Changes in mass of the preen gland in rock ptarmigans (*Lagopus muta*) in relation to sex, age and parasite burden 2007-2012

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Abstract

The rock ptarmigan (*Lagopus muta*) is the main game-bird in Iceland and has a population that varies cyclically, usually peaking every 10 years. Given these population cycles and its cultural importance, the rock ptarmigan is studied throughout the year. Ptarmigan hunting is closely monitored and commerce of ptarmigans and their related products is forbidden since 2005 to assure sustainable harvest. The ptarmigan health project, which started in 2006, has focused on the general condition of the ptarmigans and how different health parameters relate to population changes during a population cycle. One of the parameters the project is studying is the preen gland. This gland is a holocrine organ exclusive to birds that produces preen oil, a secretion that birds spread through their plumage during preening. The preen oil has been proposed to offer protection against growth of feather degrading bacteria and fungi, as well as fighting ectoparasites. The present study aims to increase the understanding of the functions of the preen gland, specifically the changes in mass of the preen gland in rock ptarmigans in relation to sex, age, year and parasite burden, using data from ptarmigans collected in North-East Iceland from 2007-2012. The mean preen gland mass was significantly higher in males than in females, as well as in adult birds than in juvenile birds, but the effects of sex and age were no longer significant once corrected for body size. The year of collection had the greatest effect on the mass of the preen gland. Moreover, it was observed that the preen gland mass showed a significant negative relationship with ectoparasite richness and ectoparasite burden, as well as with the presence of chewing lice. This study provides evidence that the gland is a part of the ptarmigan outer defenses against ectoparasites.

Keywords: preen gland, *Lagopus muta*, population changes, preen oil, ectoparasites.

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1 General Introduction

1.1 The rock ptarmigan

The rock ptarmigan (*Lagopus muta*) (hereafter referred to as ptarmigan) is a member of the grouse family Tetraonidae. This species has a circumpolar Holartic distribution, including Eurasia and North America (Voous & Thomson, 1960; BirdLife International, 2013). It is classified as a species of Least Concern by the International Union for the Conservation of Nature as the world population has been estimated to number more than 8 million individuals (Rich et al., 2003; BirdLife International, 2013).

The ptarmigan is a herbivore with different diet preferences according to the season and food availability. In spring and summer, ptarmigans eat green shoots, leaves and flowers, while in late summer they prefer the bulbils of the alpine bistort (*Polygonum viviparum*). In autumn, berries like crowberries (*Empetrum nigrum*) and blueberries (*Vaccinium* spp.) are important food items. In winter, ptarmigans feed mainly on buds, shoots and catkins of small woody shrubs, like willows (*Salix* sp.) and dwarf birch (*Betula nana*) (Garðarsson & Moss, 1970).

1.1.1 The rock ptarmigan in Iceland

Ptarmigans are widely distributed within Iceland, both in lowland and highland areas (Voous & Thomson, 1960; Ridgely et al. & BirdLife International, 2012). The ptarmigan is an important part of the Icelandic culture (Hallgrímsson, 1844) and the Icelandic ptarmigan population has been exploited by humans since the settlement (late 9th century AD) (Guðmundsson 1951 as cited by Nielsen & Pétursson, 1995). Ptarmigans were consumed domestically until 1890, when exportation to other European countries commenced, and by 1900, 100 to 200 thousand ptarmigans were being exported per year. Between the years 1924 to 1927 the export peaked with 250.000 ptarmigans per year, and in 1942 the export markets closed and did not open after World War II in 1945 (Guðmundsson 1951 as cited by Fálkasetur Íslands, 2013).

Nowadays, the ptarmigan is the most popular game-bird in Iceland (The Environment Agency of Iceland, 2011) and the only upland game-bird (Garðarsson, 1988). It is also a traditional Christmas dish in Iceland (Fréttatíminn, 2011). Hunting is regulated and between 4 to 6 thousand licensed hunters take part in the hunt. Hunters must be over 20 years of age and are required to finish two courses taught by The Environment Agency of Iceland (EAI), one regarding the responsibilities of holding a hunting license and another regarding shooting and fire arms (The Environment Agency of Iceland, 2013b). The Ministry for the Environment, advised by the Icelandic Institute of Natural History and the EAI, determines the harvest regulations (The Environment Agency of Iceland, 2012).

In 2003, a time series analysis of data from North-East Iceland showed a 4% yearly decline in population abundance since 1981 (Brynjarsdóttir et al., 2003). This decline was also observed in other parts of Iceland, which led to the ptarmigan being classified as a

vulnerable species within the country, and a collapse of the ptarmigan population was predicted based on the high mortality rates of both adults and juveniles (Nielsen et al., 2004). As a consequence, the Minister for the Environment closed the ptarmigan season in 2003 and 2004, and in 2005 the commercialization of ptarmigans and their sub-products was banned (Ministry for the Environment and Natural Resources, 2003; Alþingi, 2005).

Other conservation measures have also been taken since, such as the reduction of the number of hunting days allowed. This went from 47 days in 2005 to 12 days in 2013 (The Icelandic Institute of Natural History, 2012; The Environment Agency of Iceland, 2013a). In 2013, the hunting bag was approximately 42.000 birds, well below to previous years when the number of birds hunted peaked at over 166.000 in 1997 (The Environment Agency of Iceland, 2011, 2013a). Hunting in excess of the recommended number has been reported to occur and reached 44% in 2011 (The Icelandic Institute of Natural History, 2012).

To ensure sustainable use on the ptarmigan, the population is monitored on an annual basis. The monitoring program includes counts of territorial cocks in the spring, and estimation of age ratios in the population in the spring, late summer; and during the hunting period (Nielsen et al., 1999; Nielsen et al., 2004). These data collected are used to derive a population index, and to calculate the total population size and mortality rates (Brynjarsdóttir et al., 2003; Magnússon et al., 2004; Ministry for the Environment and Natural Resources, 2012).

1.1.2 Cyclic changes in population of the ptarmigan

In animal ecology, periodic fluctuations in population size have been a matter of interest since 1924, when Charles Elton drew the attention of the scientific community to the occurrence of this phenomenon. He proposed that the cyclic population changes were driven by exogenous factors. Climatic cyclic variations, such as sunspots, and their effect on the environmental conditions (e.g. food availability) that influence a species reproductive capacity were proposed. The influence of different types of natural selection in the population cycles was also discussed; in the peak years there would be selection for individuals by disease resistance, ability to escape from predators, male to male competition for females, etc. In contrast, during the low years, selection for resistance to unfavorable climatic conditions and mate search would be present (Elton, 1924). Since then, this has been a fruitful field of research but it is still being debated. One reason for the controversy is the difficulty of doing controlled experiments with these systems and the fact that most studies are correlative in nature (Tompkins & Begon, 1999; Nielsen, 2009).

More recently, the focus has been on the importance of interpopulation processes (trophic interactions) in driving the cycles (Berryman, 2002). An example of cyclic population changes driven by predation is the collared lemming (Dicrostonyx groenlandicus) in high-Arctic Greenland and the four different species that prey upon it; the stoat (Mustela ermine), the arctic fox (Alopex lagopus), the snowy owl (Nyctea scandiaca) and the long-tailed skua (Stercorarius longicaudus). The predators differ both in their functional and numerical response to changes in lemming numbers. The lemming population peaks every 4 years and the cycle is driven by predation. The stoat is the only predator that shows a delayed response to changes in prey density as their population reaches the maximum number the year after the lemming population, while the other three species of predators show a highly stabilizing predation in synchrony with lemming numbers (Gilg et al., 2003).

A case of cyclic population changes driven by parasitism is the larch budmoth (*Zeiraphera diniana*), known for its recurrent destructive effects on the subalpine larch-cembran pine forests in the Swiss Alps. The larch budmoth shows peaks in population abundance about every 9 years and the difference in number between low and peak abundance is 100.000-fold (Turchin et al., 2003). Parasites on the larch budmoth have a highly variable prevalence, ranging from 1–5% to 80–90% (Delucchi, 1982), and are the main drivers of the population cycles seen in the larch budmoth (Turchin et al., 2003). Prevalence of parasites peaks approximately 2 years after the budmoth peak (Turchin et al., 2003).

Experiments on host-parasite interactions done on six red grouse (*Lagopus lagopus scoticus*) populations in the United Kingdom suggest that the nematode *Trichostrongylus tenuis* (hereafter referred to as strongyle worm) drives the grouse cycle in that system. Parasitic infestation by strongyle worms negatively impacts female reproductive potential and population crashes are highly related to high parasitic infestations. The experiments consisted of administering the anthelmintic Levamisole hydrochloride during peak population levels. An estimated 15-50% of breeding adults of four of the six populations were treated in 1989. Subsequently, two of the four previously treated populations were treated in 1993, leaving four untreated. In the six treatments performed, the anthelmintic reduced the life expectancies of the strongyle worm, thus maintaining the females breeding capacity and preventing the population decline witnessed in untreated populations (Hudson et al., 1998). Similar explanations relating to host-parasite interactions have been proposed for the same grouse species in Norway (Holmstad et al., 2005).

The case of the cyclic dynamics of the snowshoe hare (*Lepus americanus*) is more complex. Peaks in this species occur every 10 years and the specialist predator is the Canada lynx (*Lynx canadensis*) (Krebs et al., 2001). Other predators such as coyotes (*Canis latrans*) also feed on the snowshoe hare, but function as generalist predators, feeding primarily on snowshoe hares when the hare population is high (Todd & Keith, 1983). Studies on the snowshoe hare have shown that the driving forces of the population cycles are system interactions involving three trophic levels that include predation and food supplies. The primary cause of death of hares is, with only few exceptions, predation and lynx populations mirror hare numbers with only a slight time-lag. The effect of food is strongly sensed during winter and is mostly indirect, given that hares infrequently die of malnutrition. Nonetheless, nutrient shortage affects body condition and can expose hares to lynxes, making them more susceptible to parasites and chronic stress, all which can affect reproductive potential. The cyclicity is the outcome of the time lag in both the direct and indirect effects of predation, where lower population numbers are due to deaths caused by predation and reproductive potential slowly being regained (Krebs et al., 2001).

Ptarmigans experience similar cyclic population changes in different areas, including Alaska, United States; Northwest Territories, Canada; United Kingdom and Iceland (Montgomerie & Holder, 2008). In Iceland, the period (i.e. frequency in which they occur) and the amplitude (i.e. the difference between the lowest point and the peak) are relatively irregular, and is the reason why they are sometimes referred to as quasi-cycles (Nisbet & Gurney, 1982). The population peaks occur approximately every 10 years and the difference in number between low and peak numbers is 3-10 fold (Fig. 1) (Nielsen & Pétursson, 1995; Nielsen, 1999; Brynjarsdóttir et al., 2003; Nielsen et al., 2004). In Iceland, the ptarmigan is the main prey of the gyrfalcon (*Falco rusticolus*), and interestingly, the gyrfalcon population is positively correlated with ptarmigan numbers with approximately a 3-year time-lag (Nielsen, 1999; Brynjarsdóttir et al., 2003). This

suggests a coupled predator-prey cycle where the gyrfalcon plays the role of the "resident specialized predator" (Andersson & Erlinge, 1977).

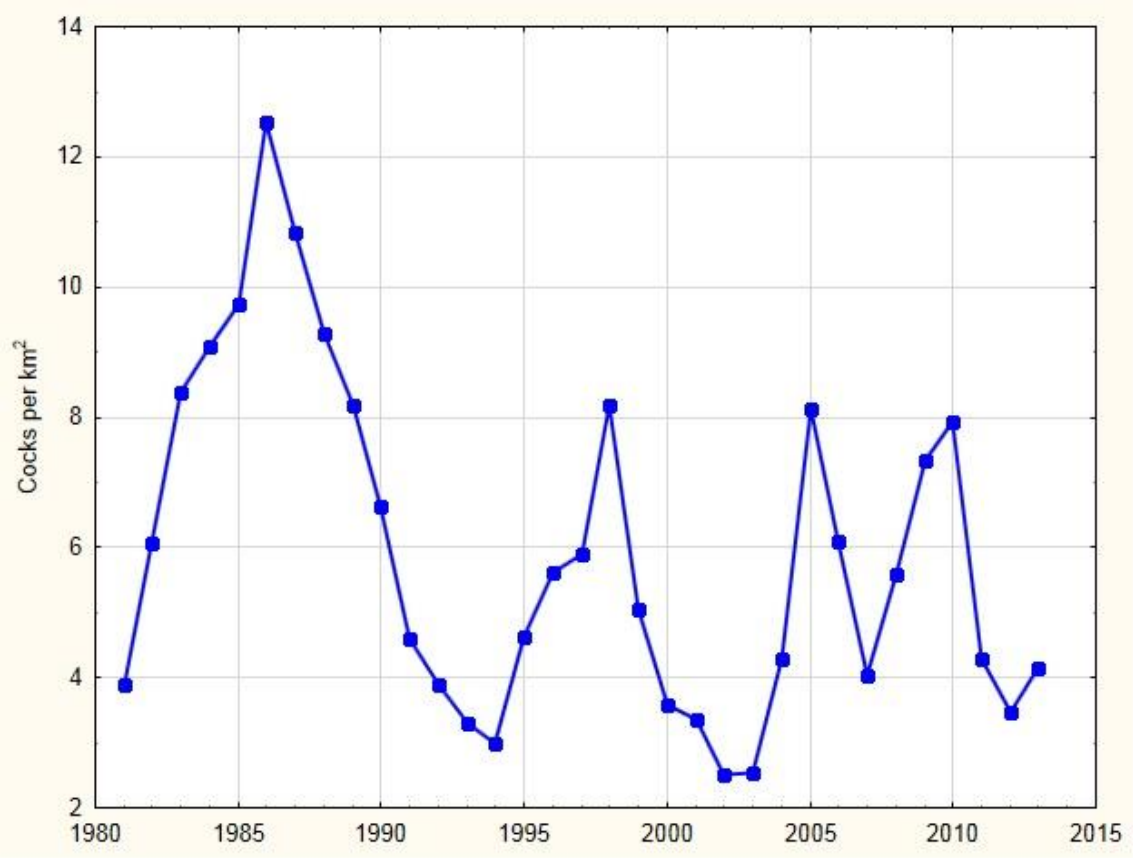

Figure 1: Mean density of rock ptarmigan cocks per km^2 on six census plots in North-East Iceland between 1981 and 2013(adapted from Nielsen 2013).

Ptarmigan population peaks were documented in Iceland in 1986, 1998, 2005 and 2010. Based on the available information, it has been predicted that the ptarmigan population will decline for several years and low population numbers should occur between 2015 and 2018. The next population peak is predicted to occur between 2020 to 2022, however it may occur earlier if the population trends seen from 2012 to 2013 continue (The Icelandic Institute of Natural History, 2012).

1.2 Ptarmigan research in Iceland

The ptarmigan has been much studied in Iceland. In the beginning, the research mostly focused on ptarmigan feeding habits, molt patterns, movement and population cycles (Guðmundsson 1937; Salomonsen 1939 and Guðmundsson 1951 as cited by Nielsen, 2009). In 1963, a big research project was started centered on the island of Hrísey in North-East Iceland. The research questions were related to demography, food habits and social behavior, and the aim was to explain what forces were driving the cycle. By 1981, studies on the predator-prey relationship of the gyrfalcon and the ptarmigan were started in North-East Iceland (Guðmundsson & Garðarsson, 1970; Nielsen, 1986; Garðarsson, 1988; Nielsen, 1999). More recently, from 1995 to 2001, other studies that have focused on the effect of hunting by radio tagging individuals have been carried out in the South-West part

of the country (Nielsen, 2000, 2001). Between 2007 and 2010 radio tagging of hens was conducted in order to study their reproductive success and survival, both in the North-East and South-West of the country (Snæþórsson, 2012).

In 2006, a study was started on ptarmigan health and population changes in North-East Iceland. Based on the theory that the driving force of a 10 year cycle should show a 2-3 year time lag with regard to the population numbers (Berryman, 2002), the goal is to study the general condition of the birds and how the different health parameters relate to population changes during one decline and increase phase (Nielsen, 2009). The annual index derived from the health parameters should indicate a better health status during the first years of the cycle (increase phase) and worsen towards the end of the cycle (decrease phase) (Nielsen, 2009).

The parameters measured include:

1. *Morphology:* the size of certain organs, including the spleen and the bursa of Fabricius, reflect the activity of the immune system, which is highly important in disease resistance and therefore related to survival rates (Cooper et al., 1966; John, 1994; Møller & Erritzøe, 2003)**.**

2. *Body condition*: the status of metabolic reserves relative to likely demands has often been linked to survival rates in birds (Newton, 1993). Different indicators for body condition are measured; weight and size of the birds, heart fat content and protein mass of pectoral muscles (Nielsen, 2009).

3. *Stress levels:* a common response to modifying factors (e.g. reduced food access, predation and bad weather conditions) among vertebrates is an increase in the production of steroid hormones by the adrenal gland; mainly corticosterone in birds (Árnason et al., 1986). Chronic stress response lead to negative effect on the body, including the immune system (Mostl & Palme, 2002), thus affecting animals under natural conditions (Blas et al., 2007).

4. *Plumage condition:* To study the plumage condition, the tail feathers are inspected and scored for hunger traces and holes (Moyer et al., 2003). Hunger traces on feathers are known to reflect stressful episodes during feather growth (Jovani & Blas, 2004).

5. *Preen gland parameters:* preen gland secretions are part of the birds defense system, offering protection both against growth of feather degrading bacteria (Martín-Platero et al., 2006) and chewing lice (Moyer et al., 2003). Studies have shown that feather degradation caused by chewing lice affects thermal regulation and metabolism (Booth et al., 1993), effects that may affect the well-being of the individual (Nielsen, 2009).

6. *Parasite burden*: parasites feed on their hosts and can cause patho-physiological damage (Bush, 2001b), and thus having a negative effect on the host by reducing growth, reproduction and survival rates (Hudson et al., 1998). Emphasis is put on the whole parasite community of the birds rather than on individual species. In a study by Holmstad et al. (2005), the parasite community of the willow ptarmigan (*Lagopus lagopus*) was analyzed, and despite that none of the parasites had an

important effect on their own, the community as a whole reduced host body mass and breeding mortality, thus reducing host fitness. The study of the parasite community also addresses public health concerns, such as the possibility of zoonotic diseases, as there are strong ptarmigan-human interactions during the ptarmigan hunting season (The Environment Agency of Iceland, 2011).

A total of 46 parasite species, including endoparasites and ectoparasites, have been described for ptarmigan around the world. Of those, 16 species have been reported for the study population in Iceland, including 6 endoparasite species and 10 ectoparasite species (Table 1) (Mironov et al., 2010; Bochkov & Skírnisson, 2011; Skírnisson et al., 2012).

