.9	87.1±2.3	86.1±1.7	67.6±3.3	61.7±3.4	64.7±2.3	41.5±3.4	40.7±3.4	41.1±2.4	1.0±0.7	0.0	0.5±0.3

Year	*Eimeria muta*			*Eimeria rjupa*			*Capillaria caudinflata*			*Trichostrongylus tenuis*			*Passerilepis lagopi*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	100.0±0.0	93.3±4.6	96.7±2.3	33.3±8.6	36.7±8.8	35.0±6.2	26.7±8.1	36.7±8.8	31.7±6.0	0.0	6.7±4.6	3.3±12.6	3.3±3.3	6.7±4.6	5.0±2.8
2007	63.3±8.8	80.0±7.3	71.7±5.8	20.0±7.3	33.3±8.6	26.7±5.7	23.3±7.7	13.3±6.2	35.0±6.2	0.0	0.0	0.0	0.0	0.0	0.0
2008	82.1±7.0	62.1±9.0	71.9±6.0	3.6±3.5	3.4±3.4	3.5±2.4	46.4±9.4	20.7±7.5	33.3±6.2	0.0	0.0	0.0	0.0	0.0	0.0
2009	79.3±7.7	76.7±7.7	78.0±5.4	6.9±4.7	10.0±5.5	8.5±3.6	17.2±7.0	16.7±6.8	16.9±4.9	3.4±3.4	13.3±6.2	8.5±12.5	3.4±3.3	0.0	1.7±1.7
2010	93.3±4.6	90.0±5.5	91.7±3.6	10.0±5.5	26.7±7.8	18.3±5.0	30.0±8.4	53.3±9.1	41.7±6.4	3.3±3.3	3.3±3.3	3.3±12.6	3.3±3.3	6.7±4.6	5.0±2.8
2011	100.0±0.0	86.7±6.2	93.3±3.2	6.7±4.6	23.3±8.1	15.0±4.6	20.0±7.3	36.7±8.8	28.3±5.8	0.0	3.3±3.3	1.7±12.9	0.0	0.0	0.0
2012	66.7±8.6	50.0±9.1	58.3±6.4	10.0±5.5	6.7±4.6	8.3±3.6	20.0±7.3	33.3±8.6	26.7±5.7	0.0	0.0	0.0	6.7±4.6	3.3±3.3	0.0
All	83.6±2.6	77.0±2.9	80.3±2.0	13.0±2.3	20.1±2.8	16.6±1.8	26.2±3.1	30.3±3.2	28.2±2.2	1.0±0.7	3.8±1.3	2.4±4.8	2.4±1.1	2.4±0.8	2.4±0.8

(C)

All

Year	*Tetraolichus lagopi*	*Strelkoviacarus holoaspis*	*Metamicrolichus islandicus*	*Myialges borealis*	*Mironovia lagopus*
2006	15.2±2.1	32.2±9.0	14.2±3.7	2.1±0.4	-
2007	23.8±2.5	35.4±8.3	14.5±5.1	3.1±0.6	-
2008	8.6±1.2	17.1±4.0	8.3±1.8	2.4±0.3	-
2009	18.9±3.3	30.0±9.4	10.7±2.4	1.9±0.4	-
2010	8.8±1.3	20.8±8.5	14.5±6.1	3.6±1.4	-
2011	9.2±1.5	19.9±5.2	6.2±2.0	2.4±0.8	-
2012	26.9±3.0	88.3±28.1	10.7±4.3	3.7±0.7	-
All	16.5±0.9	36.7±5.8	11.9±1.6	2.6±0.3	-

Year	*Amyrsidea lagopi*	*Goniodes lagopi*	*Lagopoecus affinis*	*Ornithomya chloropus*	*Ceratophyllus garei*
2006	10.8±4.2	13.8±2.2	3.4±0.6	2.3±0.2	0.0
2007	13.4±6.5	8.0±0.7	3.7±0.5	1.3±0.2	1.0±0.0
2008	11.2±4.8	7.3±1.1	5.2±1.3	1.7±0.2	0.0
2009	11.1±4.9	6.2±0.8	4.6±0.7	1.7±0.2	0.0
2010	6.7±2.1	6.4±0.7	3.2±0.5	1.6±0.2	1.0±0.0
2011	15.2±4.6	18.7±2.7	7.7±1.7	2.1±0.2	0.0
2012	14.0±9.0	8.0±1.0	4.2±0.6	1.6±0.2	0.0
All	11.8±2.5	10.2±1.0	4.7±1.2	1.8±0.1	1.0±0.0

Year	*Eimeria muta*	*Eimeria rjupa*	*Capillaria caudinflata*	*Trichostrongylus tenuis*	*Passerilepis lagopi*
2006	364.7±119.5	327.7±124.0	10.2±3.0	3.7±0.6	18.0±16.5
2007	339.7±91.8	220.3±99.0	5.3±1.7	0.0	0.0
2008	400.6±136.1	77.3±15.1	15.8±4.9	0.0	0.0
2009	167.4±34.0	201.1±107.6	16.9±6.5	1.2±0.2	7.0±0.0
2010	319.6±157.5	144.4±42.0	17.2±4.8	5.5±2.0	1.0±0.0
2011	94.5±19.9	904.5±814.0	27.7±7.1	2.0±1.0	0.0
2012	93.8±28.0	34.1±15.1	9.4±1.9	0.0	7.7±6.2
All	252.2±40.1	322.2±134.1	15.1±1.9	3.4±0.6	8.7±5.1

Adult

Year	*Tetraolichus lagopi*			*Strelkoviacarus holoaspis*			*Metamicrolichus islandicus*			*Myialges borealis*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	21.7±8.9	5.9±2.1	13.2±4.4	43.0±16.4	64.2±50.3	54.8±27.6	3.7±1.5	0.0	3.7±1.5	1.0±0.0	1.0±0.0	1.0±0.0
2007	27.0±8.9	11.5±6.1	15.6±5.2	2.3±0.3	44.4±43.3	23.3±21.5	13.0±0.0	4.0±2.7	5.8±2.7	2.0±0.0	2.0±0.0	2.0±0.0
2008	14.8±5.1	3.8±1.6	11.2±3.6	2.6±0.5	1.0±0.0	2.4±0.5	3.5±1.7	1.0±0.0	3.0±1.4	2.0±0.0	0.0	2.0±0.0
2009	33.2±20.4	4.4±1.0	14.5±7.6	20.3±9.1	2.3±1.3	11.3±5.8	0.0	1.0±0.0	1.0±0.0	0.0	1.0±0.0	1.0±0.0
2010	15.0±5.1	2.6±0.5	8.8±2.8	5.0±3.0	12.7±11.7	9.6±6.7	1.0±0.0	0.0	1.0±0.0	1.0±0.0	0.0	1.0±0.0
2011	10.4±4.5	2.3±0.5	5.8±2.1	3.4±1.3	43.8±26.4	23.6±14.2	8.0±7.0	4.0±0.0	6.7±4.3	1.0±0.0	2.5±0.5	2.0±0.6
2012	50.3±14.4	16.2±4.0	24.5±5.1	19.5±10.1	17.8±14.7	18.3±10.4	0.0	2.5±1.5	2.5±1.5	0.0	6.0±0.0	6.0±0.0
All	22.7±3.7	8.4±1.5	14.1±1.8	12.6±3.6	30.3±11.4	21.5±6.0	5.0±1.5	2.8±1.1	4.0±1.0	1.4±0.2	2.3±0.7	1.9±0.4

Year	*Amyrsidea lagopi*			*Goniodes lagopi*			*Lagopoecus affinis*			*Ornithomya chloropus*			*Ceratophyllus garei*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	4.0±0.0	0.0	4.0±0.0	5.0±1.5	2.5±0.5	3.8±0.9	2.3±0.6	2.5±0.5	2.3±0.4	3.0±0.6	2.0±0.5	2.4±0.4	0.0	0.0	0.0
2007	0.0	0.0	0.0	3.3±1.4	2.3±0.7	2.9±0.8	1.0±0.0	2.5±0.5	1.5±0.3	1.0±0.0	1.0±0.0	1.0±0.0	0.0	0.0	0.0
2008	0.0	0.0	0.0	4.8±1.6	9.0±0.0	5.2±1.5	5.8±4.4	1.0±0.0	4.2±3.0	2.8±1.4	3.0±0.0	2.8±1.1	0.0	0.0	0.0
2009	3.0±0.0	0.0	3.0±0.0	3.7±1.3	3.3±1.5	3.6±0.9	1.0±0.0	2.0±1.0	1.6±0.6	1.5±0.5	2.3±0.8	2.0±0.5	0.0	0.0	0.0
2010	0.0	0.0	0.0	4.1±1.5	2.2±0.5	2.9±0.7	1.4±0.4	3.5±2.5	2.0±0.7	1.5±0.5	1.8±0.3	1.7±0.2	0.0	0.0	0.0
2011	1.5±0.5	0.0	1.5±0.5	7.3±2.2	4.3±1.6	5.9±1.4	5.1±1.6	2.7±0.7	4.5±1.2	1.8±0.5	1.9±0.4	1.9±0.3	0.0	0.0	0.0
2012	0.0	0.0	0.0	7.7±1.2	3.3±1.2	4.1±1.1	5.0±1.0	2.6±0.8	3.1±0.7	2.0±0.0	1.4±0.3	1.5±0.2	0.0	0.0	0.0
All	2.2±0.5	0.0	2.2±0.5	5.3±0.8	3.8±0.5	4.3±0.5	3.4±0.8	2.5±0.4	3.0±0.5	2.1±0.3	1.7±0.2	1.8±0.1	0.0	0.0	0.0

Year	*Eimeria muta*			*Eimeria rjupa*			*Capillaria caudinflata*			*Trichostrongylus tenuis*			*Passerilepis lagopi*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	1101.5±805.6	99.1±36.9	561.7±377.1	271.3±256.4	2.0±0.0	163.6±155.2	21.2±13.7	1.8±0.6	11.5±7.2	3.2±1.2	4.4±1.0	3.8±0.8	0.0	0.0	0.0
2007	218.0±139.3	221.1±110.7	220.4±89.7	0.0	205.3±196.7	205.3±196.7	0.0	5.1±3.5	5.1±3.5	0.0	0.0	0.0	0.0	0.0	0.0
2008	189.7±100.9	129.0±67.9	157.3±57.7	86.0±0.0	0.0	86.0±0.0	7.8±2.5	6.6±2.2	7.1±1.5	0.0	0.0	0.0	0.0	0.0	0.0
2009	155.6±91.0	126.5±55.8	137.7±46.9	0.0	499.0±313.0	499.0±313.0	33.0±32.0	23.2±14.2	26.9±13.6	0.0	0.0	0.0	0.0	0.0	0.0
2010	1212.3±1145.1	104.2±27.2	507.1±416.0	30.5±18.5	90.0±87.0	60.3±40.2	9.3±7.6	9.8±4.1	9.6±3.7	7.5±6.5	5.0±0.0	6.3±2.8	0.0	0.0	0.0
2011	60.4±18.6	41.7±11.9	49.6±10.4	34.5±18.5	102.0±54.8	79.5±37.8	20.7±9.1	22.0±11.0	21.2±6.7	3.0±2.0	1.0±0.0	2.3±1.3	0.0	0.0	0.0
2012	19.0±8.2	99.4±68.7	83.9±55.6	75.0±NA	27.7±21.3	39.5±19.1	1.0±0.0	9.0±3.9	7.7±3.4	0.0	0.0	0.0	0.0	0.0	0.0
All	542.5±288.5	107.2±21.1	265.0±106.2	122.8±83.2	146.7±62.9	138.4±49.2	16.8±5.2	10.3±2.4	12.7±2.5	4.1±1.4	4.1±0.7	4.1±0.8	0.0	0.0	0.0

Juveniles

Year	*Tetraolichus lagopi*			*Strelkoviacarus holoaspis*			*Metamicrolichus islandicus*			*Myialges borealis*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	19.5±3.3	12.8±2.9	16.1±2.2	30.6±11.9	16.9±5.4	23.8±6.6	15.7±7.9	15.1±4.3	15.4±4.1	2.5±0.7	2.0±0.4	2.3±0.4
2007	33.0±5.1	19.9±1.9	26.4±2.8	47.4±17.7	33.1±10.2	38.3±9.0	9.3±4.3	23.1±11.3	16.0±5.9	3.4±1.2	3.0±0.8	3.2±0.7
2008	7.7±1.5	7.7±1.5	7.7±1.0	16.5±6.4	26.3±7.5	20.8±4.9	8.1±3.1	11.6±3.1	9.7±2.2	2.2±0.3	2.7±0.7	2.4±0.4
2009	24.3±5.9	22.9±4.2	20.1±3.6	46.4±19.9	18.6±5.4	33.3±11.0	15.6±3.7	6.4±2.5	11.5±2.5	2.3±0.8	1.5±0.3	1.9±0.5
2010	9.7±2.1	9.9±1.9	8.8±1.4	14.8±5.1	29.7±18.0	22.8±9.9	24.4±10.7	5.5±2.9	16.0±6.6	5.4±2.9	2.2±1.0	3.8±1.5
2011	13.5±3.1	12.0±2.5	11.3±2.0	15.9±3.9	19.8±6.5	18.1±4.0	4.0±1.9	16.0±NA	6.0±2.5	2.0±1.0	2.8±1.8	2.5±1.1
2012	31.9±5.9	22.3±4.1	28.4±3.6	63.5±18.2	154.5±64.0	115.9±38.0	8.6±4.4	16.0±9.2	12.3±5.0	2.5±1.5	3.8±0.9	3.3±0.7
All	20.7±1.8	14.4±1.2	17.5±1.1	33.5±5.5	47.8±12.7	41.1±7.2	12.2±2.1	14.3±3.0	13.2±1.8	2.9±0.5	2.5±0.3	2.7±0.3

Year	*Amyrsidea lagopi*			*Goniodes lagopi*			*Lagopoecus affinis*			*Ornithomya chloropus*			*Ceratophyllus garei*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	12.0±7.1	11.4±6.8	11.6±4.7	17.1±4.4	14.7±2.9	15.9±2.6	4.0±1.1	2.9±0.6	3.6±0.7	3.2±0.4	1.6±0.2	2.3±0.3	0.0	0.0	0.0
2007	19.3±12.7	7.5±3.3	33.4±6.5	10.3±1.2	7.5±1.0	8.7±0.8	4.5±1.0	3.7±0.7	4.1±0.6	1.4±0.3	1.4±0.3	1.4±0.2	1.0±0.0	0.0	1.0±0.0
2008	7.7±3.9	17.3±11.9	11.2±4.8	8.0±1.9	7.5±1.8	7.7±1.3	4.6±1.7	6.4±2.4	5.5±1.4	1.5±0.2	1.5±0.2	1.5±0.2	0.0	0.0	0.0
2009	6.0±4.6	18.8±10.2	11.8±5.4	6.8±1.0	6.7±1.4	6.8±0.9	4.8±1.2	5.1±1.1	4.9±0.8	1.8±0.3	1.5±0.2	1.7±0.2	0.0	0.0	0.0
2010	9.5±4.2	4.6±1.7	6.7±2.1	6.9±1.3	8.5±1.0	7.6±0.8	3.7±0.9	3.1±0.7	3.4±0.6	1.4±0.3	1.5±0.2	1.5±0.2	1.0±0.0	0.0	1.0±0.0
2011	11.8±6.0	21.3±7.2	18.5±5.4	29.2±5.5	21.8±5.0	25.3±3.7	11.4±4.1	6.1±1.7	8.6±2.1	2.6±0.6	2.1±0.3	2.3±0.3	0.0	0.0	0.0
2012	7.0±6.0	18.7±15.2	14.0±9.0	9.6±1.9	9.0±1.7	9.3±1.3	4.9±1.3	3.9±0.8	4.4±0.7	1.4±0.2	2.2±0.6	1.7±0.3	0.0	0.0	0.0
All	10.1±2.2	14.6±3.0	12.6±2.0	12.8±1.3	11.0±1.0	11.8±0.8	5.5±0.8	4.5±0.5	5.0±0.5	2.0±0.2	1.7±0.1	1.9±0.1	2.0±0.0	0.0	2.0±0.0