The ectoparasites reported for the Icelandic ptarmigan population fall in the following classification groups:

1. Feather mites (Acari): an extensive group of permanent inhabitants of most groups of birds and transmitted between hosts through close contact (Proctor, 2003). Some feed on the living tissues of the host (e.g. *Myialges borealis* and *Metamicrolichus islandicus*) while others live exclusively on the plumage and down (e.g. *Strelkoviacarus holoaspis* and *Tetraolichus lagopi*) and in the feather quill (e.g. *Mironovia lagopi*). Down mites are considered mutualists by some researchers since they feed on bacteria, excess waxes and dirt, although they can cause damage if abundant (Proctor, 2003; Galván et al., 2008), while skin mites and quill mites are classified as parasites (Kethley, 1971). In the study by Skírnisson et al. (2012), the prevalence of infection on ptarmigans was analyzed. They found that *M. islandicus* showed a higher prevalence and intensity in juveniles than in adults, while *S. holoaspis*, *M. borealis* and *T. lagopi* showed no difference between age groups. It is considered likely that *M. islandicus* causes mange in ptarmigans. The study suggests that the absence of prevalence differences among age groups is an indicator of the limited capacity of the host to control those mites. In addition, if feather mites and ptarmigan have mutualistic relations, there should not be differences in mite prevalence across host age groups (Skírnisson et al., 2012).

2. Chewing lice (Phthiraptera): parasites of birds and mammals. This is a paraphyletic taxon, composed by two major taxa, Amblycera (e.g. *Amyrsidea lagopi*) and Ischnocera (e.g., *Goniodes lagopi* and *Lagopoecus affinis*) (Barker et al., 2002; Johnson & Whiting, 2002; Johnson & Clayton, 2003). Amblycera feed on living tissue and feather barbs, ambulating directly on the bird's skin, while Ischnocera feed on feather barbs and dead skin and do not come into contact with the living tissue (Møller & Rózsa, 2005; Clayton et al., 2008). In the study by Skírnisson et al. (2012), *G. lagopi* and *L. affinis* had a higher prevalence on juvenile than on adult hosts, which suggests that the ectoparasite defense system in juveniles is less developed than in adults (Bush, 2001a). A lower prevalence as the birds become older, may be the effect of host immune system or selective mortality (Hudson et al., 1992).

3. Fleas (Siphonaptera): parasites of mammals and birds. The adult forms of fleas feed on blood while the larvae feed on debris (Durden & Traub, 2002). The only flea found on the ptarmigan is *Ceratophyllus garei* (Skírnisson et al., 2012).

4. Louse flies (Diptera): parasites that come into direct contact with the host by feeding on blood, causing a detrimental effect on the host (Baker, 1967). In the study by Skírnisson et al. (2012), *Ornithomya chloropus* had a higher prevalence on juvenile than on adult hosts but there was no difference with respect to mean intensities.

The ptarmigan parasite fauna in Iceland includes 6 ectoparasites (e.g. feather mites *Metamicrolichus islandicus, Strelkoviacarus holoaspis, Tetraolichus lagopi, Myialges borealis*, *Mironovia lagopi* and feather lice *Amyrsidea lagopi*), and 2 endoparasites (e.g. *Bastocystis* sp.and *Passerilepis serpentulus*) not reported from other parts of the range. According to Skírnisson et al. (2012), the cause for these species not being reported in other geographic areas reflects the sampling methods used. Specialists working with ptarmigan elsewhere have overlooked these parasite species and it is presumed that identical or closely related species will be encountered in other ptarmigan populations (Skírnisson et al., 2012).

Given that the community and abundance of ectoparasites may be another important driving factor regulating the ptarmigan population cycles, the next chapter will focus on a study conducted to understand the relationship between ectoparasites and the preen gland in ptarmigans.

Table 1: The ectoparasite fauna of the rock ptarmigan and geographic distribution of the different ectoparasite species (adapted from Skírnison et al. (2012).

		Geographical occurrence			
Group	**Species**	**Iceland**	**Palaearctic**	**Nearctic**	**Reference**
Feather mites					
Astigmata	*Metamicrolichus islandicus*	yes	no	no	(Mironov et al., 2010; Skírnisson et al., 2012)
Astigmata	*Strelkoviacarus holoaspis*	yes	no	no	(Mironov et al., 2010; Skírnisson et al., 2012)
Astigmata	*Tetraolichus lagopi*	yes	no	no	(Mironov et al., 2010; Skírnisson et al., 2012)
Astigmata	*Myialges borealis*	yes	no	no	(Mironov et al., 2010; Skírnisson et al., 2012)
Prostigmata	*Mironovia lagopi*	yes	no	no	(Bochkov & Skírnisson, 2011; Skírnisson et al., 2012)
Chewing lice					
Phthiraptera	*Goniodes lagopi*	yes	yes	yes	(Timmermann, 1950; Harper, 1953; Mehl, 1975; Steen, 1978; Skírnisson et al., 2012)
Phthiraptera	*Lagopoecus affinis*	yes	yes	yes	(Timmermann, 1950; Harper, 1953; Jellison & Neiland, 1965; Mehl, 1975; Steen, 1978; Holmstad, 2004; Skírnisson et al., 2012)
Phthiraptera	*Amyrsidea lagopi*	yes	no	no	(Skírnisson et al., 2012)
Flea					
Siphonaptera	*Ceratophyllus garei*	yes	yes	no	(Mehl, 1975; Steen, 1978; Skírnisson et al., 2012)
Fly					
Diptera	*Ornithomya chloropus*	yes	yes	no	(Mehl, 1975; Steen, 1978; Skírnisson et al., 2012)

References

Alþingi. (2005). Vernd, friðun og veiðar á villtum fuglum og villtum spendýrum (rjúpnaveiðar, sölubann og takmörkun veiða), 36/2005 C.F.R., Retrieved from http://www.althingi.is/dba-bin/ferill.pl?ltg=131&mnr=495

Andersson, M., & Erlinge, S. (1977). Influence of predation on rodent populations. *Oikos*, 591-597.

Árnason, S. S., Rice, G. E., Chadwick, A., & Skadhauge, E. (1986). Plasma levels of arginine vasotocin, prolactin, aldosterone and corticosterone during prolonged dehydration in the domestic flowl: effect of dietary NaCl. *Journal of Comparative Physiology B, 156*(3), 383-397.

Baker, J. R. (1967). A review of the role played by the Hippoboscidae (Diptera) as vectors of endoparasites. *The Journal of Parasitology*, 412-418.

Barker, S. C., Whiting, M., Johnson, K. P., & Murrell, A. (2002). Phylogeny of the lice (Insecta, Phthiraptera) inferred from small subunit rRNA. *Zoologica Scripta, 32*(5), 407-414.

Berryman, A. A. (2002). *Population Cycles : The Case for Trophic Interactions: The Case for Trophic Interactions*: Oxford University Press, USA.

BirdLife International. (2013). *Lagopus muta*. *IUCN Red List of Threatened Species*. Retrieved on 24.07.2013, from http://www.iucnredlist.org/details/100600291/0

Blas, J., Bortolotti, G. R., Tella, J. L., Baos, R., & Marchant, T. A. (2007). Stress response during development predicts fitness in a wild, long lived vertebrate. *Proceedings of the National Academy of Sciences of the United States of America, 104*(21), 8880-8884.

Bochkov, A., & Skírnisson, K. (2011). Description of the life stages of quill mite *Mironovia lagopus* sp. nov. (Acari: Syringophilidae) parasitizing the rock ptarmigan *Lagopus muta* (Phasianidae) from Iceland. *Parasitology Research, 108*(3), 715-722.

Booth, D. T., Clayton, D. H., & Block, B. A. (1993). Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 253*(1337), 125-129.

Brynjarsdóttir, J., Lund, S. H., Magnússon, K. G., & Nielsen, Ó. K. (2003). *Analysis of time series for rock ptarmigan and gyrfalcon populations in north-east Iceland*. Raunvísindastofnun Háskólans. RH-18-2003. pp. 19

Bush, A. O. (2001a). Parasitism: The Diversity and Ecology of Animal Parasites (pp. 13-23): Cambridge University Press.

Bush, A. O. (2001b). Parasitism: The Diversity and Ecology of Animal Parasites (pp. 24-27): Cambridge University Press.

Clayton, D. H., Adams, R. J., & Bush, S. E. (2008). Phthiraptera, the Chewing Lice. In C. T. Atkinson, N. J. Thomas & D. B. Hunter (Eds.), *Parasitic Diseases of Wild Birds* (pp. 514-526). Iowa: Wiley.

Cooper, M. D., Peterson, R. D. A., South, M. A., & Good, R. A. (1966). The functions of the thymus system and the bursa system in the chicken. *J Exp Med, 123*, 75-102.

Delucchi, V. (1982). Parasitoids and hyperparasitoids of *Zeiraphera diniana* [Lep., Tortricidae] and their pole in population control in outbreak areas. *Entomophaga, 27*(1), 77-92.

Durden, L. A., & Traub, R. (2002). Fleas (Siphonaptera). In G. R. Mullen & L. A. Durden (Eds.), *Medical and Veterinary Entomology* (Vol. 2, pp. 103-125). Amsterdam: Academic Press.

Elton, C. S. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. *Journal of Experimental Biology, 2*(1), 119-163.

Fálkasetur Íslands. (2013, 04.03.2013). Útflutningur á rjúpu. Retrieved on 07.09.2013, from http://www.falkasetur.is/rjupan/rjupan-i-menningu-islendinga/utflutningur-a-rjupu/

Fréttatíminn. (27.01 2011). Rjúpan elduð upp á gamla og nýja mátann, *Fréttatíminn*. Retrieved from http://www.frettatiminn.is/matur_og_vin/rjupan_eldud_upp_a_gamla_og_nyja_matann/

Galván, I., Barba, E., Piculo, R., Cantó, J., Cortés, V., Monrós, J., Atiénzar, F., & Proctor, H. (2008). Feather mites and birds: an interaction mediated by uropygial gland size? *Journal of Evolutionary Biology, 21*(1), 133-144.

Garðarsson, A. (1988). Cyclic population changes and some related events in rock ptarmigan in Iceland. In A. T. Bergerud & M. W. Gratson (Eds.), *Adaptive Strategies and Population Ecology of Northern Grouse* (pp. 300–329). Minneapolis: University of Minnesota Press.

Garðarsson, A., & Moss, R. (1970). Selection of food by Icelandic ptarmigan in relation to tis availability and nutritive value. In A. Watson (Ed.), *Animal Populations in Relation to their food Resources* (pp. 47-71). Oxford: Blackwell Scientific Publication.

Gilg, O., Hanski, I., & Sittler, B. (2003). Cyclic dynamics in a simple vertebrate predator-prey community. *Science, 302*(5646), 866-868.

Guðmundsson, F., & Garðarsson, A. (1970). *Cyclic phenomenon in populations of Lagopus mutus*. The Icelandic Institute of Natural History. pp. 25

Hallgrímsson, J. (1844) Retrieved from http://jonashallgrimsson.is/index.php?page=ohrasid

Harper, F. (1953). Birds of the Nueltin Lake expedition, Keewatin, 1947. *American Midland Naturalist, 49*(1), 1-116.

Holmstad, P. R. (2004). *Do parasites affect ptarmigan parasite population dynamics.* Ph.D. Thesis, University of Bergen, pp. 128.

Holmstad, P. R., Hudson, P. J., & Skorping, A. (2005). The influence of a parasite community on the dynamics of a host population: a longitudinal study on willow ptarmigan and their parasites. *Oikos, 111*(2), 377-391.

Hudson, P. J., Dobson, A. P., & Newborn, D. (1992). Do parasites make prey vulnerable to predation? Red grouse and parasites. *Journal of Animal Ecology*, 681-692.

Hudson, P. J., Dobson, A. P., & Newborn, D. (1998). Prevention of population cycles by parasite removal. *Science, 282*(5397), 2256-2258.

Jellison, W. L., & Neiland, K. A. (1965). *Parasites of Alaskan vertebrates*. Dept. of the Army and University of Oklahoma Report. pp. 73

John, J. L. (1994). The avian spleen: a neglected organ. *Quarterly Review of Biology*, 327-351.

Johnson, K. P., & Clayton, D. H. (2003). The biology, ecology, and evolution of chewing lice. In R. D. Price, R. A. Hellenthal, R. L. Palma, K. P. Johnson & D. H. Clayton (Eds.), *The chewing lice: world checklist and biological overview* (pp. 449-476): Illinois Natural History Survey Special Publication 24.

Johnson, K. P., & Whiting, M. F. (2002). Multiple Genes and the Monophyly of Ischnocera (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution, 22*(1), 101-110.

Jovani, R., & Blas, J. (2004). Adaptive allocation of stress-induced deformities on bird feathers. *Journal of Evolutionary Biology, 17*(2), 294-301.

Kethley, J. (1971). Population regulation in quill mites (Acarina: Syringophilidae). *Ecology*, 1113-1118.

Krebs, C. J., Boonstra, R., Boutin, S., & Sinclair, A. R. E. (2001). What Drives the 10-year Cycle of Snowshoe Hares? *BioScience, 51*(1), 25-35.

Magnússon, K. G., Brynjarsdóttir, J., & Nielsen, Ó. K. (2004). *Population cycles in rock ptarmigan Lagopus muta: modelling and parameter estimation*. Raunvísindastofnun Háskólans. RH-19-2004. pp. 35

Martín-Platero, A. M., Valdivia, E., Ruíz-Rodríguez, M., Soler, J. J., Martín-Vivaldi, M., Maqueda, M., & Martínez-Bueno, M. (2006). Characterization of antimicrobial substances produced by *Enterococcus faecalis* MRR 10-3, isolated from the uropygial gland of the hoopoe (*Upupa epops*). *Applied and environmental microbiology, 72*(6), 4245-4249.

Mehl, R. (1975). Rypenes ektoparasitter i Norge. *Fauna, 28*, 208-215.

Ministry for the Environment and Natural Resources. (26.9.2003). Heimild til rjúpnaveiði felld úr gildi. Retrieved from http://www.umhverfisraduneyti.is/frettir/nr/26

Ministry for the Environment and Natural Resources. (21.9.2012). Óbreytt rjúpnaveiði 2012, Press Release. Retrieved from http://www.umhverfisraduneyti.is/frettir/nr/2213

Mironov, S. V., Skírnisson, K., Þórarinsdóttir, S. T., & Nielsen, Ó. K. (2010). Feather mites (Astigmata: Psoroptidia) parasitising the rock ptarmigan *Lagopus muta* (Montin) (Aves: Galliformes) in Iceland. *Systematic Parasitology, 75*(3), 187-206.

Møller, A. P., & Erritzøe, J. (2003). Climate, body condition and spleen size in birds. *Oecologia, 137*(4), 621-626.

Møller, A. P., & Rózsa, L. (2005). Parasite biodiversity and host defenses: chewing lice and immune response of their avian hosts. *Oecologia, 142*(2), 169-176.

Montgomerie, R., & Holder, K. (2008). Rock ptarmigan (*Lagopus muta*). In A. Poole (Ed.), The Birds of North America online. Ithaca, New York, USA: Cornell Laboratory of Ornithology. Retrieved from the Birds of North America Online database: http://bna.birds.cornell.edu/bna/species/051.

Mostl, E., & Palme, R. (2002). Hormones as indicators of stress. [Review]. *Domest Anim Endocrinol, 23*(1-2), 67-74.

Moyer, B. R., Rock, A. N., Clayton, D. H., & Prum, R. (2003). Experimental test of the importance of preen oil in rock doves (*Columba livia*). *The Auk, 120*(2), 490-496.

Newton, S. F. (1993). Body condition of a small passerine bird: ultrasonic assessment and significance in overwinter survival. *Journal of Zoology, 229*(4), 561-580.

Nielsen, Ó. K. (1986). *Population ecology of the gyrfalcon in Iceland with comparative notes on the merlin and the raven.* Ph.D. Thesis, Cornell University, pp. 430.

Nielsen, Ó. K. (1999). Gyrfalcon predation on ptarmigan: numerical and functional responses. *Journal of Animal Ecology, 68*(5), 1034-1050.

Nielsen, Ó. K. (2000). Vetrarafföll rjúpna í nágrenni Reykjavíkur 1995 til 2000. *SKOTVÍS, 6*, 15-19.

Nielsen, Ó. K. (2001). Vetrarafföll rjúpna við Eyjafjörð 2000 til 2001. *SKOTVÍS, 7*, 42-45.

Nielsen, Ó. K. (2009). *Project description: Ptarmigan health studies in Northeast Iceland*. The Icelandic Institute of Natural History.

Nielsen, Ó. K., Brynjarsdóttir, J., & Magnússon, K. G. (1999). Monitoring of the ptarmigan population in Iceland. *Fjölrit Náttúrufrædistofnunar, 39*, 55.

Nielsen, Ó. K., Brynjarsdóttir, J., & Magnússon, K. G. (2004). Monitoring of the ptarmigan population in Iceland. *Fjölrit Náttúrufrædistofnunar, 47*, 110.

Nielsen, Ó. K., & Pétursson, G. (1995). Population fluctuations of gyrfalcon and rock ptarmigan: analysis of export figures from Iceland. *Wildlife Biology, 1*(2), 65-71.

Nisbet, R., & Gurney, W. (1982). *Modelling fluctuating populations*. Chichester: John Wiley & Sons.

Proctor, H. C. (2003). Feather mites: (Acari: Astigmata): Ecology, Behavior, and Evolution. *Annual Review of Entomology, 48*(1), 185-209.

Rich, T. D., Beardmore, C., Berlanga, H., Blancher, P., Bradstreet, M., Butcher, G., Demarest, D., Dunn, E., Hunter, W., & Iñigo-Elias, E. (2003). Partners in Flight North American landbird conservation plan. *Partners in Flight, Ithaca, NY*.

Ridgely et al., & BirdLife International. (2012). Bird species distribution maps of the world: *Lagopus muta Digital Distribution Maps of the Birds of the Western Hemisphere, version 5.0.* IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1.

Skírnisson, K., Þórarinsdóttir, S. T., & Nielsen, Ó. K. (2012). The Parasite Fauna of Rock Ptarmigan (*Lagopus muta*) in Iceland: Prevalence, Intensity, and Distribution Within the Host Population. *Comparative Parasitology, 79*(1), 44-55.

Snæþórsson, A. Ö. (2012). *Reproductive success and survival of hen rock ptarmigan (Lagopus muta) during summer.* M.Sc. thesis, Faculty of Life and Environmental Sciences, University of Iceland, pp. 42.

Steen, J. B. (1978). *Ryper. Rypeliv og rypejakt.* Oslo: Gyldendal Norsk Forlag.

The Environment Agency of Iceland. (2011, n.d.). Veiðitölur. Retrieved on 29.07.2013, from http://ust.is/einstaklingar/veidi/veiditolur/

The Environment Agency of Iceland. (2012, n.d.). Veiðitímabil. Retrieved on 29.07.2013, from http://www.ust.is/einstaklingar/veidi/veiditimabil/

The Environment Agency of Iceland. (25.09.2013). Fyrirkomulag rjúpnaveiða 2013 - Hófsemi í fyrirrúmi. Retrieved from https://www.ust.is/einstaklingar/frettir/frett/2013/09/25/Fyrirkomulag-rjupnaveida-2013-Hofsemi-i-fyrirrumi/

The Environment Agency of Iceland. (2013b). Veiðikort og skotveiði. Retrieved on 16.09.2013, from http://www.ust.is/einstaklingar/veidi/veidikortanamskeid/

The Icelandic Institute of Natural History. (2012). *Mat á veiðiþoli rjúpnastofnsins haustið 2012: greinargerð Náttúrufræðistofnunar Íslands*. The Icelandic Institute of Natural History. pp. 8

Timmermann, V. G. (1950). Beiträge zur Kentniss der Ektoparsitenfauna Isländischer Säugetiere und Vögel, 3. *Miscellaneous papers on Icelandic Zoology, 1*, 1-8.

Todd, A. W., & Keith, L. B. (1983). Coyote Demography during a Snowshoe Hare Decline in Alberta. *The Journal of Wildlife Management, 47*(2), 394-404.

Tompkins, D. M., & Begon, M. (1999). Parasites Can Regulate Wildlife Populations. *Parasitology Today, 15*(8), 311-313.

Turchin, P., Wood, S. N., Ellner, S. P., Kendall, B. E., Murdoch, W. W., Fischlin, A., Casas, J., McCauley, E., & Briggs, C. J. (2003). Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. *Ecology, 84*(5), 1207-1214.

Voous, K. H., & Thomson, S. A. L. (1960). Atlas of European birds.

2 Changes in mass of the preen gland in rock ptarmigans (*Lagopus muta*) in relation to sex, age and parasite burden 2007-2012

2.1 The preen gland

In birds, preening behavior mainly consists of drawing one or more feathers through their bill with fast movements that last between 1-1.5 seconds. It also includes head rubbing, head and body shaking, scratching, and stretching. Preening and allopreening (birds preening each other) are costly activities in terms of energy and time (Goldstein, 1988), and the resources that birds allocate into preening are redrawn from other activities (e.g. foraging and vigilance) (Redpath, 1988).

The preen gland is the only holocrine glandular organ in the bird integument (Jacob & Ziswiler, 1982; Johnston, 1988). The preen oil, the secretion of the preen gland, is transferred by the beak to the feathers during preening (Clayton et al., 2010). Most bird species have a preen gland but in some species the preen gland is only present during the embryonic phase of development. For example, in nine families of birds, including parrots (Psittacidae), ostriches (Struthionidae), pigeons and doves (Columbiade) among others, some or all members are without the preen gland (Jacob & Ziswiler, 1982; Johnston, 1988).

2.1.1 Anatomy

The preen gland is positioned dorsally and medially in the synsacrocaudal region, normally rostral to the pygostyle over the posterior caudal vertebrae (Fig. 2). Its location is distinguished by a "C" shaped line of feather follicles of the upper median and major tail converts. The main arterial supply is provided to the gland by the caudal artery (*Arteria caudae lateralis*). The caudal artery branches out including two coccygeal arteries (*Aa. intersegmentales caudales*), which before reaching the gland divide into an upper, lower and medial branch (*R.r. glandulares uropygiales*), reaching the gland dorsally, ventrally and medially, respectively. The venous drainage goes through a dorsal and ventral web of vessels (*Vv. glandulares uropygiales*) that join to become two parallel veins and then merge into the renal portal vein system (Kossmann 1871, Gadow & Selenka 1891 and Paris 1913 as cited by Jacob & Ziswiler, 1982). The gland is innerved by the *Nervous glangulae uropygialis*, which originates from both the medullary and sympathetic nervous system (Kossman 1871 and Paris 1913 as cited by Jacob & Ziswiler, 1982).

Enclosed by a connective tissue capsule, the typical gland consists of two lobes divided by the interlobular septum, the papilla, and the preen circlet or feather tuft (Lucas & Stettenheim, 1972; Jacob & Ziswiler, 1982). The lobes are rounded cranially to slender caudally at the preen canal entrance (Lucas & Stettenheim, 1972; Getty, 1975). The lobes

are usually clearly divided from the papilla by a firm band of connective tissue; the isthmus (Lucas & Stettenheim, 1972). Each lobe is composed by radially arranged secretory tubules where secretions collect into a central cavity. From this central cavity, a main preen duct is connected to the papilla at the posterior end of the preen gland. The papilla opens to the exterior at its tip in two preen pores (Lucas & Stettenheim, 1972; Menon et al., 1981; Jacob & Ziswiler, 1982).

Figure 2: Exposed preen gland of a rock ptarmigan still attached to the tail.Image courtesy of Ólafur Karl Nielsen.

The preen gland varies greatly in size, mass, shape and presence of a tuft of feathers (Jacob & Ziswiler, 1982). Age has also been demonstrated to be an important factor influencing the gland´s mass, histology and quantity of preen oil produced (in chickens *Gallus gallus domesticus*). The absolute preen gland weight increases as the chickens get older and larger, whereas the relative preen gland weight (as a percentage of body weight) shows little variation after 5 weeks of age (Sandilands et al., 2004).

2.1.2 Histology

A four-layer structure can be recognized within each secretory tubule. First, the germinative layer, which consists of one or two cell lines where new cells are created through mitosis and then pushed towards the lumen of the tubule. Second, the intermediate layer, which is formed by polygonal cell lines (1-5 lines) with a basophilic cytoplasm. Third, the secretory area, where one to ten rows of large polygonal cells and their secretion granules are found. Fourth, a degenerative or transitional layer, where keratohyalin granules are found in the cell cytoplasm, the nucleus are pyknotic, the cell walls are broken and the whole mass is pushed into the lumen of the tubule (Fig. 3) (Lucas & Stettenheim, 1972; Jacob & Ziswiler, 1982).

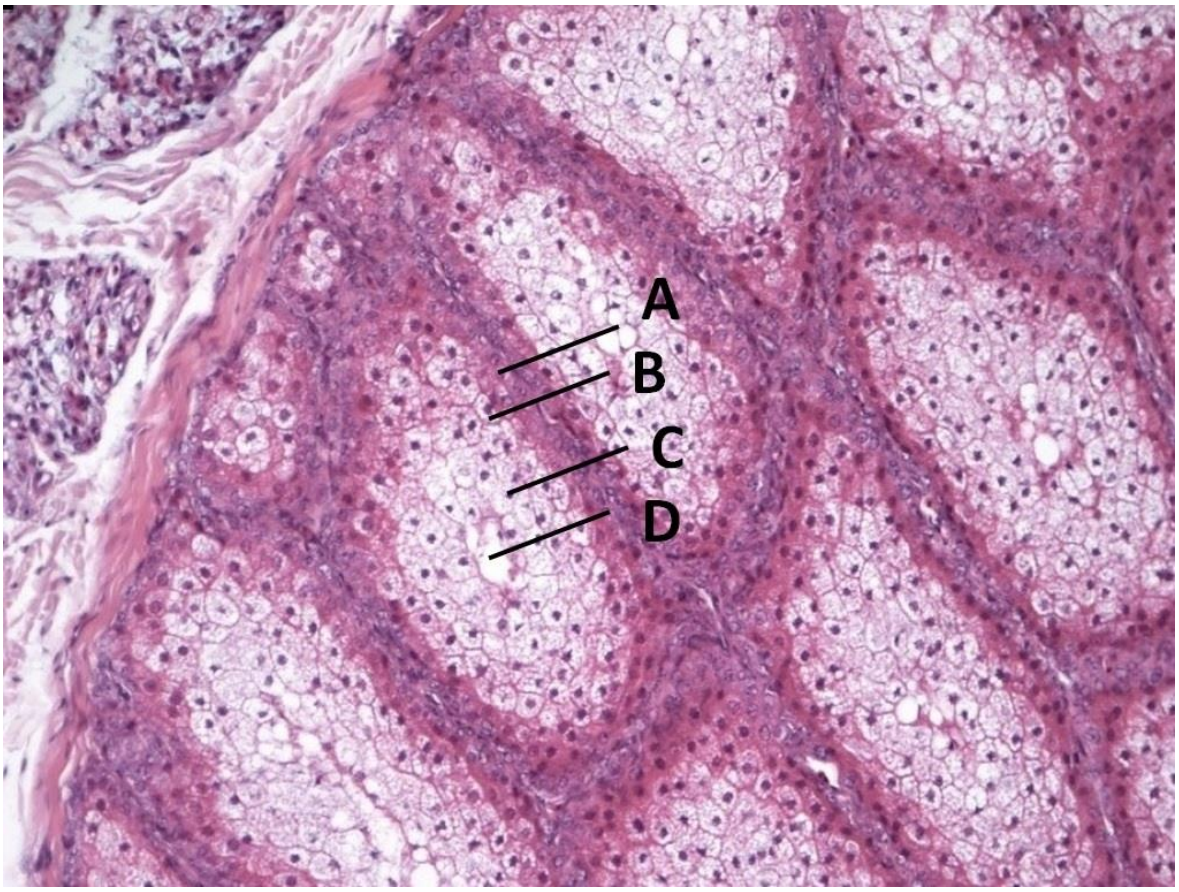

Figure 3: Transverse section of secretory tubules from the outer edge of a ptarmigan preen gland, fixed in 10% neutral buffered formalin and stained with haematoxylin-eosin (HE). A = germinative layer, B = intermediate layer, C = secretory area, D = lumen of the tubule. Magnification: 200x. Image courtesy of Ólöf Sigurðardóttir.

2.1.3 Physiology

Adrenal corticosteroids play a fundamental role in regulating the function and the maintenance of the preen gland (Asnani & Ramachandran, 1993). The gland synthesizes a complex oleaginous secretion that birds spread on to their plumage during the preening act. The daily excreted oil amount is highly variable and has been reported to range between 0.5 mg (Passeriformes) and 600 mg (Laridae) (Jacob, 1976). Previous studies have postulated that preen glands of greater dimensions secrete larger amounts of waxes in comparison to smaller glands (Elder, 1954; Sandilands et al., 2004; Martín-Vivaldi et al., 2009). Alternatively, it has been proposed that the physiological function of the gland may be determined by the chemical composition of the preen oil rather than the gland mass itself (Montalti & Salibián, 2000).

2.1.4 Preen oil composition

The preen oil is composed of non-lipoid and lipoid compounds. The non-lipoid compounds include proteins, inorganic salts and cell fragments (King & McLelland, 1975). The lipoid compounds are mostly monoester, diester and triester waxes (long chain molecules which have one, two or three ester bonds, respectively) of aliphatic alcohols and fatty acids (Haahti & Fales, 1967; Stevens, 2000). The chemical composition of the preen oil varies

greatly within and among species (Reneerkens et al., 2002; Haribal et al., 2005; Montalti et al., 2005). The diester waxes are particularly common in Galliformes, where they are normally made of unbranched fatty acids of up to 24 carbon atoms with 1, 2- and 2, 3-diols (two alcohol fractions on the first and second, or second and third, carbon atom of the fatty acid, respectively) (Jacob & Ziswiler, 1982).

In a study conducted in Iceland, preen oil samples from ptarmigans were collected and analyzed for composition from 2007-2009. Results showed that the proportion of the saturated fatty acid in the preen oil was higher than the proportion of unsaturated fatty acids, especially the myristic acid. Notable differences in the fatty acid composition were found among years and bird age. Compared between years, samples from 2007 had the greatest proportion of palmitic acid (16:0), whereas samples collected in 2008 had the highest proportion of myristic acid (14:0). In addition, samples collected in 2009 had the highest proportion of linoleic acid (18:2n-6). Adult individuals had a higher proportion of mono and polyunsaturated fatty acids than juveniles. No correlation was observed between parasite load and proportion of saturated fatty acids present in the ptarmigan preen oil (Runólfsdóttir, 2012).

Various factors that affect the preen oil´s fatty acid compound have been described in different species (Sandilands et al., 2004; Haribal et al., 2009). For example, in laying hens that are victims of feather pecking (a behavioral problem where a bird is excessively bitten by others), experiments have found the fatty acid proportion to be higher than in individuals that are not feather pecked. This could be caused by some birds "tasting" better than others, and therefore making them more exposed to feather pecking. In the same study, the age of the hens also affected the composition of fatty acids in the preen oil, which may be due to hen´s hormonal profile and sexual maturity at the time of the analysis (Sandilands et al., 2004).

In a study conducted by Haribal et al. (2009), a total of 40 samples of preen oil from tropical birds (e.g. antbirds (Thamnophilidae and Formicaridae), manakins (Pipridae), woodcreppers (Dendrocolaptidae) and a flycatcher (Tyrannidae)) were analyzed to gain better understanding of the differences in composition of the preen oil among birds that inhabit tropical habitats, as well as with species that inhabit temperate habitats. Results indicated that the preen oil of some tropical birds was formed by long chain esters. These compounds were of higher molecular weight than the preen oil described for multiple temperate species (monoesters) (Haribal et al., 2005). It was therefore concluded that the molecular composition of the long chain esters in tropical birds is likely influenced by ambient temperature (Haribal et al., 2009).

2.1.5 Phenology and associated functions of the preen oil

Both increased weight and activity have been seen in the preen gland during the breeding season (Asnani & Ramachandran, 1993). A variation from monoester in winter to diester waxy components in spring and summer (breeding season) has been observed in sandpipers (Scolopacidae) such as red knots (*Calidris canutus*) (Kolattukudy & Rogers, 1978; Reneerkens et al., 2002; Reneerkens et al., 2007). A similar chemical shift has also been described for female and male mallards (*Anas platyrhynchos*) and has been associated with sexual pheromone production (Kolattukudy et al., 1987; Bohnet et al., 1991). A different chemical shift in preen oil has been described for the darked-eyed junco (*Junco*

hyemalis), where an increase in linear alcohols (volatile compounds) during the breeding season has been reported (Soini et al., 2007).

Monoester waxes are more volatile than diester waxes and it has been proposed for sandpipers that this seasonal chemical shift has to do with predator avoidance during the incubation and nestling period, given that diester waxes emit less odor than monoester waxes (Reneerkens et al., 2002, 2005). This has also been suggested for female green woodhoopoes (*Phoeniculus purpureus*) (Burger et al., 2004) and for female hoopoe (*Upupa epops*). A particular trait in the preen oil of the hoopoe and green woodhoopoe is that along with the chemical shift during the breeding season, there is also a change in coloration and fluidity, becoming brown and thicker.

The changes in the preen oil during the breeding season also affect the plumage coloration and have proposed to act as a "cosmetic" (by improving the bird´s appearance), thus becoming a sexual signal (Simpson et al., 2002; Montgomerie, 2006; Delhey et al., 2007). For example in sandpipers, diester waxes present in the preen oil during the breeding season may alter the way it reflects ultra violet light, and therefore affect its visual attractiveness, and sexual selection (Reneerkens et al., 2002).

2.1.6 Other functions of the preen oil

Several other different functions have been assigned to the preen oil but results have been debated by various researchers throughout the years (Jacob & Ziswiler, 1982; Urich, 1994; Montalti & Salibián, 2000). One function is that it serves as a defense against pathogens, both fungi and bacteria, as well as against parasites. An *in vitro* experiment conducted by Jacob et al. (1997) showed that preen oil from the order Pelecaniformes had an antagonist effect over fungal dermatophytes (e.g. *Trichophyton* sp. and *Microsporum gypseym*), as well as an antibacterial effect over Gram-positive bacteria. Additionally, it has been proposed that bacteria are controlled through the action of certain bacteria that live in the preen gland (Jacob & Ziswiler, 1982; Bandyopadhyay & Bhattacharyya, 1996; Shawkey et al., 2003; Ruiz-Rodríguez et al., 2009). A symbiotic bacteria isolated from the brown preen oil from nestling hoopoes, *Enterococcus faecalis*, has an antagonistic effect through the production of bacteriocins that act against *Bacillus licheniformis*, a feather degrading bacteria (Martín-Platero et al., 2006). In addition, another study on the hoopoe that looked at the action of volatile compounds, present in the dark preen oil produced during the breeding season concluded that such compounds provided this species with strong antimicrobial action (Martín-Vivaldi et al., 2010).

The antibacterial property of the preen oil might be relevant in the hygiene of the nest and therefore in hatching success, since bacteria are an important factor affecting egg survival, both under natural and captive conditions (Baggott & Graeme-Cook, 2002; Cook et al., 2003, 2005). The difference between female and male secretion in the hoopoe and green woodhoopoe could also be connected to the fact that females incubate the eggs and brood the chicks and they use the same nests for years, therefore females may have a greater risk of pathogenic infections (Cramp, 1998; Burger et al., 2004). Møller et al. (2010) found that species with a proportionally larger preen gland enjoy a higher hatching success compared with species with a proportionally smaller gland, thus supporting the hypothesis that preen oil serves in controlling bacteria. In contrast, an experiment on red knots by Reneekens et al. (2008) suggests that preen oil maintains feather integrity by imposing a physical barrier to bacteria rather than through the chemical properties of the oil.

Experiments where the preen gland has been removed or blocked have been performed. In studies conducted on rock doves (Moyer et al., 2003) and mallards (Giraudeau et al., 2010), results indicated that after gland removal, individuals suffered from elevated degrees of fungal and bacterial colonization of feathers, as well as greater levels of feather degeneration. Contrary to this, no severe effects were recorded after gland removal in goslings (*Anser* sp.), chickens and some passerine birds (Jacob, 1976; Chen et al., 2003). A recent study on male house sparrows (*Passer domesticus*) found that gland removal had no important effects on feather-degrading bacteria but it did influence the abundance of other-cultivable bacteria. This study suggests that the antimicrobial function of the preen oil covers a broader range than was originally believed and that by controlling overall bacterial loads, the preen gland may have a role in fighting potentially detrimental bacteria (Czirják et al., 2013). The interaction between the preen gland and ectoparasites will be discussed further in section 2.1.7.

Another suggested function of the preen oil is that it helps maintain feather flexibility and it has been observed that preening without secretions leads feathers to become uneven and fragile (Moyer et al., 2003). The preen oil also acts as a water repellant for the feathers, which relates to the fact that aquatic species were thought to have proportionally larger preen glands than terrestrial birds (Jacob & Ziswiler, 1982). Nonetheless, a study showed that there is no clear relationship between the relative gland weight and the degree of aquaticity of the species in question, despite looking at more than a thousand individuals belonging to 126 different species (Montalti & Salibián, 2000). More recently however, the original hypothesis regarding the link between preen gland size and degree of aquaticity was confirmed by Møller et al. (2010), where terrestrial species had smaller preen glands (relatively to body mass) than aquatic species, and partially aquatic species showed intermediate gland sizes.