Year	*Eimeria muta*			*Eimeria rjupa*			*Capillaria caudinflata*			*Trichostrongylus tenuis*			*Passerilepis lagopi*		
	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All	Female	Male	All
2006	302.1±70.7	248.9±41.0	276.4±41.4	576.8±293.4	175.8±82.9	366.8±149.2	15.6±4.8	5.1±2.6	9.5±2.7	0.0	3.0±1.0	3.0±1.0	51.0±0.0	1.5±0.5	18.0±16.5
2007	346.4±153.5	404.0±176.0	378.5±118.1	31.7±28.1	339.4±179.0	224.0±116.6	5.4±2.1	5.3±3.6	5.4±1.8	0.0	0.0	0.0	0.0	0.0	0.0
2008	678.8±315.7	247.9±96.9	489.6±183.4	48.0±0.0	98.0±0.0	73.0±25.0	13.2±4.5	34.5±19.9	19.9±7.0	0.0	0.0	0.0	0.0	0.0	0.0
2009	233.1±75.1	118.5±34.2	175.8±41.7	64.0±62.0	94.0±74.6	82.0±45.9	15.4±6.3	2.4±0.9	8.9±3.7	1.0±0.0	1.3±0.3	1.2±0.2	7.0±0.0	0.0	7.0±0.0
2010	230.3±75.8	183.1±37.7	207.1±42.5	151.0±57.5	184.0±72.0	175.0±53.3	23.1±9.4	18.6±8.9	20.2±6.5	1.0±0.0	7.0±0.0	4.0±3.0	1.0±0.0	1.0±0.0	1.0±0.0
2011	74.6±18.4	174.4±61.3	120.9±30.5	141.0±138.5	1829.6±1744.5	1454.4±1355.5	26.8±23.9	34.7±11.8	31.9±11.0	0.0	1.0±0.0	1.0±0.0	0.0	0.0	0.0
2012	109.1±43.0	90.7±26.1	101.2±26.7	7.3±5.8	63.5±62.5	29.8±24.3	9.0±2.8	11.8±3.1	10.8±2.2	0.0	0.0	0.0	11.0±9.0	1.0±0.0	7.7±6.2
All	274.5±50.8	215.5±32.3	246.0±30.6	255.3±116.5	478.9±292.6	391.4±183.4	15.4±3.3	17.3±3.8	16.5±2.6	1.0±0.0	2.4±0.8	2.1±0.6	16.2±9.3	0.4±0.2	8.7±5.1

(D)

Year	*Tetraolichus lagopi*			*Strelkoviacarus holoaspis*			*Metamicrolichus islandicus*			*Myialges borealis*			*Mironovia lagopus*		
	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All
2006	0.511	0.679	0.582	0.824	0.87	0.866	0.823	0.903	0.874	0.822	0.875	0.861	-	-	-
2007	0.411	0.59	0.471	0.815	0.89	0.849	0.847	0.827	0.866	0.828	0.857	0.853	-	-	-
2008	0.526	0.691	0.601	0.76	0.72	0.814	0.815	0.856	0.851	0.831	0.923	0.872	-	-	-
2009	0.571	0.697	0.616	0.817	0.824	0.841	0.571	0.850	0.846	0.837	0.900	0.867	-	-	-
2010	0.559	0.785	0.661	0.854	0.932	0.898	0.925	0.951	0.954	0.909	0.951	0.941	-	-	-
2011	0.657	0.742	0.710	0.814	0.917	0.882	0.934	0.938	0.946	0.916	0.921	0.931	-	-	-
2012	0.479	0.573	0.525	0.821	0.896	0.874	0.917	0.941	0.945	0.911	0.951	0.939	-	-	-
All	0.531	0.680	0.636	0.866	0.937	0.893	0.833	0.895	0.917	0.886	0.958	0.913	-	-	-

Year	*Amyrsidea lagopi*			*Goniodes lagopi*			*Lagopoecus affinis*			*Ornithomya chloropus*			*Ceratophyllus garei*		
	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All
2006	0.922	-	0.944	0.548	0.712	0.656	0.649	0.821	0.866	0.642	0.783	0.699	-	-	-
2007	0.929	-	0.947	0.455	0.743	0.556	0.645	0.735	0.698	0.807	0.762	0.811	-	-	-
2008	0.912	-	0.938	0.597	0.737	0.656	0.783	0.874	0.825	0.657	0.846	0.739	-	-	-
2009	0.923	-	0.938	0.513	0.658	0.567	0.637	0.775	0.699	0.735	0.742	0.749	-	-	-
2010	0.882	-	0.929	0.487	0.406	0.617	0.685	0.871	0.773	0.748	0.722	0.747	-	-	-
2011	0.866	-	0.915	0.591	0.674	0.684	0.697	0.798	0.761	0.614	0.624	0.628	-	-	-
2012	0.952	-	0.971	0.564	0.772	0.669	0.626	0.821	0.717	0.706	0.703	0.713	-	-	-
All	0.931	-	0.953	0.608	0.756	0.682	0.707	0.866	0.768	0.723	0.763	0.738	-	-	-

Year	*Eimeria muta*			*Eimeria rjupa*			*Capillaria caudinflata*			*Trichostrongylus tenuis*			*Passerilepis lagopi*		
	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All	Juv	Ad	All
2006	0.573	0.871	0.755	0.902	0.934	0.926	0.861	0.883	0.884	-	-	-	-	-	-
2007	0.829	0.871	0.832	0.929	0.901	0.936	0.823	0.897	0.894	-	-	-	-	-	-
2008	0.823	0.750	0.835	0.954	0.923	0.957	0.875	0.736	0.872	-	-	-	-	-	-
2009	0.722	0.698	0.731	0.949	0.881	0.954	0.918	0.814	0.920	-	-	-	-	-	-
2010	0.647	0.894	0.818	0.894	0.935	0.924	0.850	0.873	0.877	-	-	-	-	-	-
2011	0.697	0.623	0.708	0.964	0.908	0.975	0.892	0.853	0.893	-	-	-	-	-	-
2012	0.777	0.853	0.827	0.961	0.921	0.957	0.836	0.843	0.855	-	-	-	-	-	-
All	0.775	0.898	0.827	0.974	0.964	0.976	0.909	0.894	0.906	-	-	-	-	-	-