A final potential function is that the gland may capture and deposit lipophilic compounds, such as chlorinated hydrocarbon pesticides and pollutants (Charnetski & Stevens, 1974; Johnston, 1976, 1978). Experiments where sub-lethal doses of lindane have been injected into rock doves have shown accumulation of the insecticide in the gland (as well as liver enlargement) (Gutiérrez et al., 1998). These results suggest a repository and regulatory function, which may be of relevance in wild species occupying contaminated habitats (Pilastro et al., 1993; Dauwe et al., 2002).

2.1.7 Preen gland and ectoparasites

Preening behavior and scratching are the first means that birds have to defend themselves from the broad variety of ectoparasites that infest them (Rothschild & Clay, 1952; Clayton et al., 2010). Some groups of ectoparasites move slowly on the bird´s plumage or skin and therefore are rather easy to remove by preening (Marshal 1981 as cited by Clayton et al., 2010). Other mechanisms to fight ectoparasites in birds include body maintenance behaviors (e.g. sunning, anting and dusting), characteristics associated with plumage (e.g. feather molt, feather toughness, feather toxins, odorous feathers and preen oil) and the existence of a pectinate claw (Clayton et al., 2010).

It has been suggested that preen oil could act as a physical barrier against ectoparasites by limiting their ability to move on the bird´s plumage or skin (Clayton et al., 2010). It has also been proposed that preen oil could kill ectoparasites by blocking their spiracles (breathing pores), since an insecticide effect has been achieved by applying mineral oil on

chewing lice (B. R. Moyer unpubl. data as cited by Moyer et al., 2003). Another feature of the preen oil that has been mentioned that possibly influences ectoparasites is the unpleasant smell that characterizes the preen oil in some species (Clayton et al., 2010).

Feather mites are a common group of ectoparasites that infest birds (Blanco et al., 2001). Preen oil has been described to play an important role in the commensalistic relationship that some species of feather mites hold with their hosts (Galván et al., 2008). Feather mites feeding habits would benefit the host by preventing preen oil from accumulating excessively in the bird's plumage, which has been proved to reduce its heat retention capacity (Blanco et al., 2001; Proctor, 2003; Sandilands et al., 2004; Sweeney et al., 2004). Accordingly, the amount of feather mites and preen gland size have been described to be positively correlated, both intra- and interspecifically (Galván & Sanz, 2006; Galván et al., 2008; Møller et al., 2010; Haribal et al., 2011). Aditionally, Galván & Sanz (2006) showed that in great tits (*Parus major*) the abundance of feather mites was also positively correlated with the color intensity of the plumage.

Chewing lice are strictly parasitic and therefore hold different relationships than the ones described for some species of feather mites. In a study made by Moyer et al. (2003) the effect of preen oil on two species of chewing lice (e.g. *Columbicola columbae* and *Campanulotes bidentatus compar*) exclusive for rock doves, was tested *in vivo* and *in vitro*. The preen oil showed no significant insecticide effect on chewing lice *in vivo* but it had an insecticide effect when tested *in vitro*. In the same study, it is discussed that the difference between the results obtained under the two conditions could be attributed to pure chance and that further research is needed to test the insecticide effect of the preen oil.

In a study conducted by Møller et al. (2010) it was also described that the relative size of the preen gland size was positively correlated with the species richness of chewing lice from the genera Amblycera, but not from the sub-order Ischnocera. In the same study, it was described that the differences between the two groups could be attributed to the effect of biochemical compounds from the immune system and the preen oil that lice from the genera Amblycera are exposed to given their life habits of feeding on living tissues and coming into contact with the host´s immune system (Møller & Rózsa, 2005; Møller et al., 2010).

To summarize, it has been described that preen oil has an antagonistic effect over some species of feather degrading bacteria (e.g. *Bacillus* sp.) (Shawkey et al., 2003). In addition, feather mites have been described to feed on preen oil, as well as on bacteria killed by preen oil (Proctor, 2003). Finally, chewing lice have been reported to feed on feather mites, at least to some degree (Møller et al., 2010).

2.1.8 Research question

Preen gland tissue is mostly formed by secretory capsules, and it has been suggested that a gland size increases by the propagation of these capsules (Sandilands et al., 2004; Martín-Vivaldi et al., 2009). The main assumption is that gland mass reflects gland activity and therefore larger preen glands secrete more preen oil than smaller glands (Elder, 1954; Sandilands et al., 2004; Martín-Vivaldi et al., 2009). The aim of this study is to quantify the size of the preen gland in ptarmigans and to determine how variability in mass is related to age and sex of the birds and ectoparasite burden. The effect of year on the preen gland mass is also studied due to the cyclic population changes that characterize the ptarmigan. My prediction is that one of the primary functions of the preen gland in the

ptarmigan is related to the control of pathogens and parasites. Based on this prediction, the mass of the preen gland in ptarmigans should not only reflect body size of the bird but also age, year and ectoparasite burden. Individuals should allocate their resources in a way that defenses are induced when needed. To address these predictions, a data set on ptarmigans from North-East Iceland from 2007 to 2012 was analyzed.

2.2 Methods

2.2.1 Study area

The study area was located in North-East Iceland. The majority of the ptarmigans were collected in the lava fields and highlands east and north of Lake Mývatn (Fig. 4). The field headquarters and laboratory were at the Lake Mývatn Nature Research Station at Skútustaðir (65°34´N, 17°03´ W).

2.2.2 Ptarmigan population index

Territorial ptarmigan cocks have been counted since 1981 on six census plots within the general study area of the ptarmigan health project, covering a total of 26.8 km^2. This is a part of the monitoring program for the ptarmigan in Iceland. The counts are done in May and each plot is counted once either early in the morning hours or late in the afternoon (Nielsen et al. 2004). The index is the mean density of cocks for the six plots each year.

2.2.3 Collection of birds for the ptarmigan health project

Birds have been collected for the project during the first week of October since 2006. Collection of birds has been done under a special license issued by the Icelandic Institute of Natural History. The annual sample analyzed has been 71-101 individuals, both adults and juveniles. Juveniles are approximately 3 months old and adults are 15 months or older (Nielsen et al., 2013).

To avoid blood contamination an absorbing paper plug was inserted down the bird´s throat. The carcass was then completely wrapped in multiple layers of absorbing paper and then placed in a paper bag with the bird´s identification number written on it. Bags were transported to the laboratory by car in Styrofoam cooling boxes, at 4°C (Nielsen et al., 2013).

2.2.4 Processing and measuring at the laboratory

Processing of the birds was always performed within three days from collection and it took approximately 40 minutes for each bird (Nielsen et al., 2013). The birds were sexed by the loral stripe and size and color of the combs (Montgomerie & Holder, 2008). The criteria used for determining the age of the birds was based on the pigmentation of the primaries (Weeden & Watson, 1967). Sex and age were verified during dissection by examination of the gonads and presence or absence of the bursa of Fabricius (Skírnisson et al., 2012). Samples of different organs and tissues were collected during dissection for later analyses, including preen glands and tails (Nielsen et al., 2013).

The scales used to record mass were AND Fx-3000 (precision 0.01 g) or AND HR-120 (precision 0.0001 g). The tools that were used to measure size were vernier calipers (accuracy 0.01 mm) and a steel ruler with a zero-stop (accuracy 1 mm) (Nielsen et al., 2013).

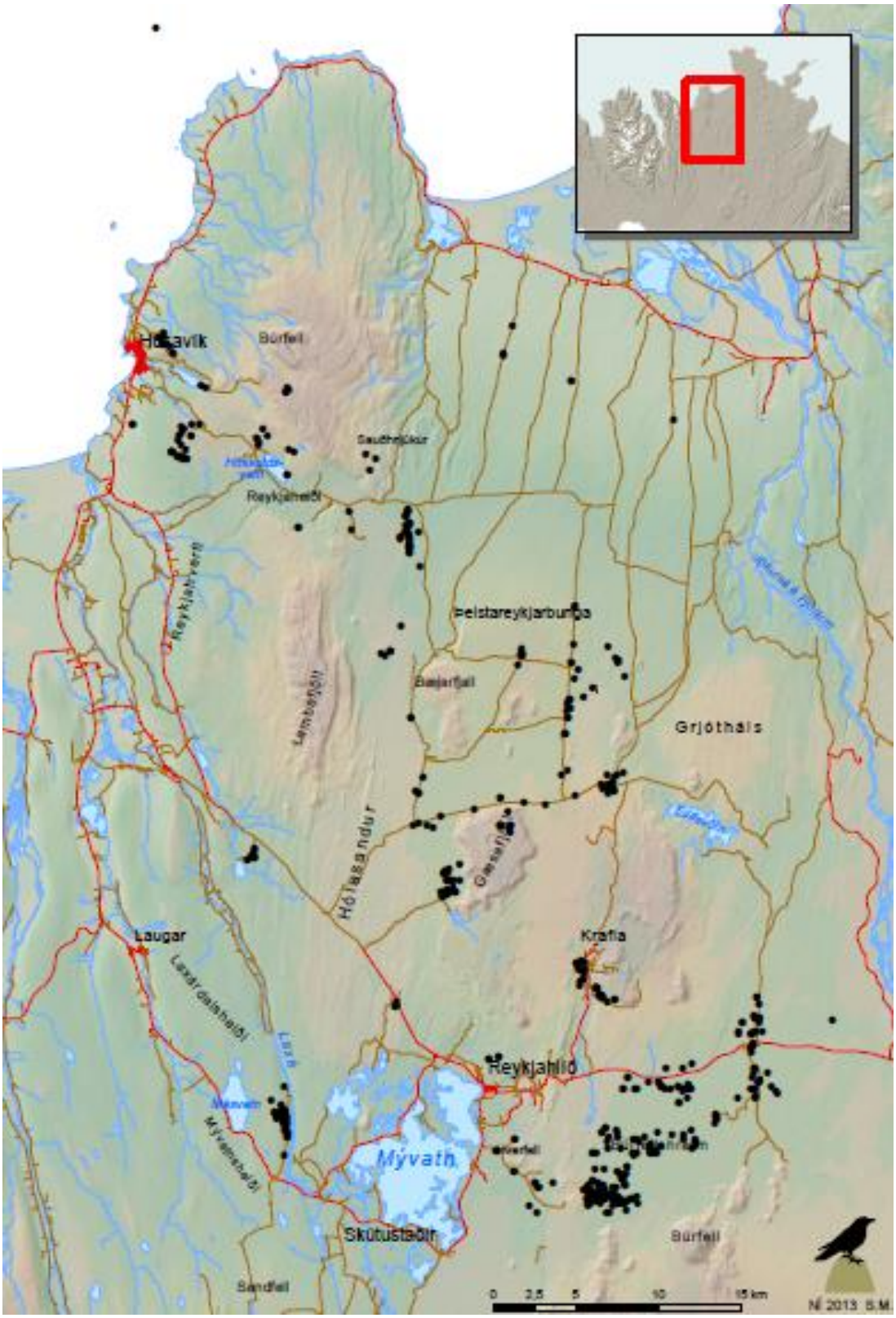

Figure 4: Rock ptarmigan study area in North-East Iceland 2007-2012. Black dots are collection sites of the ptarmigans. A dot can represent more than one bird.

The body measurements used for this study were all taken during dissection of the birds at Lake Mývatn and are:

1. *Head + bill*: measured with vernier calipers, from the hindmost point of the head to the tip of the bill (positioned horizontally to the head).
2. *Tarsus*: measured with the aid of vernier calipers, from the articulation between tarsus and toes to the intertarsal articulation; both the toes and the tibia were flexed inversely at approximately 90° to the tarsus.
3. *Tarsus + mid toe*: measured with a zero stop ruler, from the joint to the base of the central claw (to facilitate reading, the claw was cut off at the base). The intertarsal joint was held down to the stop, and the tarsus and the toes extended on the ruler (Nielsen et al., 2013).
4. *Sternum length*: measured with vernier calipers, from the end of *Spina externa* through the middle line to *Margo caudalis*.
5. *Sternum-coracoid length*: measured with vernier calipers, from the middle line of *Margo caudalis* to the cranial end of the *Coracoideum*, which was first released from the shoulder articulation. Anatomical terms are following Baumel (1979).

"*Body size*" refers to the supporting tissues of the body form, primarily the skeleton. The five size variables listed above were selected to represent body size. To determine body size based on these five body measurements, a principle component analysis (PCA) was conducted. Five different factors were calculated from the PCA. The factor that showed the highest correlation with the five body measurements was Factor 1; 70.12 % of the variance in the body measurements was explained by this factor (Table 2). Therefore, Factor 1 reflected body measurements and is a descriptor of body size, and whenever body size is mentioned in the text it refers to the Factor 1 of the PCA (Table 3).

Table 2: Eigenvalues of the correlation matrix (and related statistics) derived from the principle component analysis based on five body measurements of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Factor	Eigenvalue	% total-variance	Cumulative - Eigenvalue	Cumulative - %
1	3.51	**70.12**	3.51	**70.12**
2	0.64	12.84	4.15	82.96
3	0.51	10.21	4.66	93.17
4	0.33	6.66	4.99	99.83
5	0.01	0.17	5.00	100

Table 3: Factor coordinates of the variables, based on correlations with five body measurements of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Body measurement	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Head + bill	**0.828**	-0.156	-0.165	0.512	-0.017
Tarsus length	**0.693**	0.526	0.488	0.070	0.011
Tars + middle toe length	**0.715**	0.478	-0.480	-0.173	-0.020
Sternum length	**0.885**	-0.337	0.124	-0.214	-0.206
Sternum – coracoid length	**0.908**	-0.306	0.036	-0.176	0.224

2.2.5 External parasite collection and quantification

Although in the ptarmigan health project internal and external parasites were collected, for the purposes of this study only ectoparasites are of relevance, because endoparasites do not come into contact with the defense mechanism of the preen gland secretions (Møller et al., 2010). The ectoparasite data were provided by Dr. Karl Skírnisson, at the Institute for Experimental Pathology of the University of Iceland, and Ute Stenkewitz at the Icelandic Institute of Natural History.

During the packing process, the presence of hippoboscid flies was recorded and whenever possible the flies were collected and fixed in 70% ethanol. After unwrapping the birds, the examiner always looked for the presence of flies and chewing lice, both in the wrapping material and the bird itself (Skírnisson et al., 2012; Nielsen et al., 2013). After un-wrapping each bird it was then systematically vacuumed for approximately a minute with a modified handheld Princess® (Type 2755) vacuum cleaner. The vacuum was modified by attaching a spout (4 x 1.5 cm) and a placing a 100 cm^2 filter. The filter, its content, and the bird´s wrapping were stored in a plastic bag at -20°C. The elements stored in the filter, such as feathers, skin and blood flakes, and parasites were moved to a 400 ml glass jar. To prevent accidental loss of particles, the filter was washed onto a Petri dish and then the liquid was poured into a 400 ml glass jar along with more water until in total, 100 ml were reached. To encourage particle settling and diminish adhesive forces, seven drops of the surfactant TritonH X-100 were combined to the mixture. A lid was placed on the jar and it was agitated manually. Feathers were taken individually from the mixture, washed with water over the jar and then cast away. The mixture was then softly stirred, in order to remove air bubbles and particles from the surface, and left to stand for one hour (Skírnisson et al., 2012).

Parasite collection from the sediments was performed under a stereoscope at x10–35 magnification and specimens fixed in ethanol. The lice sample included individuals found in the vacuum filters and picked manually, either from the birds or their wrappings in the laboratory. All mites, except for *Tetraolichus lagopi*, were gathered from the vacuum filters (Skírnisson et al., 2012). *T. lagopi* was so numerous that a scale was used to quantify its infestation intensity. The value obtained by each bird in the scale was derived from direct counts and from infestation scores that were given after looking at the underwing coverts, the main areas where *T. lagopi* resides. The scale has four values that range from 0 to 3, where 0 means absence of the parasite, 1 is an estimated infestation of 1-25 %, 2 is an estimated infection intensity of 26-75 %, and 3 is an estimated infection intensity of 76-100 % (Stenkewitz, 2013).

Identification was done following methods by different authors (Skírnisson et al., 2012). Mites were mounted in Hoyer's medium (Gaud & Atyeo, 1996) and identified following Mironov et al. (2010). The chewing lice *Gonoides lagopi* and *Lagopoecus affinis* were identified according to Timmermann (1950). Identification of *Amyrsidea lagopi* presence was confirmed by Ricardo L. Palma, from the Museum of New Zealand Te Papa Tongarewa (Skírnisson et al., 2012). The hippoboscid fly *Ornithomya chloropus* was identified according to Theodor and Oldroyd (1964).

2.2.6 Processing of the preen gland

A total of 526 preen glands were analyzed in the laboratory for this study. Dr. Ólafur Karl Nielsen provided preen gland data for 2007-2010 and for this study the preen glands from 2011 and 2012 were analyzed. Preen glands were transported from Mývatn to Garðabær still attached to the tails and preserved frozen at -20°C. Prior to processing, the tails were left at room temperature for approximately 10 minutes. The gland was exposed and carefully detached from the muscle. Immediately after extraction, the gland was weighed on a precision balance to the nearest 0.001 g. Subsequently, the papilla was cut off and the gland was weighed again. Preen oil was collected in individual tubes by gently squeezing the gland and frozen immediately after extraction. The glands were weighed again after all the oil was extracted. For this study, intact gland mass (preen gland, preen oil and papilla) (g) was used as an indicator of gland size in all the analyses.

2.2.7 Statistical analyses

All statistical tests were conducted with STATISTICA 12 (Statsoft, 2012), using an alpha level of 0.05. The distribution of the gland mass data and their transformed values using $\log_{10}$ were explored through a Chi-square test to determine if normality assumptions were satisfied. Variance homogeneity was tested using Levene's test of homogeneity and the Brown-Forsythe test of homogeneity. Preen gland data were grouped into four categories according to age and sex (e.g. adult females, juvenile females, adult males and juvenile males). The mass of the preen gland between age groups (adult versus juvenile) and sex (female versus male) were compared with an analysis of variance (ANOVA) and significant differences were examined further with Tukey's honest significant test.

Simple linear regression analyses were performed to explore different relationships, such as the one between preen oil mass (g) and preen gland mass (g) after the oil had been extracted. For this analysis, the dependant (response) variable was oil mass (g) and the independent variable (covariate) was preen gland mass (g) after oil extraction. A regression analysis was also performed to study the relationship between preen gland mass and body size of the ptarmigans, where the dependant variable was the mass of the preen gland ($\log_{10}$- transformed) and the independent variable was body size. Furthermore, the relationship between preen gland mass and body size was studied separately in the two age groups (e.g. juveniles and adults) through two simple linear regression analyses.