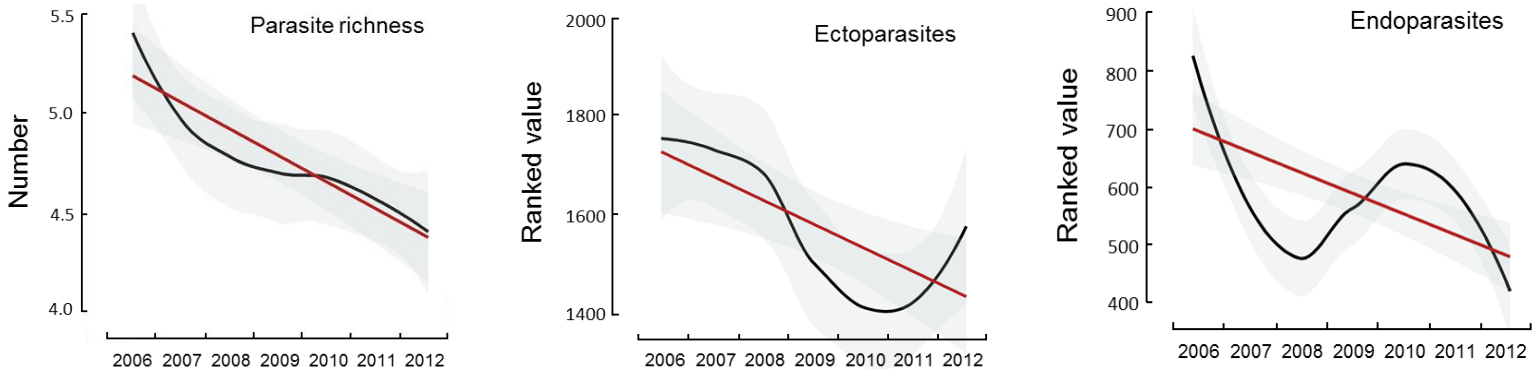
Appendix B

Sources of variation for (A) parasite measures (ranked values; abundance), and (B) ectoparasite and (C) and endoparasite prevalence and mean intensities from hurdle models illustrated through gg-plots of rock ptarmigan in northeast Iceland October 2006–2012.

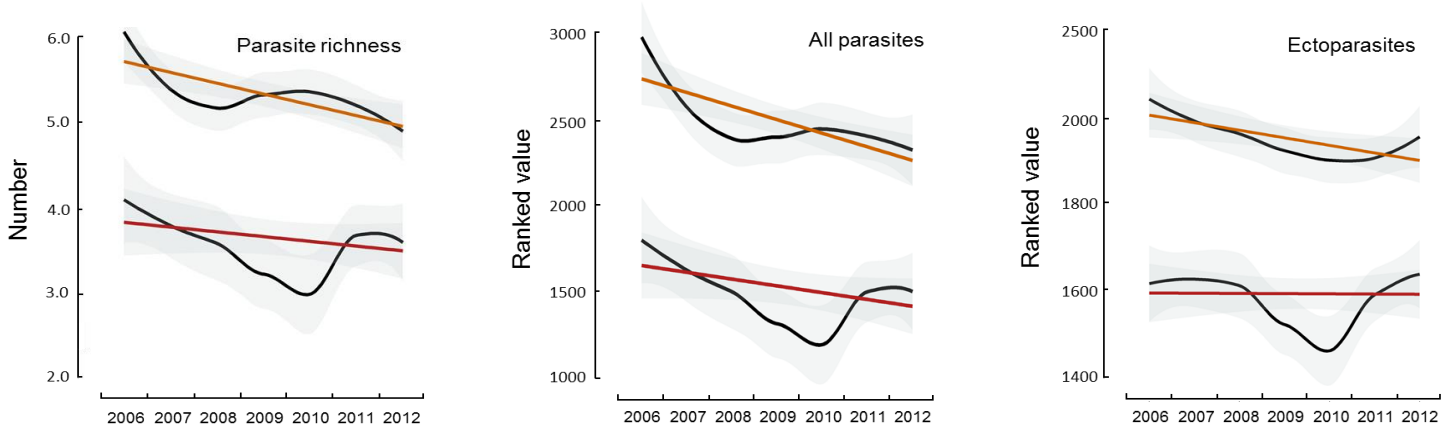
Linear regression lines: blue = males, lila = females, orange = juveniles, red = adults
Underlying smooth regression lines: black

(A)

Year



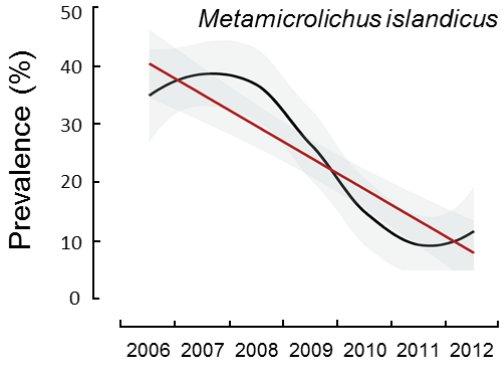
Age: year



(B)

Prevalence

Year



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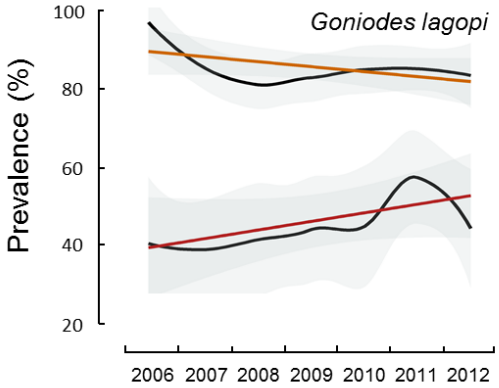
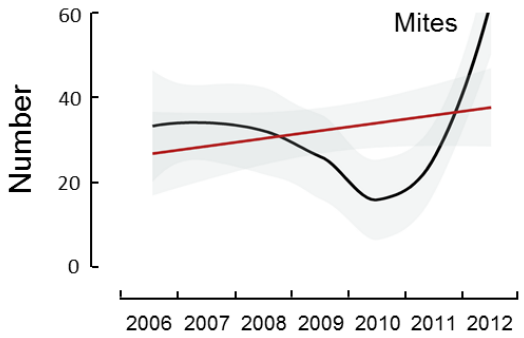
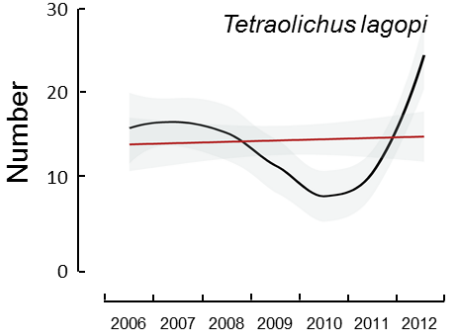
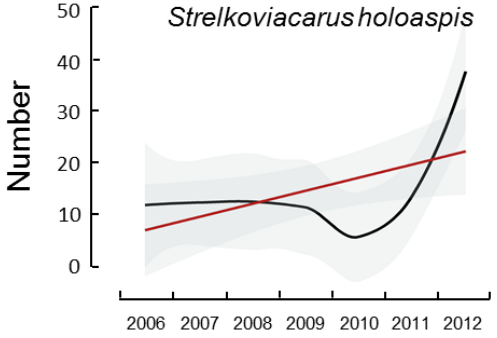


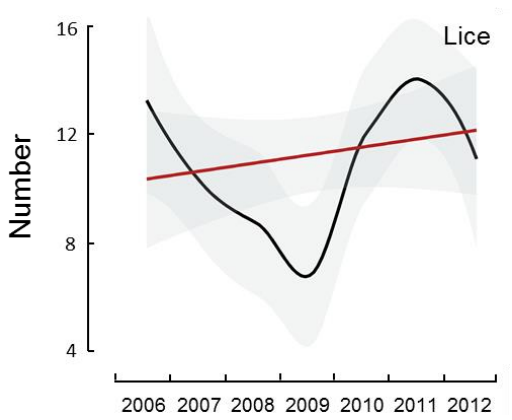
Mean Intensity

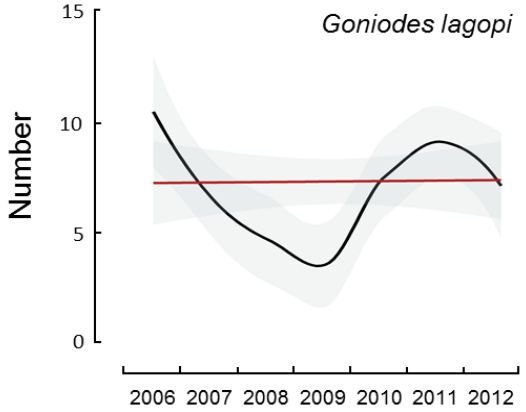
Year



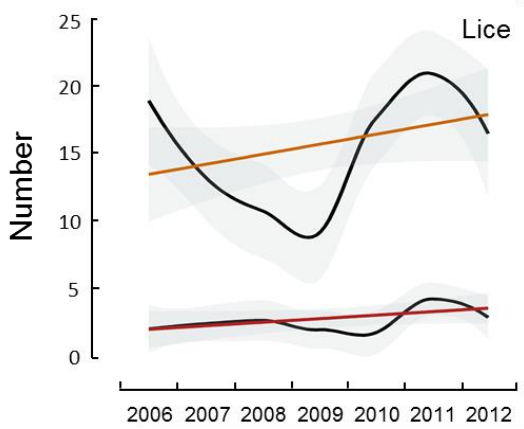


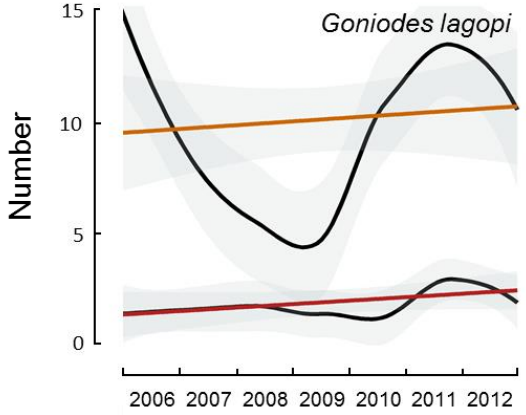


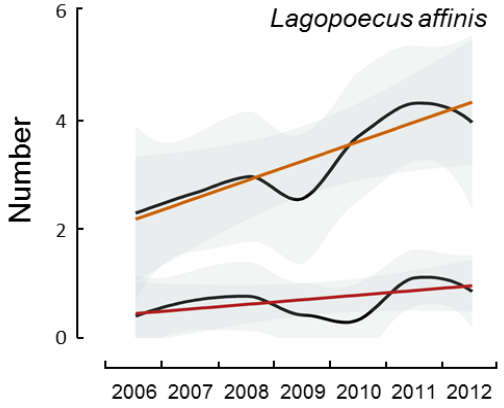

Lice
Number
16
12
8
4
2006 2007 2008 2009 2010 2011 2012

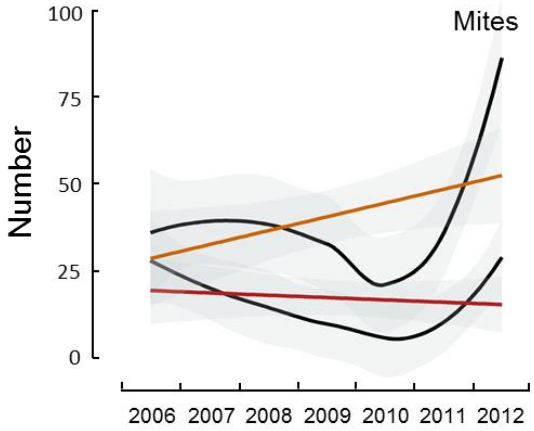

Goniodes lagopi
Number
15
10
5
0
2006 2007 2008 2009 2010 2011 2012

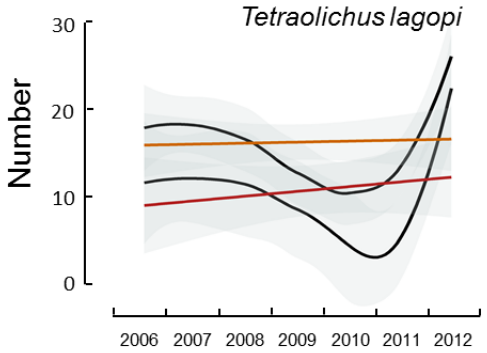
Age: year

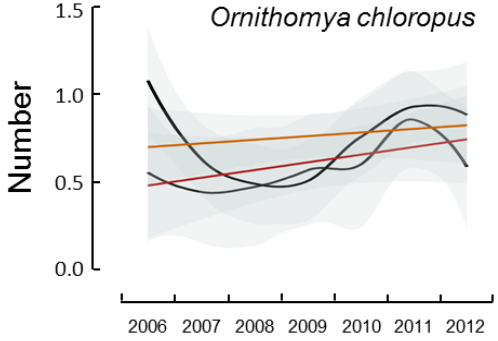

Lice
Number
25
20
15
10
5
0
2006 2007 2008 2009 2010 2011 2012


Goniodes lagopi
Number
15
10
5
0
2006 2007 2008 2009 2010 2011 2012


Lagopoecus affinis
Number
6
4
2
0
2006 2007 2008 2009 2010 2011 2012



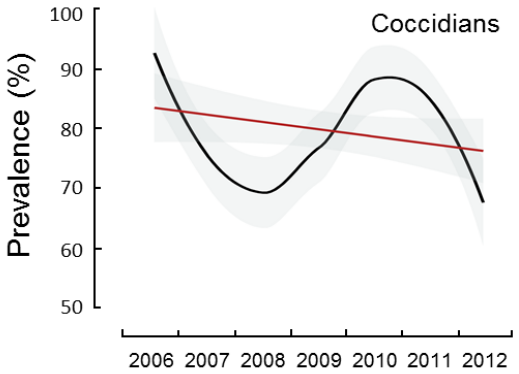


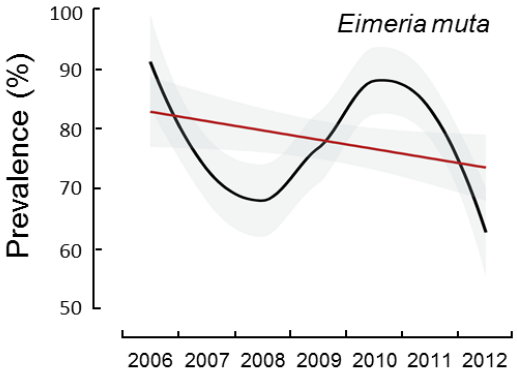


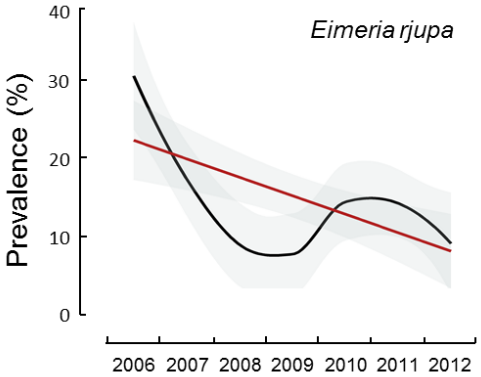
(C)