A general linear model analysis was performed to explore the factors influencing the variability in preen gland mass. One model used the mass of the preen gland ($\log_{10}$-transformed) as the dependant variable, and sex, age, collection year (hereafter referred to year) and their interactions as independent variables. A second general linear model was also developed, where mass of the preen gland ($\log_{10}$-transformed) was the dependant variable and the independent variables were sex, age, year, body size and only the interaction between age and year. Subsequently, different measures of parasite infestation

were added one by one to the second general linear model (Table 8) and the model was run multiple times (Table 9). The measures included ectoparasite species richness, ectoparasite load, ectoparasite presence/absence and ectoparasite burden. These measures included 10 different ectoparasite species (Table 1), except for ectoparasite load, which included only nine ectoparasite species (the flea *Ceratophyllus garei* was excluded from that measure due to too few observations). Ectoparasite species richness refers to the number of species encountered on one host, while ectoparasite load refers to the abundance of a particular ectoparasite species on the host. Ectoparasite presence/absence refers to whether a host has a particular species or not. Ectoparasite burden covers these three measures and is obtained by adding the ranked values of all individual species. Ectoparasite burden refers to the combined parasite community, thus giving an infestation intensity index.

2.3 Results

2.3.1 Preen gland

Among the four age and sex groups, the heaviest mean preen gland was found in adult males, while the lightest occurred in juvenile females (Fig. 5). The glands were heaviest in 2011, followed by 2012, 2007, 2010, 2009 and 2008 (Table 4).

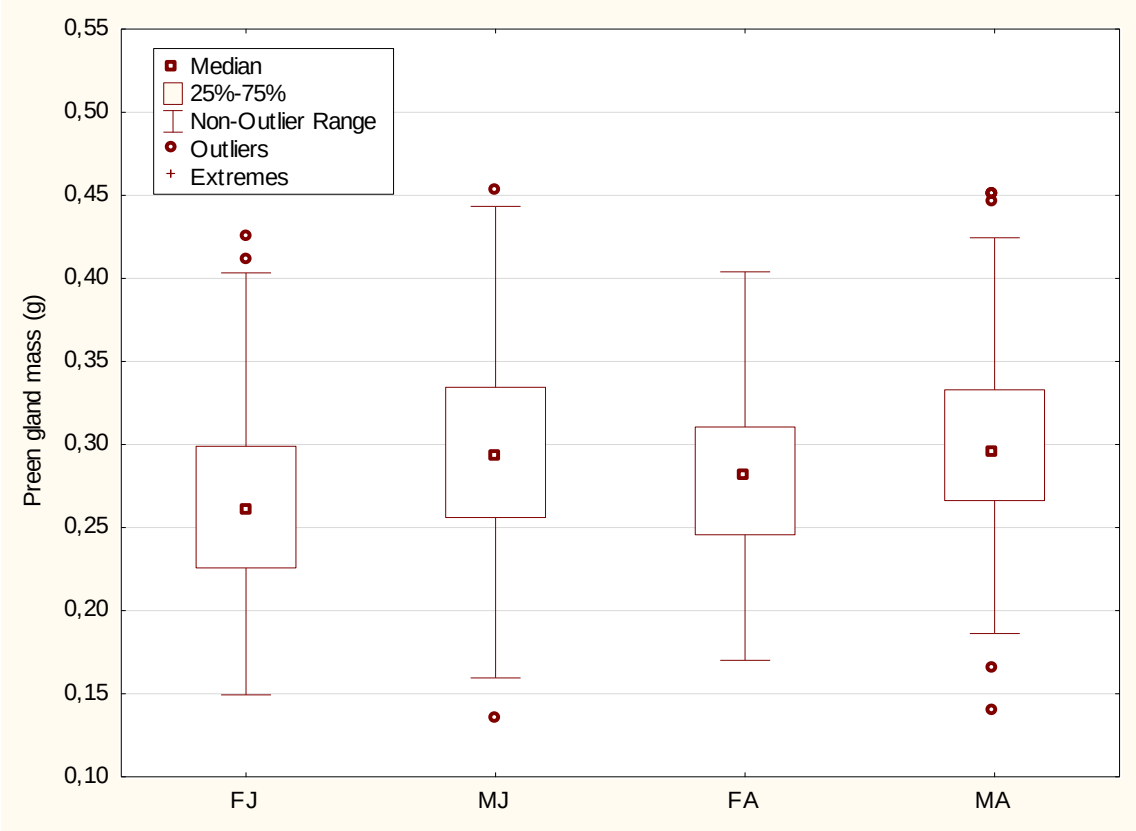

Figure 5: Preen gland mass according to age and sex of rock ptarmigans collected in North-East Iceland in October 2007-2012. FJ are juvenile females, MJ are juvenile males, FA are adult females and MA are adult males.

Table 4: Total mass of the preen gland (g) in rock ptarmigans collected in North-East Iceland in October 2007-2012, grouped by years, age and sex. FJ are juvenile females, MJ are juvenile males, FA are adult females and MA are adult males. Sample size, mean, range and standard deviation (SD) for each group are shown.

Year/ Sex-age group	Sample size (n)	Mean (g)	Minimum (g)	Maximum (g)	SD
2007	**71**	**0.287**	**0.135**	**0.451**	**0.066**
FA	4	0.295	0.255	0.359	0.049
FJ	28	0.269	0.175	0.426	0.058
MA	13	0.353	0.244	0.451	0.064
MJ	26	0.271	0.135	0.419	0.060
2008	**83**	**0.261**	**0.171**	**0.411**	**0.050**
FA	13	0.246	0.184	0.343	0.047
FJ	29	0.251	0.182	0.411	0.053
MA	11	0.262	0.186	0.325	0.043
MJ	30	0.277	0.171	0.368	0.046
2009	**78**	**0.276**	**0.168**	**0.424**	**0.057**
FA	6	0.283	0.232	0.404	0.066
FJ	30	0.262	0.168	0.370	0.053
MA	13	0.256	0.198	0.317	0.040
MJ	29	0.298	0.208	0.424	0.059
2010	**96**	**0.282**	**0.149**	**0.453**	**0.066**
FA	13	0.296	0.212	0.377	0.048
FJ	27	0.248	0.149	0.365	0.055
MA	26	0.292	0.164	0.451	0.063
MJ	30	0.297	0.160	0.453	0.075
2011	**101**	**0.305**	**0.170**	**0.519**	**0.056**
FA	16	0.291	0.170	0.370	0.048
FJ	30	0.297	0.173	0.519	0.065
MA	25	0.315	0.216	0.421	0.054
MJ	30	0.312	0.176	0.443	0.052
2012	**97**	**0.304**	**0.140**	**0.450**	**0.061**
FA	9	0.294	0.211	0.401	0.056
FJ	29	0.275	0.174	0.395	0.060
MA	30	0.319	0.140	0.450	0.063
MJ	29	0.322	0.229	0.440	0.052
Total	**526**	**0.287**	**0.135**	**0.519**	**0.061**

The preen gland mass deviated significantly from the normal distribution (Chi square test = 26.206, df = 12, p = 0.01). The preen gland mass was therefore log_{10}-transformed (Chi square test = 10.828, df = 8, p = 0.212). Levene's test of homogeneity implied that the variances were homogeneous (p = 0.738). The ANOVA detected a significant difference among both age and sex groups but not the interaction term (Table 5). Males had bigger glands than females and adults had bigger glands than juveniles. The mean gland mass for males was 0.300 g (SD = 0.062), while for females was 0.275 g (SD = 0.056). The mean gland mass for adults was 0.293 g (SD = 0.002) while for juveniles was 0.282 g (SD = 0.06). The Tukey test indicated that the main significant contrast was encountered between juvenile females and both adult and juvenile males (Table 6).

Table 5: ANOVA results comparing preen gland mass (g) from rock ptarmigans collected in North-East Iceland in October 2007-2012 relative to age and sex Significant values (alpha < 0.05) are emphazised.

Effect	SS	Degree(s) of Freedom	MS	F	p
Intercept	133.502	1	133.502	15860.077	**0.000**
Sex	0.157	1	0.157	18.690	**0.000**
Age	0.035	1	0.035	4.143	**0.042**
Sex*Age	0.007	1	0.007	0.881	0.348
Error	4.394	522	0.008		

Table 6: Tukey test results given a p-value for preen gland mass (g) from rock ptarmigans collected in North-East Iceland in October 2007-2012, grouped by sex and age.FJ are juvenile females, MJ are juvenile males, FA are adult females and MA are adult males. Significant p-values (alpha < 0.05) are emphazised.

Effect	Sex	Age	1	2	3	4
1	F	J		0.226	**0.000**	**0.000**
2	F	A	0.226		0.458	0.171
3	M	J	**0.000**	0.458		0.817
4	M	A	**0.000**	0.171	0.817	

2.3.2 Oil mass and preen gland mass

The amount of oil found in the preen gland had a significant negative relationship with the mass of the empty preen gland after the oil had been extracted (Fig. 6). This indicates that proportionally more oil was squeezed out of smaller glands compared with bigger glands.

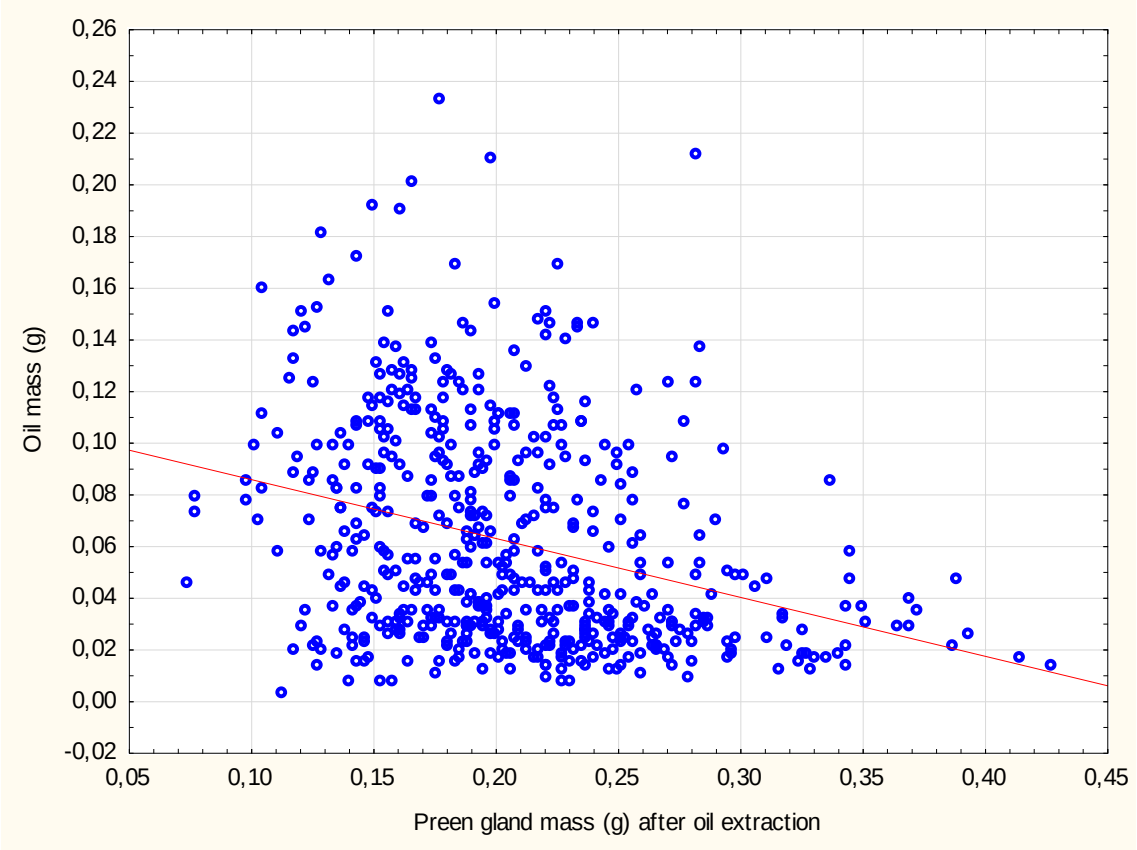

Figure 6: *Preen oil mass (g) in relation to preen gland mass after oil extraction (g) in rock ptarmigans collected in North-East Iceland in October 2007-2012. The red line indicates the regression fit (r^2=0.098; p=0.000.Regression equation: Oil mass (g) = 0.1087 - 0.228*preen gland mass after oil extraction (g)).*

2.3.3 Preen gland mass and body size

Results indicate that there was a significant positive relationship between preen gland mass and body size of the birds, in both age groups combined (e.g. juveniles and adults) (Fig. 7). The mass of the preen gland increased with body size, and therefore bigger birds had bigger glands, and 5.3% of the variability of the preen gland mass was explained by body size.

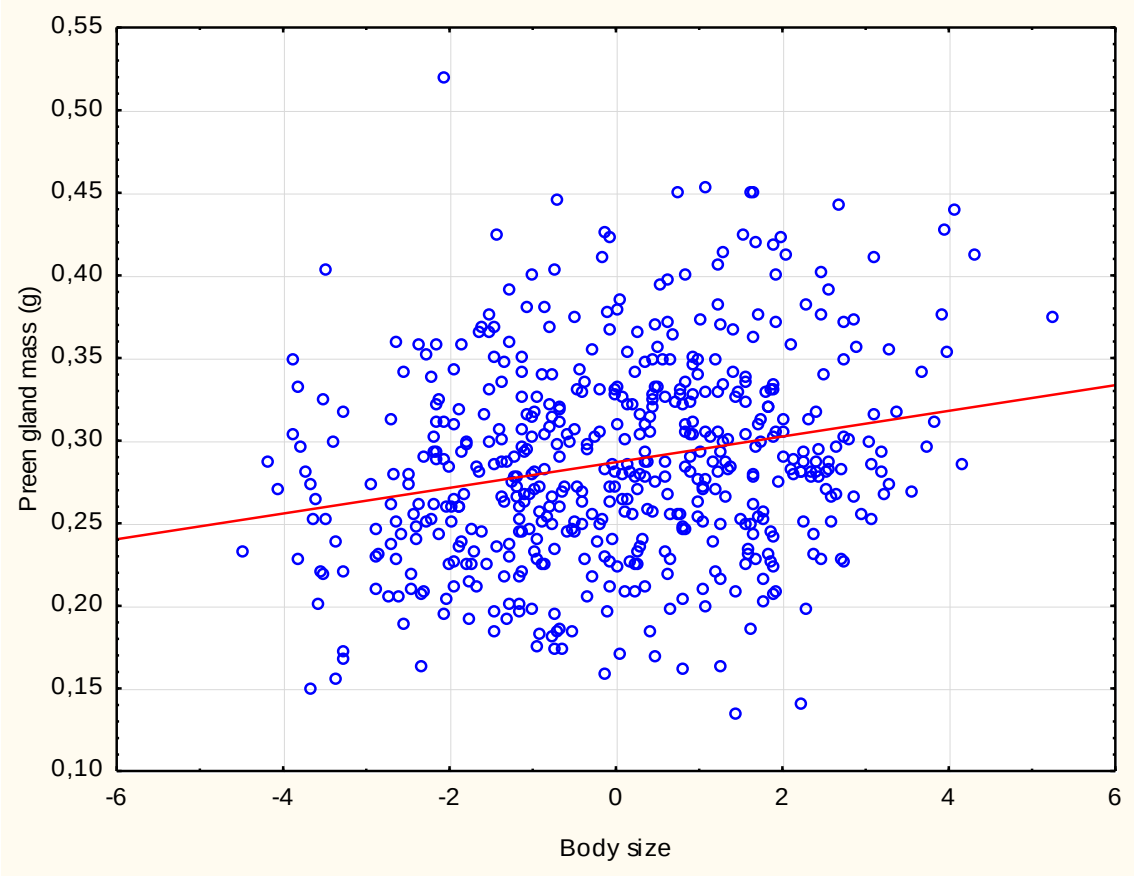

Figure 7: *Preen gland mass (g) in relation to body size of rock ptarmigans collected in North-East Iceland in October 2007-2012. The red line indicates the regression fit (r^2=0.053; p=0.000. Regression equation: Preen gland mass (g) = -0.287 + 0.0078*body size).*

2.3.4 Factors affecting preen gland mass

The first general linear model indicates that sex and year was highly negatively correlated with preen gland mass (log_{10}-transformed). Some years were positively correlated (2007 and 2011), while others were negatively correlated with preen gland mass (2008, 2009 and 2010). In addition, the interaction of age and year was also correlated with preen gland mass (Table 7).

Table 7: Results of the general linear model exploring the effects of sex, age, year, and their interactions, in preen gland mass (log_{10}-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Variables	Parameter coefficients	SS	Degree of Freedom	MS	F	p
Intercept	**-0.552**	**115.829**	**1**	**115.829**	**14947.34**	**0.000**
Sex	**-0.017**	**0.104**	**1**	**0.104**	**13.45**	**0.000**
Age	-0.008	0.027	1	0.027	3.44	0.064
Year		**0.259**	**5**	**0.051**	**6.68**	**0.000**
2007	0.015					
2008	-0.042					
2009	-0.017					
2010	-0.007					
2011	0.027					
Sex*Age	-0.006	0.016	1	0.016	2.03	0.155
Sex* Year		0.017	5	0.003	0.43	0.829
2007	-0.003					
2008	-0.002					
2009	0.013					
2010	0.000					
2011	0.002					
Age*Year		**0.092**	**5**	**0.018**	**2.36**	**0.039**
2007	-0.032					
2008	0.017					
2009	0.016					
2010	-0.011					
2011	0.009					

Sex*Age*Year		0.069	5	0.014	1.79	0.113
2007	0.025					
2008	0.002					
2009	-0.018					
2010	-0.015					
2011	0.009					
Error		3.890	502	0.007		

Based on this general linear model a new model was developed, this time including body size and the only significant interaction in the previous model (between age and year). Neither sex nor age were significant once body size was included as a covariate in the model, but the effect of year was still highly significant (Fig 8). Preen gland mass was also positively correlated to body size. There was also a significant correlation between preen gland mass and the interaction between age and year. This correlation was negative for the years 2007 and 2010 and positive for the years 2008, 2009 and 2011 (Table 8). The annual variability in preen gland mass is shown in Fig. 8, where preen gland mass drops in 2008 and then continuously increases until 2011, to decrease in 2012.