Prevalence

Year

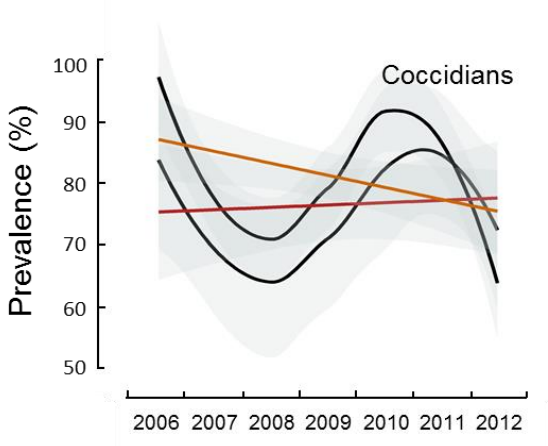


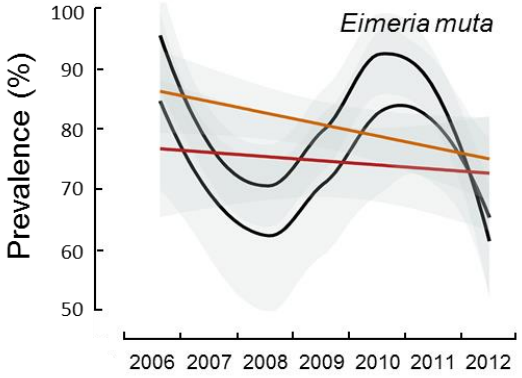


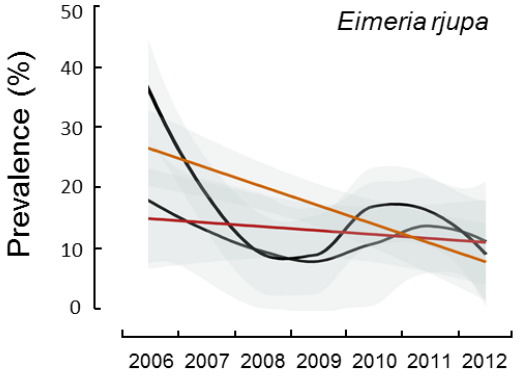



Helminths
Prevalence (%)
50
40
30
20
2006 2007 2008 2009 2010 2011 2012

Age: year

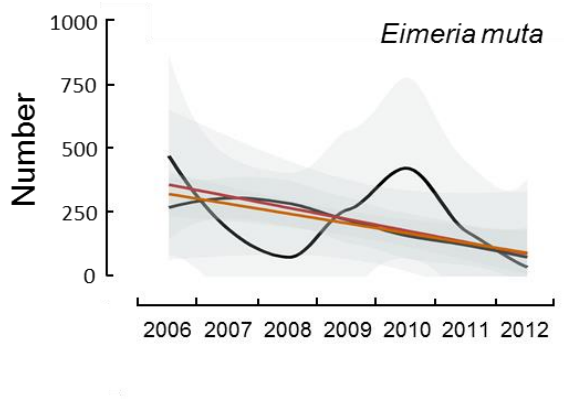

Coccidians
Prevalence (%)
100
90
80
70
60
50
2006 2007 2008 2009 2010 2011 2012


Eimeria muta
Prevalence (%)
100
90
80
70
60
50
2006 2007 2008 2009 2010 2011 2012

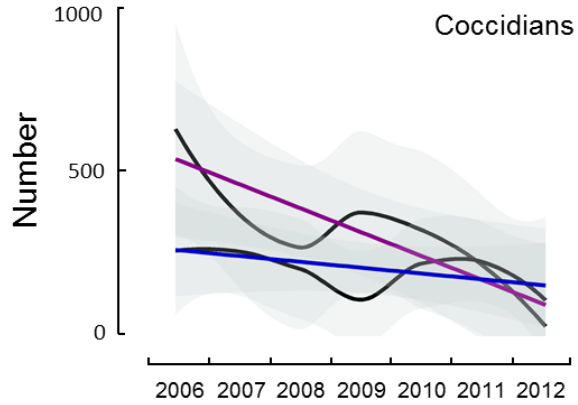

Eimeria rjupa
Prevalence (%)
50
40
30
20
10
0
2006 2007 2008 2009 2010 2011 2012

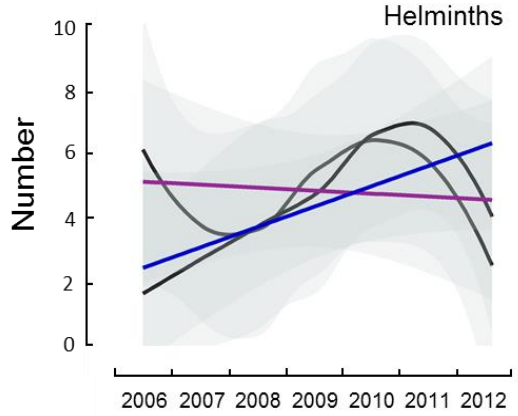
Mean Intensity

Age: year



Sex:year





Appendix C

Spearman's rank correlation pyramids of annual parasite associations of rock ptarmigan in northeast Iceland October 2006–2012.

Top value: Spearman rho. Bottom value: p-value. Significant p-values highlighted in red.

2006

	Em	Er	Cc	Tl	Sh	Mi	Mb	Gl	La	Al
Er	0.082									
	0.440									
Cc	-0.055	0.079								
	0.607	0.459								
Tl	-0.003	0.000	**0.291**							
	0.978	0.999	**0.005**							
Sh	-0.054	-0.159	0.177	0.167						
	0.613	0.132	0.094	0.114						
Mi	0.166	0.133	-0.008	**0.267**	0.044					
	0.116	0.209	0.939	**0.011**	0.680					
Mb	-0.054	-0.064	-0.061	0.181	0.097	**0.332**				
	0.609	0.548	0.567	0.087	0.363	**0.001**				
Gl	**0.313**	-0.060	**0.220**	**0.362**	-0.010	0.114	0.098			
	0.003	0.574	**0.036**	**0.000**	0.924	0.280	0.355			
La	0.009	-0.037	0.132	**0.314**	0.124	0.055	0.191	**0.585**		
	0.935	0.725	0.212	**0.002**	0.240	0.602	0.070	**0.000**		
Al	0.000	0.045	**0.400**	0.110	0.053	-0.098	0.024	**0.239**	0.097	
	0.999	0.670	**0.000**	0.299	0.616	0.357	0.823	**0.023**	0.358	
Oc	-0.066	0.038	0.072	0.087	-0.037	**-0.253**	-0.036	**0.288**	0.189	0.023
	0.534	0.723	0.498	0.411	0.731	**0.016**	0.735	**0.006**	0.073	0.832

2007

	em	er	cc	tl	sh	mi	mb	gl	la	al
er	0.127									
	0.262									
cc	0.011	-0.036								
	0.924	0.756								
tl	-0.201	-0.015	-0.199							
	0.073	0.897	0.078							
sh	0.102	0.013	-0.164	**0.223**						
	0.369	0.909	0.148	**0.047**						
mi	0.066	-0.023	0.059	0.290	0.011					
	0.563	0.840	0.606	0.009	0.921					
mb	0.091	0.047	0.174	0.203	0.011	**0.581**				
	0.420	0.676	0.126	0.071	0.924	**0.000**				
gl	-0.088	-0.016	-0.048	**0.337**	0.189	-0.050	-0.003			
	0.439	0.886	0.673	**0.002**	0.093	0.657	0.977			
la	0.021	-0.000	-0.122	**0.371**	**0.305**	0.037	0.057	**0.460**		
	0.850	0.998	0.285	**0.001**	**0.006**	0.743	0.617	**0.000**		
al	0.043	-0.092	-0.167	-0.058	0.092	-0.179	-0.070	0.018	0.120	
	0.703	0.417	0.140	0.608	0.419	0.112	0.536	0.872	0.290	
oc	0.195	-0.015	0.035	-0.148	-0.087	-0.112	-0.070	-0.106	-0.124	-0.054
	0.084	0.893	0.762	0.190	0.445	0.321	0.540	0.348	0.273	0.632