Table 8: Results of the general linear model exploring the effects of sex, age, year, body size and the interaction between age and year, in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Variables	Parameter coefficients	SS	Degree of Freedom	MS	F	p
Intercept	**-0.552**	**127.874**	**1**	**127.874**	**16561.23**	**0.000**
Sex	-0.009	0.018	1	0.002	2.35	0.126
Age	-0.006	0.017	1	0.017	2.22	0.137
Year		**0.310**	**5**	**0.062**	**8.03**	**0.000**
2007	0.021					
2008	-0.042					
2009	-0.021					
2010	-0.010					
2011	0.029					
Body size	**0.008**	**0.051**	**1**	**0.051**	**6.63**	**0.010**
Age*Year		**0.132**		**0.026**	**3.41**	**0.005**
2007	-0.040					
2008	0.013					
2009	0.021					
2010	-0.007					
2011	0.011					
Error		3.953	512	0.007		

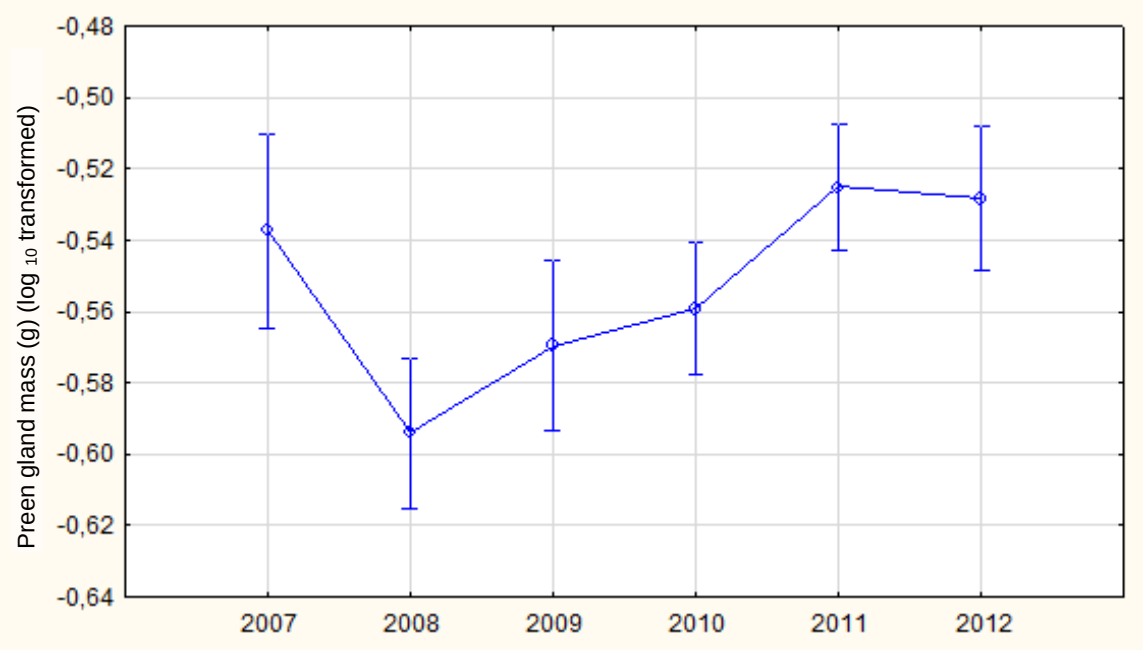

Figure 8: Overview of the annual changes in preen gland mean mass (g) (log_{10}-transformed) corrected for sex, age and body size of rock ptarmigans collected in North-East Iceland in October 2007-2012.

2.3.5 Preen gland mass and ectoparasites

Overall, nine general linear models that included ectoparasite variables showed a significant relationship with preen gland mass (Tables 9-18). Examinations of these correlations shed light on the relationship between preen gland mass and certain ectoparasite variables. For example, ectoparasite richness showed a significant and negative relationship with preen gland mass. The higher the number of ectoparasite species per host, the smaller the preen gland. In terms of the ectoparasite load, the only species that showed a significant relationship was the feather mite *Metamicrolichus islandicus*. This relationship was positive, meaning that the higher the load of *M. islandicus*, the bigger the preen gland. Among feather mites presence, *Myialges borealis* and *Strelkoviacarus holoaspis* were positively correlated with preen gland mass. Hence, ptarmigans that had feather mites of these two species had bigger preen glands. All of the chewing lice species and their combined index were negatively correlated with preen gland mass, therefore birds that had chewing lice had smaller glands (Tables 9-18). Finally, ectoparasite burden (total parasite community), had a significant and negative relationship with preen gland mass, indicating that birds that had heavier ectoparasite infestations had smaller glands (Table 17 and Fig. 9).

Table 9: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and ectoparasite richness in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Variables	Parameter coefficients	SS	Degree of Freedom	MS	F	p
Intercept	**-0.530**	**15.999**	**1**	**15.999**	**2085.04**	**0.000**
Sex	-0.007	0.012	1	0.012	1.53	0.217
Age	-0.002	0.002	1	0.02	0.21	0.649
Year		**0.322**	**5**	**0.064**	**8.39**	**0.000**
2007	0.022					
2008	-0.044					
2009	-0.020					
2010	-0.012					
2011	0.031					
Age*Year		**0.136**	**5**	**0.027**	**3.54**	**0.004**
2007	-0.040					
2008	0.013					
2009	0.023					
2010	-0.007					
2011	0.019					
Body size	**0.008**	**0.055**	**1**	**0.055**	**7.17**	**0.008**
Ectoparasite richness	**-0.006**	**0.032**	**1**	**0.032**	**4.24**	**0.040**
Error		3.953	512	0.007		

Table 10: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and load of Metamicrolichus islandicus in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Variables	Parameter coefficients	SS	Degree of Freedom	MS	F	p
Intercept	**-0.557**	**103.851**	**1**	**103.851**	**13562.73**	**0.000**
Sex	-0.009	0.021	1	0.021	2.74	0.099
Age	-0.007	0.023	1	0.023	3.00	0.084
Year		**0.323**	**5**	**0.065**	**8.44**	**0.000**
2007	0.017					
2008	-0.044					
2009	-0.021					
2010	-0.008					
2011	0.031					
Age*Year		**0.128**	**5**	**0.027**	**3.34**	**0.006**
2007	-0.039					
2008	0.012					
2009	0.020					
2010	-0.006					
2011	0.011					
Body size	**0.008**	**0.049**	**1**	**0.055**	**6.43**	**0.012**
***Metamicrolichus islandicus* load**	**0.011**	**0.041**	**1**	**0.032**	**5.30**	**0.022**
Error		3.875	506	0.008		

Table 11: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and presence of Myialges borealis in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Variables	Parameter coefficients	SS	Degree of Freedom	MS	F	p
Intercept	**-0.555**	**115.52**	**1**	**115.52**	**15047.94**	**0.000**
Sex	-0.009	0.018	1	0.018	2.34	0.126
Age	-0.008	0.024	1	0.024	3.10	0.079
Year		**0.315**	**5**	**0.027**	**8.21**	**0.000**
2007	0.020					
2008	-0.043					
2009	-0.021					
2010	-0.009					
2011	0.030					
Age*Year		**0.133**	**5**	**0.049**	**3.47**	**0.004**
2007	-0.039					
2008	0.012					
2009	0.022					
2010	-0.007					
2011	0.011					
Body size	**0.008**	**0.049**	**1**	**0.031**	**6.38**	**0.012**
***Myialges borealis* presence**	**0.023**	**0.031**	**1**	**0.008**	**3.98**	**0.047**
Error		3.884	506	0.008		

Table 12: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and presence of Strelkoviacarus holoaspis in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Variables	**Parameter coefficients**	**SS**	**Degree of Freedom**	**MS**	**F**	**p**
Intercept	**-0.555**	**78.757**	**1**	**78.757**	**10266.33**	**0.000**
Sex	-0.009	0.015	1	0.015	1.91	0.168
Age	-0.008	0.008	1	0.008	1.07	0.302
Year		**0.295**	**5**	**0.060**	**7.69**	**0.000**
2007	0.020					
2008	-0.043					
2009	-0.021					
2010	-0.009					
2011	0.030					
Age*Year		**0.137**	**5**	**0.027**	**3.56**	**0.004**
2007	-0.039					
2008	0.012					
2009	0.022					
2010	-0.007					
2011	0.011					
Body size	**0.008**	**0.056**	**1**	**0.056**	**7.26**	**0.007**
***Strelkoviacarus holoaspis* presence**	**0.023**	**0.033**	**1**	**0.033**	**4.34**	**0.047**
Error		3.882	506	0.008		

Table 13: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and presence/absence of Gonoides lagopi in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Variables	**Parameter coefficients**	**SS**	**Degree of Freedom**	**MS**	**F**	**p**
Intercept	**-0.540**	**40.428**	**1**	**40.428**	**5267.22**	**0.000**
Sex	-0.007	0.013	1	0.013	1.72	0.190
Age	-0.003	0.003	1	0.003	0.39	0.533
Year		**0.320**	**5**	**0.064**	**8.34**	**0.000**
2007	0.020					
2008	-0.043					
2009	-0.020					
2010	-0.010					
2011	0.031					
Age*Year		**0.124**	**5**	**0.025**	**3.24**	**0.007**
2007	-0.037					
2008	0.013					
2009	0.022					
2010	-0.007					
2011	0.010					
Body size	**0.008**	**0.053**	**1**	**0.053**	**6.87**	**0.009**
***Gonoides lagopi* presence**	**-0.019**	**0.031**	**1**	**0.031**	**4.08**	**0.044**
Error		3.884	506	0.008		

Table 14: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and presence of Lagopoecus affinis in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012.

Variables	**Parameter coefficients**	**SS**	**Degree of Freedom**	**MS**	**F**	**p**
Intercept	**-0.540**	**67.211**	**1**	**67.211**	**8860.53**	**0.000**
Sex	-0.007	0.013	1	0.013	1.67	0.197
Age	-0.001	0.001	1	0.001	0.08	0.775
Year		**0.343**	**5**	**0.069**	**9.05**	**0.000**
2007	0.021					
2008	-0.046					
2009	-0.019					
2010	-0.013					
2011	0.032					
Age*Year		**0.136**	**5**	**0.027**	**3.58**	**0.003**
2007	-0.039					
2008	0.010					
2009	0.023					
2010	-0.007					
2011	0.012					
Body size	**0.008**	**0.048**	**1**	**0.048**	**6.32**	**0.012**
***Lagopoecus affinis* presence**	**-0.027**	**0.077**	**1**	**0.077**	**10.13**	**0.002**
Error		3.838	506	0.008		

Table 15: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and presence of Amyrsidea lagopi in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012

Variables	**Parameter coefficients**	**SS**	**Degree of Freedom**	**MS**	**F**	**p**
Intercept	**-0.550**	**115.421**	**1**	**115.421**	**15033.57**	**0.000**
Sex	-0.008	0.015	1	0.015	1.95	0.164
Age	-0.004	0.008	1	0.008	0.98	0.324
Year		**0.314**	**5**	**0.063**	**8.17**	**0.000**
2007	0.020					
2008	-0.046					
2009	-0.020					
2010	-0.010					
2011	0.031					
Age*Year		**0.134**	**5**	**0.027**	**3.50**	**0.004**
2007	-0.039					
2008	0.013					
2009	0.022					
2010	-0.006					
2011	0.011					
Body size	**0.008**	**0.056**	**1**	**0.056**	**7.35**	**0.007**
***Amyrsidea lagopi* presence**	**-0.023**	**0.030**	**1**	**0.030**	**3.93**	**0.048**
Error		3.885	506	0.008		

Table 16: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and presence of chewing lice (combined in one group) in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012

Variables	Parameter coefficients	SS	Degree of Freedom	MS	F	p
Intercept	**-0.550**	**24.820**	**1**	**24.820**	**3303.98**	**0.000**
Sex	-0.008	0.010	1	0.010	1.30	0.255
Age	-0.004	0.001	1	0.001	0.09	0.767
Year		**0.328**	**5**	**0.066**	**8.74**	**0.000**
2007	0.020					
2008	-0.046					
2009	-0.020					
2010	-0.010					
2011	0.031					
Age*Year		**0.110**	**5**	**0.022**	**2.92**	**0.013**
2007	-0.039					
2008	0.013					
2009	0.022					
2010	-0.006					
2011	0.011					
Body size	**0.008**	**0.052**	**1**	**0.052**	**6.91**	**0.009**
Total chewing lice presence	**-0.023**	**0.114**	**1**	**0.114**	**15.15**	**0.000**
Error		3.801	506	0.008		

Table 17: Results of the general linear model exploring the effects of sex, age, year, the interaction between age and year, body size and ectoparasite burden in preen gland mass (log10-transformed) of rock ptarmigans collected in North-East Iceland in October 2007-2012

Variables	Parameter coefficients	SS	Degree of Freedom	MS	F	p
Intercept	**-0.527**	**22.094**	**1**	**22.094**	**2901.92**	**0.000**
Sex	-0.007	0.010	1	0.010	1.34	0.247
Age	0.001	0.000	1	0.000	0.03	0.867
Year		**0.328**	**5**	**0.066**	**8.61**	**0.000**
2007	0.020					
2008	-0.044					
2009	-0.020					
2010	-0.011					
2011	0.034					
Age*Year		**0.123**	**5**	**0.025**	**3.25**	**0.007**
2007	-0.037					
2008	0.012					
2009	0.022					
2010	-0.008					
2011	0.011					
Body size	**0.008**	**0.050**	**1**	**0.050**	**6.59**	**0.011**
Ectoparasite burden	**-0.000039**	**0.063**	**1**	**0.063**	**8.21**	**0.004**
Error		3.852	506	0.008		

Table 18: Significant associations between preen gland mass (log10-transformed) and parasite richness, parasite load, presence/absence of ectoparasite species and ectoparasite burden in rock ptarmigans collected in North-East Iceland in October 2007-2012.Results are based on the general linear models shown in Tables 9-17.

Independent Variables	**Preen Gland (Response Variable)**		
	F	**p**	**Relationship**
Ectoparasite richness	4.235	0.040	(-)
Ectoparasite load			
Feather mites			
Metamicrolichus islandicus	5.30	0.022	**(+)**
Ectoparasite presence/absence			
Feather mites			
Myialges borealis	3.98	0.047	**(+)**
Strelkoviacarus holoaspis	4.34	0.038	**(+)**
Chewing lice			
Gonoides lagopi	4.075	0.044	**(-)**
Lagopoecus affinis	10.125	0.002	**(-)**
Amyrsidea lagopi	3.93	0.048	**(-)**
Total chewing lice	15.151	0.000	**(-)**
Ectoparasite burden	8.214	0.004	**(-)**

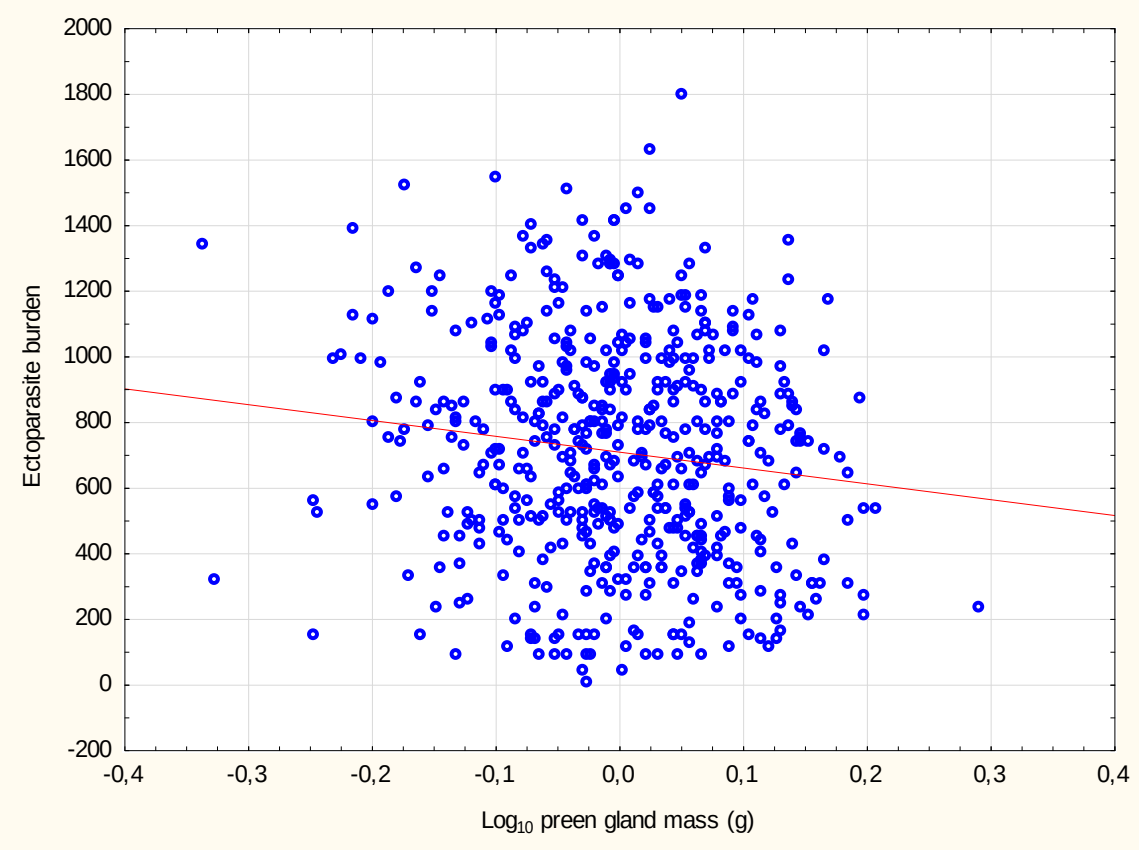

Figure 9: Ectoparasite burden in relation to preen gland mass (log_{10}-transformed)of rock ptarmigans collected in North-East Iceland in October 2007-2012(r^2= 0.017; p= 0.0031. Regression equation: Ectoparasite burden = 709.655 – 482.7787 Log_{10} preen gland mass (g))*

2.3.6 Preen gland mass in relation to ptarmigan density

In 2007 the population was at low levels, and numbers increased until a peak was reached in 2010. In 2011, the ptamigan population showed an abrupt decrease and continued decreasing in 2012. In June 2013, numbers increased by at least 20% in relation to 2012 (Fig. 1). Preen gland mass values decreased from 2008 to 2009 and increased until a peak was reached in 2011. Preen gland mass shows a similar pattern to mean density numbers with a two years time lag (Fig. 10). Mean ectoparasite burden numbers are highly variable among years, and peaked in 2009 and 2011. Based on Fig. 10 there does not seem to be an obvious relationship between ectoparasite burden and the the other two variables (spring density and preen gland mass). This suggests that ectoparasite burden is not the factor driving the main changes that are observed in preen gland mass.

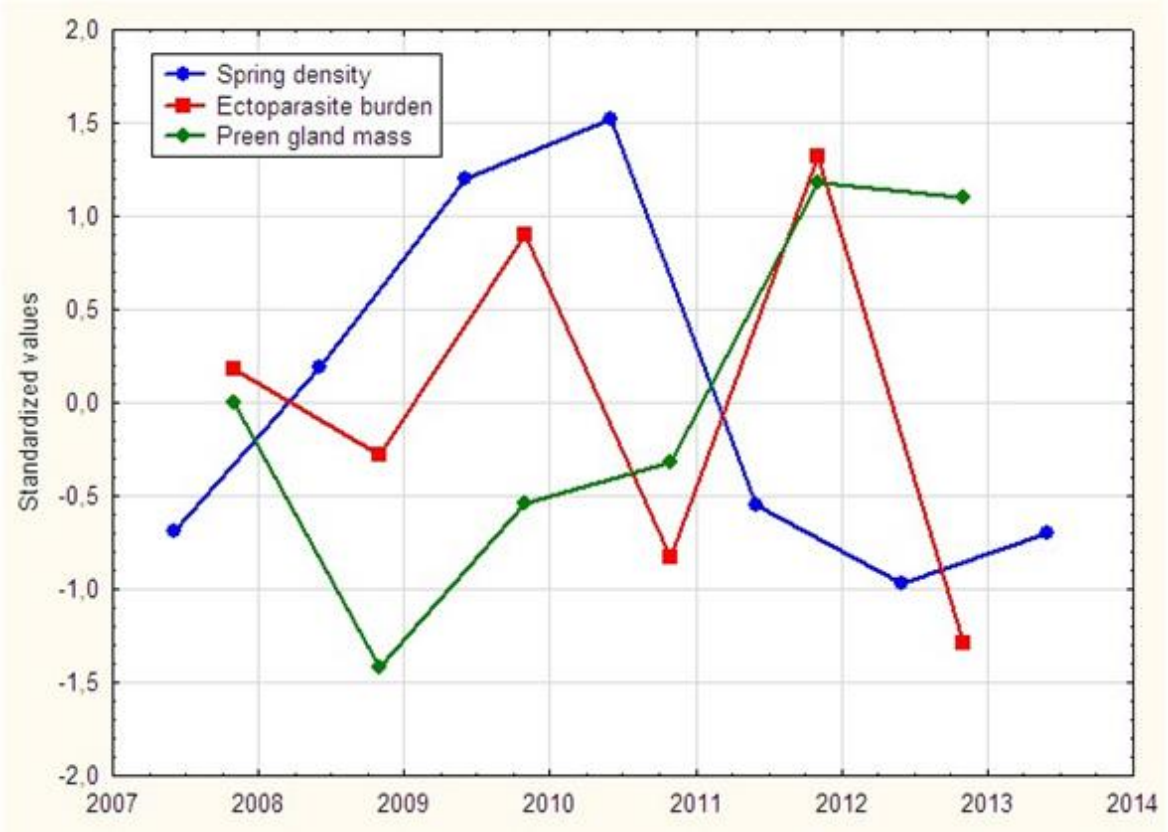

Figure 10: Mean density of territorial rock ptarmigans, ectoparasite burden and preen gland mass (log10-trasformed) of rock ptarmigans collected in North-East Iceland in 2007-2012. Values are standarized to zero mean and unit variance. Densities are measured in May and ptarmigans for the Ptarmigan health project (ectoparasite burden and preen gland mass values) are collected in October.

2.4 Discussion

The main findings of this research were that neither sex nor age of the ptarmigan showed a significant relation with gland size when controlling for body size. The variables found to have a significant effect on preen gland mass were year, body size and the interaction between age and year. Certain measures of parasite infestations (e.g. ectoparasite richness and ectoparasite burden), as well as presence of chewing lice (individual species and chewing lice as a group), had a negative and significant effect on preen gland size. There was a positive relationship between preen gland mass and the load of one species of feather mites (e.g. *Metamicrolichus islandicus*), and the presence of two species of feather mites (e.g. *Myialges borealis* and *Strelkoviacarus holoaspis*).

As previously stated, the main assumption of this research was that preen gland mass represents preen gland activity and oil production. Several authors have supported this assumption. Preen gland tissue is mostly formed by secretory capsules that synthesize the lipoid compounds of the preen oil and the propagation of these secretory capsules cause increase of preen gland size (Sandilands et al., 2004; Martín-Vivaldi et al., 2009). Furthermore, Özcan et al. (2004) performed a study in rock partridges (*Alectoris graeca*) in which results indicate a positive correlation between the size of the gland and the diameter of its main artery. In other words, when oxygen demand of the gland increases (due to increased preen gland activity/preen oil production), resources are allocated into growing a bigger artery to meet this demand. In addition, the mass of the preen gland has been shown to increase with body mass (Møller et al., 2010). In rhinoceros auklets (*Cerorhinca monocerata*), preen gland mass has been shown to be positively correlated with preen oil mass (Oka & Okuyama, 2000). The present project´s results show a negative correlation between preen oil and gland mass (after oil extraction) and therefore does not support that bigger glands produce more oil. This could be related to the oil extraction method; it is a possibility that part of the inner tissue of the gland was expelled with the oil when the gland was squeezed and more so in small than in big glands.

Preen gland mass

Møller et al. (2010) conducted a study where preen gland mass and body mass of 212 bird species were included. In that study, they report the mean mass of the ptarmigan preen gland to be 0.384 g and a relative gland mass of 0.09 % (in relation to body mass). The largest relative preen gland mass was 0.61 % and belonged to the little grebe (*Tachybaptus ruficollis*) and the smallest relative gland mass was 0.01% and belonged to the spoonbill (*Platalea leucorodia*) and the little auk (*Alle alle*). Ptarmigans had a small relative preen gland mass compared to the other species included in this study.

Ptarmigans show sexual dimorphism, males are bigger than females and have a larger body size (Nielsen et al., 2013). Martín-Vivaldi et al. (2009) conducted a study where the factors affecting preen gland morphology in hoopoes were explored. Males had bigger glands than females during the pre-breeding period, although the amount of secreted preen oil was not significantly different between sexes. In the present study, it was found that preen gland mass was significantly higher in males than females and positively correlated with body size, but this difference disappears when controlling for body size.

Alternatively, in a study conducted by Moreno-Rueda (2010) in house sparrows, the relationship between preen gland size and body size was analyzed, as well as the

abundance of feather holes, among others. During the breeding period, reproducing females had up to 8 times larger glands than males and non-reproducing females. It is possible that these results relate to the antibacterial function that has been attributed to the dark secretion produced by this species (Cramp, 1998; Burger et al., 2004). Results by Moreno-Rueda (2010) indicate that there was a sexual dimorphism for preen gland size only in one of the two years of the study, where females were found to have larger preen glands than males. In addition, he suggests that preen gland size was positively correlated with body mass (body condition) in both sex groups in one year of the study. Preen gland size was found to be independent of body size (tarsus length) in both years of the study.

Preen gland and ectoparasites

One of the functions that have been attributed to the preen oil is defence against ectoparasites. Larger individuals have a larger body size and therefore hold a larger surface for parasite establishment (Galván et al., 2008). One would expect *a priori* that ptarmigan males should have heavier loads of parasites than females. Sex and body size were included in the general linear models in order to correct for these parameters. Among the nine ectoparasites included in this research, there were five feather mites (e.g. two down mites, two skin mites and one quill mite), three chewing lice and a fly. Feather mites are a large group of permanent inhabitants of most birds,and have adapted to live in different regions of the bird´s body (Dabert & Mironov, 1999; Proctor, 2003). Various authors have reported a positive correlation between feather mite abundance and preen gland size (Galván & Sanz, 2006; Galván et al., 2008; Møller et al., 2010; Haribal et al., 2011).

Some down mites live exclusively within the plumage and down, and two species included in this project belong to this group, *Strelkoviacarus holoaspis* and *Tetraolichus lagopi*. Such down mites are considered symbionts by some researchers, although they have been suggested to cause damage when in abundance. Down mites have been proposed to benefit from the host by feeding on excess waxes, bacteria and dirt (Proctor, 2003; Galván et al., 2008), and excess wax has been reported to negatively affect the plumage´s capacity to retain heat (Sandilands et al., 2004). In the present study, only the presence of *S. holoaspis*, showed a positive and signicant relationship with preen gland size, in a accordance to a mutualistic relationship, as a larger gland means more food supply for this mite.

Other groups of feather mites are considered strictly parasitic, such as skin mites and quill mites. Skin mites live exclusively on the bird´s skin and feed on body fluids. Two species included in this project belong to this group; *Myialges borealis* and *Metamicrolichus islandicus*. Female *M. borealis* lay eggs on louse flies and chewing lice, thus spreading between hosts (Whiteman et al., 2006). *M. borealis* presence was found to be positively correlated with preen gland mass. *M. islandicus* was recently described by Mironov et al. (2010) and is considered likely to cause mange in ptarmigans (Skírnisson et al., 2012). Mange is a disease that causes skin irritation, itching and discomfort, and can lead to significant mortality in birds (Gilardi et al., 2001). *M. islandicus* was the only feather mite whose numbers were positively correlated with preen gland mass. That is, birds with larger glands had heavier loads of *M. islandicus*. The results of the present research for *M. islandicus* corroborate the findings of other studies where feather mite abundance was positively correlated with preen gland size (Galván & Sanz, 2006; Galván et al., 2008; Møller et al., 2010; Haribal et al., 2011). Nonetheless, *M. islandicus* is considered strictly parasitic and if the preen gland is part of the defense system that birds have to protect themselves against ectoparasites a different pattern would be expected; there should be a

negative correlation between preen gland mass and *M. islandicus* abundance. Quill mites live in the feather quill or calamus (portion of the feather inserted in the skin) and feed on body fluids by making holes in the wall of the quill (Kethley, 1971). One quill mite included in the study was *Mironovia lagopi*, a quill mite recently described by Bochkov and Skírnisson (2011).

Chewing lice (formerly Mallophaga) are a group that spend their entire life cycle on their host. It is a taxon composed by two major taxa, Amblycera (e.g. *Amyrsidea lagopi*) and Ischnocera (e.g. *Goniodes lagopi* and *Lagopoecus affinis*) (Barker et al., 2002; Johnson & Whiting, 2002; Johnson & Clayton, 2003). Chewing lice feed on feather keratin (structural protein of the feathers) and dead skin (Clayton et al., 2008). Amblycera also feed on living tissue (e.g. blood) and ambulate directly on the bird's skin, while Ischnocera do not come into contact with the living tissue (Møller & Rózsa, 2005; Clayton et al., 2008). When birds are heavily infested by Amblycera, they can present severe skin irritation (dermititis), itching, discomfort and increased preening (Clayton et al., 2008).

Chewing lice make feather holes by eating the feathers, thus deteriorating the plumage (Møller, 1991). Studies conducted on barn swallows (*Hirundo rustica*) have reported that feather holes negatively affect birds by weakening feathers (Kose & Møller, 1999), and thus affecting flight (Barbosa et al., 2002) and causing delayed arrival dates when migrating and late breeding initiation (Møller et al., 2004; Pap et al., 2005), as well as reduced host survival (Pap et al., 2005). Other effects have also been described in other species, such as a reduction of the plumage´s thermoregulatory capacity (Booth et al., 1993), and reduction of body condition (Potti & Merino, 1995). In the study on house sparrows conducted by Moreno-Rueda (2010), a negative correlation between the number of feather holes and preen gland size was found in both years of the study, suggesting that the preen oil is a part of this species defense system against chewing lice, therefore maintaining plumage condition.

The results of this research indicate a negative correlation between chewing lice presence and preen gland mass. This study confirms the association described by Martín-Vivaldi et al. (2009) and Moreno-Rueda (2010), where individuals with larger preen gland size were better protected from chewing lice. Given the fact that chewing lice have been described to have detrimental effects on the host, a bigger gland, and therefore more preen oil would act against chewing lice and would benefit birds´s fitness. By causing the listed above effects, chewing lice also cause an energetic cost to their hosts (Booth et al., 1993). Birds with larger glands are therefore more shielded against chewing lice, and should designate more resources into enhance their body condition. One hippoboscid fly, *Ornithomya chloropus* was included in the study. This fly feeds on blood and therefore is in close contact with the host (Baker, 1967) Results indicate that there was no significant relationship between preen gland size and this species.

To summarize, two species in the study are considered commensals while the rest are considered to be strictly parasitic. When taking into account total ectoparasite burden, the general infestation index, a negative correlation was found with preen gland mass. This suggests that individuals with larger glands, and therefore able to produce more preen oil, are more resistant to ectoparasite infestations. The growth and maintenance of a large preen gland is energetically expensive (Piault et al., 2008) and in low parasitic loads maintaining a big gland would mean that energy resources were detracted from other functions (principle of allocation, Cody, 1966). Another possibility is that individuals have

allocated their resources into growing bigger glands as a response to heavier ectoparasite loads. Heavy parasite infestations cause stress in hosts (Bush, 2001) and preen gland activity (oil production) is regulated by adrenal corticoids (Asnani & Ramachandran, 1993). Stress induces an increase in steroid hormones (mainly corticosterone in birds) by the adrenal gland (Árnason et al., 1986) and should trigger preen gland activity and preen oil production in order to fight parasite infestations.

Inter-annual variation in preen gland mass

Interestingly, the preen gland mass was largely influenced by year, to a much greater extent than by body size. Year is holistic factor, since it summarizes and includes several other factors, including weather conditions, density, food availability, predation, parasite infestations, as well as bacteria and fungi loads. Results of the present study indicate that preen gland mass tracked population size with at least a two year time lag, suggesting that preen gland activity is responding to some stimulus related to population change. If preen gland variation is a part of the ptarmigan characteristic population cycle one would expect the lag to be approximately three years.

Various other functions have been attributed to the preen oil, including antibacterial functions, fighting pathogens and maintenance of feather condition and a role in sexual selection (Jacob & Ziswiler, 1982; Urich, 1994; Montalti & Salibián, 2000). Increased weight and activity during the breeding season has been observed for some birds (Asnani & Ramachandran, 1993) and it is thought to reflect the role of the gland in fighting bacteria threatening the clutch. The ptarmigan preen gland has not been measured during summer; therefore conclusions of that kind cannot be drawn from the present research.

In a study by Burtt and Ichida (1999) on feather degrading bacteria (*Bacillus* sp.) in 32 bird species, strong seasonal variations in bacteria loads were described. Bacilli degrade feathers in a higher extent during summer, since warm and humid conditions are favorable for this class. In Iceland ptarmigan counts are done each year in May (spring) while ptarmigans for gland measurements are hunted in October (fall). It could be that feather degrading bacteria loads are different in ptarmigans between those two times of the year.

In addition, another study in the hoopoe where the action of volatile compounds, present in the dark preen oil produced during the breeding season was tested, concluded that such compounds provided this species with strong antimicrobial action. Researchers found that all volatile compounds had a strong antimicrobial effect. Among those, four saturated fatty acids (e.g. butanoic acid, 2-methyl butanoic acid, 4-methyl pentanoic acid and propanoic acid), and six other compounds (e.g. benzaldehyde, phenol, phenyl acetaldehyde, indole, 3-phenyl and 4-chloro indole) (Martín-Vivaldi et al., 2010). In a study conducted by Runólfsdóttir (2012) on ptarmigans in Iceland, preen oil was found to have more saturated fatty acid compounds than the proportion of unsaturated fatty acids, especially the myristic acid. Marked inter annual variations were also detected; for example, in 2007 the proportion of palmitic acid was the highest, and preen gland mass was also considerably higher than in 2008 and 2009. In 2008, the proportion of myristic acid was the highest and preen gland mass was the lowest among all the years studied (Runólfsdóttir, 2012) Although no correlation was found by Runólfsdóttir (2012) between ectoparasite burden and saturated fatty acid proportion, a relationship between saturated fatty acid and bacterial loads could be present and therefore saturated fatty acids in ptarmigan preen oil could play a role in fighting bacteria.

It has been suggested that there is a gap in the knowledge regarding the ectoparasite fauna in ptarmigans in other parts of the distribution range (e.g. no feather mites have been reported for ptarmigans outside of Iceland) (Skírnisson et al., 2012). Additionally, to my knowledge, there are no previous studies on the preen gland of grouse. The present project gives a further understanting of the preen gland, its functions and how it is related to ectoparasite infestations in the ptarmigan. As a component of the Ptarmigan health project, it might be of aid in increasing the understanding of ptarmigan population changes.

In conclusion, after analyzing the effect of different factors on the variability in preen gland mass, it is possible to say that the preen gland/preen oil constitutes a defense mechanism against overall ectoparasite burden and chewing lice presence in the ptarmigan in Iceland. There is a significant interannual variation in preen gland mass and resources are being allocated into growing and maintaining a bigger gland in some years. The pattern suggests a time lag of at least two years between population density and preen gland mass. Annual changes in mean ectoparasite burden suggest that ectoparasites are not driving these major changes in preen gland mass.

References

Árnason, S. S., Rice, G. E., Chadwick, A., & Skadhauge, E. (1986). Plasma levels of arginine vasotocin, prolactin, aldosterone and corticosterone during prolonged dehydration in the domestic flowl: effect of dietary NaCl. *Journal of Comparative Physiology B, 156*(3), 383-397.

Asnani, M. V., & Ramachandran, A. V. (1993). Roles of Adrenal and Gonadal Steroids and Season in Uropygial Gland Function in Male Pigeons, Columba livia. *General and Comparative Endocrinology, 92*(2), 213-224.

Baggott, G. K., & Graeme-Cook, K. (2002). Microbiology of natural incubation. In D. C. Deeming (Ed.), *Avian Incubation: Behaviour, Environment, and Evolution* (pp. 179-191): Oxford University Press, Incorporated.

Baker, J. R. (1967). A review of the role played by the Hippoboscidae (Diptera) as vectors of endoparasites. *The Journal of Parasitology*, 412-418.

Bandyopadhyay, A., & Bhattacharyya, S. (1996). Influence of fowl uropygial gland and its secretory lipid components on growth of skin surface bacteria of fowl. *Indian journal of experimental biology, 34*(1), 48-52.

Barbosa, A., Merino, S., Lope, F., Møller, A., & Moore, F. (2002). Effects of feather lice on flight behavior of male barn swallows (*Hirundo rustica*). *The Auk, 119*(1), 213-216.

Barker, S. C., Whiting, M., Johnson, K. P., & Murrell, A. (2002). Phylogeny of the lice (Insecta, Phthiraptera) inferred from small subunit rRNA. *Zoologica Scripta, 32*(5), 407-414.

Baumel, J. J. (1979). *Nomina anatomica avium*. London: Academic Press.

Blanco, G., Tella, J. L., Potti, J., & Baz, A. (2001). Feather mites on birds: costs of parasitism or conditional outcomes? *Journal of Avian Biology, 32*(3), 271-274.

Bochkov, A. V., & Skírnisson, K. (2011). Description of the life stages of quill mite *Mironovia lagopus* sp. nov.(Acari: Syringophilidae) parasitizing the rock ptarmigan *Lagopus muta* (Phasianidae) from Iceland. *Parasitology Research, 108*(3), 715-722.

Bohnet, S., Rogers, L., Sasaki, G., & Kolattukudy, P. (1991). Estradiol induces proliferation of peroxisome-like microbodies and the production of 3-hydroxy fatty acid diesters, the female pheromones, in the uropygial glands of male and female mallards. *Journal of Biological Chemistry, 266*(15), 9795-9804.

Booth, D. T., Clayton, D. H., & Block, B. A. (1993). Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 253*(1337), 125-129.

Burger, B. V., Reiter, B., Borzyk, O., & du Plessis, M. A. (2004). Avian Exocrine Secretions. I. Chemical Characterization of the Volatile Fraction of the Uropygial Secretion of the Green Woodhoopoe, *Phoeniculus purpureus*. *Journal of Chemical Ecology, 30*(8), 1603-1611.