2008

	em	er	cc	tl	sh	mi	mb	gl	la	al
er	-0.083									
	0.459									
cc	0.392	0.000								
	0.000	1.000								
tl	0.112	0.146	0.140							
	0.317	0.192	0.210							
sh	-0.064	0.245	0.088	0.292						
	0.569	**0.027**	0.432	**0.008**						
mi	0.132	0.019	0.169	0.263	0.068					
	0.238	0.868	0.129	**0.017**	0.543					
mb	0.091	-0.084	0.148	0.160	0.027	0.737				
	0.414	0.452	0.185	0.152	0.810	**0.000**				
gl	-0.111	0.117	0.020	0.180	0.295	0.015	0.181			
	0.319	0.296	0.859	0.105	**0.007**	0.891	0.104			
la	-0.028	0.186	-0.188	0.369	0.452	0.014	-0.039	0.183		
	0.805	0.093	0.092	**0.001**	**0.000**	0.898	0.731	0.099		
al	0.113	-0.076	-0.161	0.144	0.039	-0.132	-0.170	0.103	0.181	
	0.313	0.495	0.150	0.196	0.727	0.238	0.128	0.357	0.104	
oc	0.163	0.122	0.144	0.109	0.234	-0.065	-0.010	0.045	0.104	-0.091
	0.144	0.273	0.196	0.328	**0.035**	0.562	0.928	0.691	0.352	0.418

2009

	em	er	cc	tl	sh	mi	mb	gl	la	al
er	0.117									
	0.307									
cc	0.160	-0.077								
	0.163	0.501								
tl	-0.042	-0.130	0.039							
	0.714	0.256	0.733							
sh	**-0.263**	-0.158	0.007	0.099						
	0.020	0.168	0.949	0.389						
mi	0.015	-0.027	0.019	**0.343**	0.025					
	0.893	0.817	0.866	**0.002**	0.830					
mb	0.065	0.082	0.133	0.192	-0.102	**0.649**				
	0.570	0.474	0.246	0.093	0.376	**0.000**				
gl	-0.077	-0.225	-0.085	**0.278**	0.199	-0.036	0.012			
	0.505	0.048	0.458	**0.014**	0.081	0.755	0.916			
la	0.016	-0.146	-0.011	0.162	0.144	0.120	0.102	**0.455**		
	0.889	0.201	0.927	0.157	0.210	0.294	0.375	**0.000**		
al	0.088	-0.013	-0.147	0.141	-0.010	0.030	0.213	0.167	0.192	
	0.442	0.909	0.200	0.219	0.931	0.795	0.062	0.144	0.093	
oc	-0.026	-0.132	0.056	0.142	-0.039	**-0.361**	-0.169	0.046	0.142	0.051
	0.819	0.249	0.628	0.214	0.735	**0.001**	0.139	0.692	0.214	0.659

2010

	em	er	cc	tl	sh	mi	mb	gl	la	al
er	**0.219**									
	0.029									
cc	0.046	0.183								
	0.650	0.069								
tl	0.113	0.019	0.132							
	0.264	0.854	0.190							
sh	-0.154	-0.106	0.074	**0.360**						
	0.126	0.293	0.462	**0.000**						
mi	0.185	-0.139	0.027	**0.301**	0.146					
	0.065	0.167	0.788	**0.002**	0.146					
mb	0.080	-0.061	0.141	**0.336**	0.191	**0.569**				
	0.430	0.549	0.161	**0.001**	0.057	**0.000**				
gl	0.055	0.040	0.117	**0.360**	0.158	-0.032	0.104			
	0.584	0.690	0.248	**0.000**	0.118	0.749	0.302			
la	0.066	0.022	**0.207**	**0.424**	**0.282**	-0.004	0.045	**0.495**		
	0.517	0.828	**0.039**	**0.000**	**0.004**	0.972	0.658	**0.000**		
al	0.105	-0.087	0.196	**0.304**	**0.243**	**0.352**	**0.412**	**0.206**	0.124	
	0.298	0.392	0.051	**0.002**	**0.015**	**0.000**	**0.000**	**0.040**	0.218	
oc	0.059	-0.080	-0.093	**-0.229**	0.058	**-0.229**	**-0.241**	-0.031	-0.093	**-0.225**
	0.559	0.430	0.359	**0.022**	0.567	**0.022**	**0.016**	0.760	0.358	**0.024**

2011

	em	er	cc	tl	sh	mi	mb	gl	la	al
er	-0.056									
	0.576									
cc	**0.222**	-0.007								
	0.026	0.947								
tl	0.047	0.022	0.159							
	0.637	0.824	0.112							
sh	-0.070	-0.127	0.151	**0.339**						
	0.486	0.205	0.132	**0.001**						
mi	-0.046	-0.130	-0.019	0.165	**0.287**					
	0.645	0.195	0.852	0.100	**0.004**					
mb	-0.059	-0.145	-0.069	0.083	0.191	**0.592**				
	0.557	0.148	0.491	0.408	0.055	**0.000**				
gl	0.117	0.096	0.154	**0.457**	0.135	-0.072	-0.059			
	0.244	0.339	0.125	**0.000**	0.178	0.472	0.558			
la	0.049	0.013	**0.315**	**0.261**	0.193	-0.173	-0.169	**0.536**		
	0.630	0.897	**0.001**	**0.008**	0.053	0.083	0.091	**0.000**		
al	0.021	0.165	0.019	0.095	-0.043	-0.159	-0.109	**0.265**	**0.381**	
	0.834	0.099	0.849	0.344	0.666	0.113	0.279	**0.007**	**0.000**	
oc	-0.015	**-0.259**	-0.096	0.192	0.023	-0.106	-0.039	-0.011	-0.045	-0.040
	0.885	**0.009**	0.342	0.054	0.816	0.290	0.700	0.912	0.656	0.695

2012

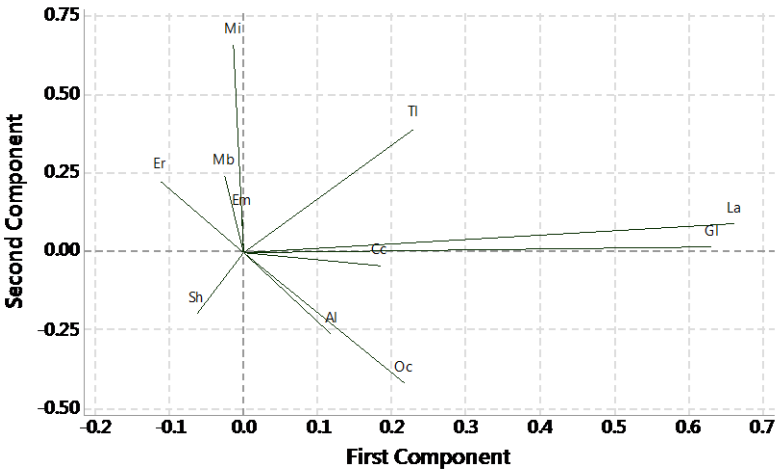
	em	er	cc	tl	sh	mi	mb	gl	la	al
er	-0.095									
	0.345									
cc	-0.149	-0.017								
	0.140	0.863								
tl	0.075	0.133	-0.161							
	0.459	0.187	0.111							
sh	-0.020	0.104	0.057	**0.320**						
	0.845	0.302	0.570	**0.001**						
mi	0.121	-0.004	-0.097	0.008	-0.008					
	0.229	0.972	0.336	0.938	0.938					
mb	0.107	0.046	-0.073	0.088	0.103	**0.658**				
	0.288	0.647	0.470	0.386	0.308	**0.000**				
gl	0.032	-0.009	-0.050	**0.272**	0.042	-0.012	-0.050			
	0.750	0.926	0.620	**0.006**	0.680	0.905	0.619			
la	-0.160	0.076	-0.081	**0.200**	0.162	0.110	0.024	**0.246**		
	0.112	0.455	0.425	**0.046**	0.107	0.275	0.809	**0.014**		
al	-0.035	0.108	0.108	0.007	0.099	-0.084	-0.063	-0.013	0.156	
	0.730	0.286	0.286	0.941	0.326	0.403	0.534	0.894	0.122	
oc	**-0.202**	-0.053	0.118	0.079	0.158	-0.021	0.055	-0.062	0.031	-0.182
	0.044	0.603	0.241	0.437	0.117	0.839	0.588	0.540	0.758	0.070