Burtt, E. H., & Ichida, J. M. (1999). Occurrence of feather-degrading bacilli in the plumage of birds. *The Auk*, 364-372.

Bush, A. O. (2001). Parasitism: The Diversity and Ecology of Animal Parasites (pp. 24-27): Cambridge University Press.

Clayton, D. H., Adams, R. J., & Bush, S. E. (2008). Phthiraptera, the Chewing Lice. In C. T. Atkinson, N. J. Thomas & D. B. Hunter (Eds.), *Parasitic Diseases of Wild Birds* (pp. 514-526). Iowa: Wiley.

Clayton, D. H., Koop, J. A., Harbison, C. W., Moyer, B. R., & Bush, S. E. (2010). How birds combat ectoparasites. *Open Ornithol J, 3*, 41-71.

Cody, M. L. (1966). A general theory of clutch size. *Evolution*, 174-184.

Cook, M. I., Beissinger, S. R., Toranzos, G. A., Rodríguez, R. A., & Arendt, W. J. (2003). Trans–shell infection by pathogenic micro–organisms reduces the shelf life of non–incubated bird's eggs: a constraint on the onset of incubation? *Proceedings of the Royal Society of London. Series B: Biological Sciences, 270*(1530), 2233-2240.

Cook, M. I., Beissinger, S. R., Toranzos, G. A., Rodríguez, R. A., & Arendt, W. J. (2005). Microbial infection affects egg viability and incubation behavior in a tropical passerine. *Behavioral Ecology, 16*(1), 30-36.

Cramp, S. (1998). *The complete birds of the western Palearctic*: OptiMedia.

Czirják, G. Á., Pap, P. L., Vágási, C., Giraudeau, M., Mureşan, C., Mirleau, P., & Heeb, P. (2013). Preen gland removal increases plumage bacterial load but not that of feather-degrading bacteria. *Naturwissenschaften, 100*(2), 145-151.

Charnetski, W. A., & Stevens, W. E. (1974). Organochlorine insecticide residues in preen glands of ducks: Possibility of residue excretion. *Bulletin of Environmental Contamination and Toxicology, 12*(6), 672-676.

Chen, Y., Kou, M., Pan, F., & Lu, L. (2003). Effects of uropygial gland removal on the growth performance and plasma characteristics in female white roman goslings from 3 to 10 weeks of age. *Tunghai Journal, 44*, 7-13.

Dabert, J., & Mironov, S. (1999). Origin and evolution of feather mites (Astigmata). In J. Bruin, L. P. S. Geest & M. W. Sabelis (Eds.), *Ecology and Evolution of the Acari* (Vol. 55, pp. 89-103): Springer Netherlands.

Dauwe, T., Bervoets, L., Blust, R., & Eens, M. (2002). Tissue Levels of Lead in Experimentally Exposed Zebra Finches (*Taeniopygia guttata*) with Particular Attention on the Use of Feathers as Biomonitors. *Archives of Environmental Contamination and Toxicology, 42*(1), 88-92.

Delhey, K., Peters, A., & Kempenaers, B. (2007). Cosmetic coloration in birds: occurrence, function, and evolution. *The American Naturalist, 169*(S1), S145-S158.

Elder, W. H. (1954). The oil gland of birds. *The Wilson Bulletin, 66*(1), 6-31.

Galván, I., Barba, E., Piculo, R., Cantó, J., Cortés, V., Monrós, J., Atiénzar, F., & Proctor, H. (2008). Feather mites and birds: an interaction mediated by uropygial gland size? *Journal of Evolutionary Biology, 21*(1), 133-144.

Galván, I., & Sanz, J. J. (2006). Feather mite abundance increases with uropygial gland size and plumage yellowness in Great Tits *Parus major*. *Ibis, 148*(4), 687-697.

Gaud, J., & Atyeo, W. T. (1996). *Feather mites of the world (Acarina, Astigmata): the supraspecific taxa.* Proceedings of the Annales-Musee Royal de l'Afrique Centrale. Sciences Zoologiques 277:

Getty, R. (1975). The anatomy of the domestic animals (5 ed., Vol. 2, pp. 1811-1997): Saunders.

Gilardi, K., Gilardi, J. D., Frank, A., Goff, M. L., & Boyce, W. M. (2001). Epidermoptid mange in Laysan Albatross fledglings in Hawaii. *Journal of wildlife diseases, 37*(1), 185-188.

Giraudeau, M., Duval, C., Guillon, N., Bretagnolle, V., Gutierrez, C., & Heeb, P. (2010). Effects of access to preen gland secretions on mallard plumage. *Naturwissenschaften, 97*(6), 577-581.

Goldstein, D. L. (1988). Estimates of daily energy expenditure in birds: the time-energy budget as an integrator of laboratory and field studies. *American Zoologist, 28*(3), 829-844.

Gutiérrez, A. M., Montalti, D., Reboredo, G. R., Salibián, A., & Catalá, A. (1998). Lindane Distribution and Fatty Acid Profiles of Uropygial Gland and Liver of *Columba livia* after Pesticide Treatment. *Pesticide biochemistry and physiology, 59*(3), 137-141.

Haahti, E. O., & Fales, H. M. (1967). The uropygiols: identification of the unsaponifiable constituent of a diester wax from chicken preen glands. *Journal of lipid research, 8*(2), 131-137.

Haribal, M., Dhondt, A., & Rodriguez, E. (2009). Diversity in chemical compositions of preen gland secretions of tropical birds. *Biochemical Systematics and Ecology, 37*(2), 80-90.

Haribal, M., Dhondt, A. A., Rosane, D., & Rodríguez, E. (2005). Chemistry of preen gland secretions of passerines: different pathways to same goal? why? *Chemoecology, 15*(4), 251-260.

Haribal, M., Proctor, H., Dhondt, A. A., & Rodríguez, E. (2011). Biology of House Finch feather mites, *Proctophyllodes pinnatus* (Acari: Proctophyllodidae), parallels variation in preen gland secretions. *International Journal of Acarology, 37*(1), 75-90.

Jacob, J. (1976). Bird waxes. In P. E. Kolattukudy (Ed.), *Chemistry and biochemistry of natural waxes* (pp. 93-146): Elsevier Scientific Pub. Co.

Jacob, J., Eigener, U., & Hoppe, U. (1997). The structure of preen gland waxes from pelecaniform birds containing 3, 7-dimethyloctan-1-ol: an active ingredient against dermatophytes. *Zeitschrift für Naturforschung. C. A journal of biosciences, 52*(1-2), 114-123.

Jacob, J., & Ziswiler, V. (1982). The uropygial gland. In J. Jacob & V. Ziswiler (Eds.), *Avian biology* (Vol. 6, pp. 199-324). New York: Academic Press.

Johnson, K. P., & Clayton, D. H. (2003). The biology, ecology, and evolution of chewing lice. In R. D. Price, R. A. Hellenthal, R. L. Palma, K. P. Johnson & D. H. Clayton (Eds.), *The chewing lice: world checklist and biological overview* (pp. 449-476): Illinois Natural History Survey Special Publication 24.

Johnson, K. P., & Whiting, M. F. (2002). Multiple Genes and the Monophyly of Ischnocera (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution, 22*(1), 101-110.

Johnston, D. W. (1976). Organochlorine pesticide residues in uropygial glands and adipose tissue of wild birds. *Bulletin of Environmental Contamination and Toxicology, 16*(2), 149-155.

Johnston, D. W. (1978). Organochlorine pesticide residues in Florida birds of prey, 1969-76. *Pesticides monitoring journal, 12*(1), 8.

Johnston, D. W. (1988). *A Morphological Atlas of the Avian Uropygial Gland* (Vol. 54): British Museum (Natural History).

Kethley, J. (1971). Population regulation in quill mites (Acarina: Syringophilidae). *Ecology*, 1113-1118.

King, A., & McLelland, J. (1975). Uropygial gland (preen gland or oil gland) and other cutaneous glands. *Outlines of Avian Anatomy, Balliere Tindall, London*, 6-7.

Kolattukudy, P., Bohnet, S., & Rogers, L. (1987). Diesters of 3-hydroxy fatty acids produced by the uropygial glands of female mallards uniquely during the mating season. *Journal of lipid research, 28*(5), 582-588.

Kolattukudy, P. E., & Rogers, L. (1978). Biosynthesis of fatty alcohols, alkane-1,2-diols and wax esters in particulate preparations from the uropygial glands of white-crowned sparrows (*Zonotrichia leucophrys*). *Archives of biochemistry and biophysics, 191*(1), 244-258.

Kose, M., & Møller, A. P. (1999). Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow (*Hirundo rustica*). *Behavioral Ecology and Sociobiology, 45*(6), 430-436.

Lucas, A. M., & Stettenheim, P. R. (1972). Avian Anatomy Integument (Vol. 362, pp. 613-626): Agricultural Research Branch.

Martín-Platero, A. M., Valdivia, E., Ruíz-Rodríguez, M., Soler, J. J., Martín-Vivaldi, M., Maqueda, M., & Martínez-Bueno, M. (2006). Characterization of antimicrobial substances produced by *Enterococcus faecalis* MRR 10-3, isolated from the uropygial gland of the hoopoe (*Upupa epops*). *Applied and environmental microbiology, 72*(6), 4245-4249.

Martín-Vivaldi, M., Peña, A., Peralta-Sánchez, J. M., Sánchez, L., Ananou, S., Ruiz-Rodríguez, M., & Soler, J. J. (2010). Antimicrobial chemicals in hoopoe preen secretions are produced by symbiotic bacteria. *Proceedings of the Royal Society B: Biological Sciences, 277*(1678), 123-130.

Martín-Vivaldi, M., Ruiz-Rodríguez, M., Soler, J. J., Peralta-Sánchez, J. M., Méndez, M., Valdivia, E., Martín-Platero, A. M., & Martínez-Bueno, M. (2009). Seasonal, sexual and developmental differences in hoopoe *Upupa epops* preen gland morphology and secretions: evidence for a role of bacteria. *Journal of Avian Biology, 40*(2), 191-205.

Menon, G., Aggarwal, S., & Lucas, A. (1981). Evidence for the holocrine nature of lipoid secretion by avian epidermal cells: a histochemical and fine structural study of rictus and the uropygial gland. *Journal of Morphology, 167*(2), 185-199.

Mironov, S. V., Skírnisson, K., Þórarinsdóttir, S. T., & Nielsen, Ó. K. (2010). Feather mites (Astigmata: Psoroptidia) parasitising the rock ptarmigan *Lagopus muta* (Montin) (Aves: Galliformes) in Iceland. *Systematic Parasitology, 75*(3), 187-206.

Møller, A. P. (1991). Parasites, sexual ornaments and mate choice in the barn swallow *Hirundo rustica*. In J. E. Loye & M. Zuk (Eds.), *Bird-parasite Interactions: Ecology, Evolution, and Behaviour*: Oxford University Press.

Møller, A. P., de Lope, F., & Saino, N. (2004). Parasitism, immunity, and arrival date in a migratory bird, the barn swallow. *Ecology, 85*(1), 206-219.

Møller, A. P., Erritzøe, J., & Rózsa, L. (2010). Ectoparasites, uropygial glands and hatching success in birds. *Oecologia, 163*(2), 303-311.

Møller, A. P., & Rózsa, L. (2005). Parasite biodiversity and host defenses: chewing lice and immune response of their avian hosts. *Oecologia, 142*(2), 169-176.

Montalti, D., Gutiérrez, A. M., Reboredo, G., & Salibian, A. (2005). The chemical composition of the uropygial gland secretion of rock dove *Columba livia*. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology, 140*(3), 275-279.

Montalti, D., & Salibián, A. (2000). Uropygial gland size and avian habitat. *Ornitología Neotropical, 11*, 297-306.

Montgomerie, R. (2006). Analyzing colors. In G. E. Hill & K. J. McGraw (Eds.), *Bird Coloration: Function and evolution* (Vol. 1, pp. 80-147). Massachusetts: Harvard University Press.

Montgomerie, R., & Holder, K. (2008). Rock ptarmigan (*Lagopus muta*). In A. Poole (Ed.), The Birds of North America online. Ithaca, New York, USA: Cornell

Laboratory of Ornithology. Retrieved from the Birds of North America Online database: http://bna.birds.cornell.edu/bna/species/051.

Moreno-Rueda, G. (2010). Uropygial gland size correlates with feather holes, body condition and wingbar size in the house sparrow *Passer domesticus*. *Journal of Avian Biology, 41*(3), 229-236.

Moyer, B. R., Rock, A. N., Clayton, D. H., & Prum, R. (2003). Experimental test of the importance of preen oil in rock doves (*Columba livia*). *The Auk, 120*(2), 490-496.

Nielsen, Ó. K., de Pelsmaeker, N., & Guðmundsson, G. A. (2013). *Rock ptarmigan (Lagopus muta) health studies in Northeast Iceland 2012: morphology and body reserves*. University of Iceland, North East Iceland Nature Center, East Iceland Nature Center. pp. 40

Oka, N., & Okuyama, M. (2000). Nutritional Status of Dead Oiled Rhinoceros Auklets (*Cerorhinca monocerata*) in the Southern Japan Sea. *Marine Pollution Bulletin, 40*(4), 340-347.

Özcan, S., Aslan, K., Aksoy, G., & Kürtül, İ. (2004). Arterial Vascularization of the Uropygial Glands (Gl. Uropygialis) in the Rock Partridge (*Alectoris graeca*) Living in Turkey. *Anatomia, Histologia, Embryologia, 33*(3), 155-157.

Pap, P. L., Tökölyi, J., & Szep, T. (2005). Frequency and consequences of feather holes in Barn Swallows *Hirundo rustica*. *Ibis, 147*(1), 169-175.

Piault, R., Gasparini, J., Bize, P., Paulet, M., McGraw, K. J., & Roulin, A. (2008). Experimental support for the makeup hypothesis in nestling tawny owls (*Strix aluco*). *Behavioral Ecology, 19*(4), 703-709.

Pilastro, A., Congiu, L., Tallandini, L., & Turchetto, M. (1993). The use of bird feathers for the monitoring of cadmium pollution. *Archives of Environmental Contamination and Toxicology, 24*(3), 355-358.

Potti, J., & Merino, S. (1995). Louse loads of pied flycatchers: effects of host's sex, age, condition and relatedness. *Journal of Avian Biology*, 203-208.

Proctor, H. C. (2003). Feather mites: (Acari: Astigmata): Ecology, Behavior, and Evolution. *Annual Review of Entomology, 48*(1), 185-209.

Redpath, S. (1988). Vigilance levels in preening dunlin *Calidris alpina*. *Ibis, 130*(6), 555-557.

Reneerkens, J., Piersma, T., & Damste, J. S. S. (2007). Expression of annual cycles in preen wax composition in red knots: constraints on the changing phenotype. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology, 307*(3), 127-139.

Reneerkens, J., Piersma, T., & Damsté, J. S. S. (2002). Sandpipers (Scolopacidae) switch from monoester to diester preen waxes during courtship and incubation, but why? *Proceedings of the Royal Society of London. Series B: Biological Sciences, 269*(1505), 2135-2139.

Reneerkens, J., Piersma, T., & Damsté, J. S. S. (2005). Switch to diester preen waxes may reduce avian nest predation by mammalian predators using olfactory cues. *Journal of Experimental Biology, 208*(22), 4199-4202.

Reneerkens, J., Versteegh, M. A., Schneider, A. M., Piersma, T., & Burtt Jr, E. H. (2008). Seasonally changing preen-wax composition: red knots'(*Calidris canutus*) flexible defense against feather-degrading bacteria. *The Auk, 125*(2), 285-290.

Rothschild, M., & Clay, T. (1952). *Fleas, flukes and cuckoos. A study of bird parasites*. London: Collins.

Ruiz-Rodríguez, M., Valdivia, E., Soler, J. J., Martín-Vivaldi, M., Martín-Platero, A., & Martínez-Bueno, M. (2009). Symbiotic bacteria living in the hoopoe's uropygial

gland prevent feather degradation. *Journal of Experimental Biology, 212*(22), 3621-3626.
Runólfsdóttir, M. S. (2012). *Fitusýrusamsetning fituefna í stélrótarkirtli íslensku rjúpunnar (Lagopus muta). Baccalaureus Scientiarum*, Science Department, University of Iceland, pp. 34.
Sandilands, V., Powell, K., Keeling, L., & Savory, C. (2004). Preen gland function in layer fowls: factors affecting preen oil fatty acid composition. *British poultry science, 45*(1), 109-115.
Shawkey, M. D., Pillai, S. R., & Hill, G. E. (2003). Chemical warfare? effects of uropygial oil on feather degrading bacteria. *Journal of Avian Biology, 34*(4), 345-349.
Simpson, J. A., Weiner, E. S. C., & Oxford University Press. (2002). *The Oxford English Dictionary*: Clarendon Press.
Skírnisson, K., Þórarinsdóttir, S. T., & Nielsen, Ó. K. (2012). The Parasite Fauna of Rock Ptarmigan (*Lagopus muta*) in Iceland: Prevalence, Intensity, and Distribution Within the Host Population. *Comparative Parasitology, 79*(1), 44-55.
Soini, H. A., Schrock, S. E., Bruce, K. E., Wiesler, D., Ketterson, E. D., & Novotny, M. V. (2007). Seasonal variation in volatile compound profiles of preen gland secretions of the dark-eyed junco (*Junco hyemalis*). *Journal of Chemical Ecology, 33*(1), 183-198.
Statsoft. (2012). Statistica 12. Retrieved on 15.08.13, from http://www.statsoft.com/Products/STATISTICA-Features/Version-12/
Stenkewitz, U. (2013, 16.10.2013). [Regarding *Tetraolichus lagopi* scores].
Stevens, L. (2000). Lipids and their metabolism. *Avian biochemistry and molecular biology. Cambridge University Press, London*, 54-60.
Sweeney, R. J., Lovette, I. J., Harvey, E. L., & Zink, R. M. (2004). Evolutionary variation in feather waxes of passerine birds. *The Auk, 121*(2), 435-445.
Theodor, O., & Oldroyd, H. (1964). Hippoboscidae. *Die Fliegen der paläarktischen Region 65*, 1-70.
Timmermann, V. G. (1950). Beiträge zur Kentniss der Ektoparsitenfauna Isländischer Säugetiere und Vögel, 3. *Miscellaneous papers on Icelandic Zoology, 1*, 1-8.
Urich, K. (1994). *Comparative Animal Biochemistry*: U.S. Government Printing Office.
Weeden, R. B., & Watson, A. (1967). Determining the age of Rock Ptarmigan in Alaska and Scotland. *The Journal of Wildlife Management*, 825-826.
Whiteman, N. K., Sánchez, P., Merkel, J., Klompen, H., & Parker, P. G. (2006). Cryptic host specificity of an avian skin mite (Epidermoptidae) vectored by louseflies (Hippoboscidae) associated with two endemic Galapagos bird species. *Journal of Parasitology, 92*(6), 1218-1228.