Appendix D

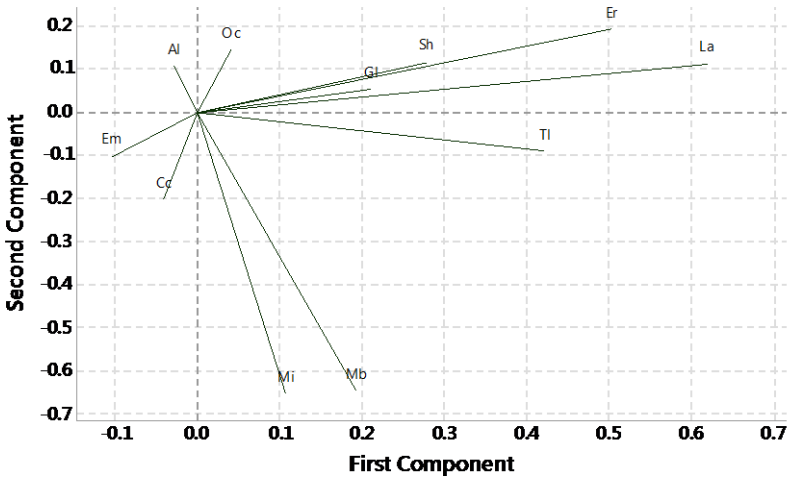
Results from Principal Component Analyses exploring annual association of parasites of rock ptarmigan in northeast Iceland October 2006–2012 Loading plots of first and second principal component per year.

Al = Amyrsidea lagopi, Cc = Capillaria caudinflata, Em = Eimeria muta, Er = Eimeria rjupa, Gl = Goniodes lagopi, La = Lagopoecus affinis, Mb = Myialges borealis, Mi = Metamicrolichus islandicus, Oc = Ornithomya chloropus, Sh = Strelkoviacarus holoaspis, Tl = Tetraolichus lagopi, Tt = Trichostrongylus tenuis

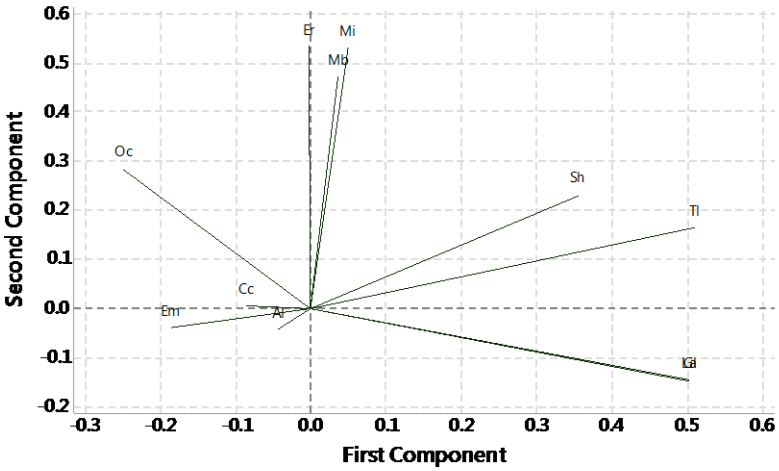
2006



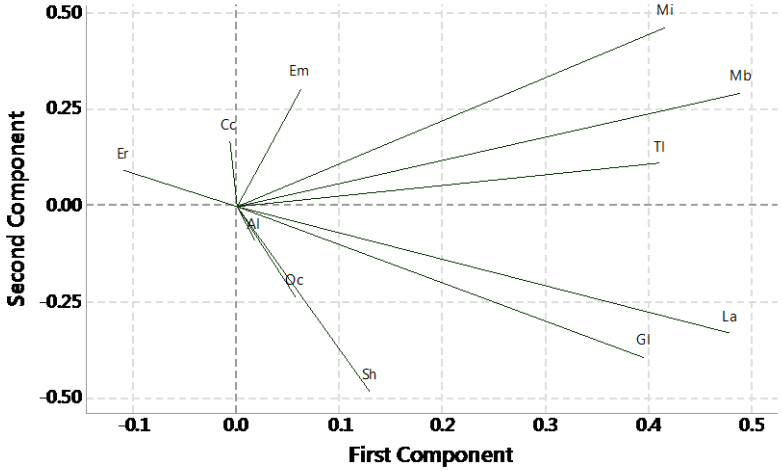
2008



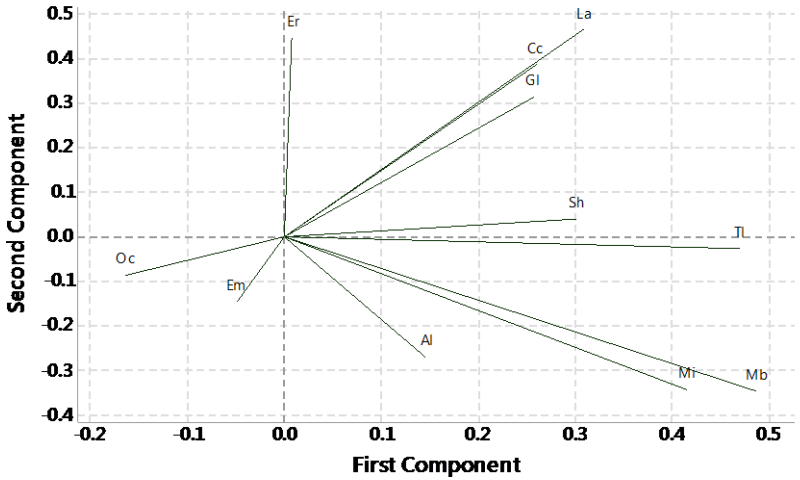
2007



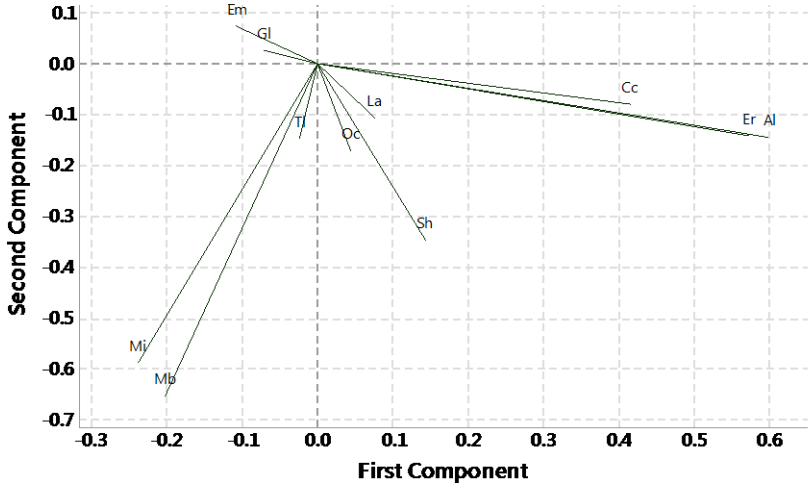
2009



2010



2012



2011