Grit, Gizzard, Gut and Grouse
- a study of the Icelandic rock ptarmigan
(*Lagopus muta*)

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Abstract

Rock ptarmigan (*Lagopus muta*) feed on digestively resistant diet which is grinded in the gizzard with help of grit the birds ingest. The composition of the grit in gizzard has previously been observed to change with quality of the food along with the size of the digestive organs, gizzard and gut. The aim of this study was to: 1) investigate the grit characteristic (number, weight and morphology), gizzard mass and gut length of the rock ptarmigan in Iceland; and 2) test if there was inter-annual variation of the grit characteristic, gizzard mass and gut length; and 3) test if there were differences between sex and age classes of the birds. Further, the inter-annual variations, if present, were compared to the changes in the ptarmigan population density. The ptarmigans for the study were collected during the first week of October 2006-2013. The number of grit and their weight was analyzed for each bird along with the morphology parameters: size, ruggedness and roundness. Grit was found in 92% of the birds and significant difference between the sex and age of the bird was detected for some of the grit variables and for the gizzard mass and gut length. The adult males were observed to have the shortest gut and the juveniles the longest. It is likely that the adult males are more dominant territorially and have better access to food of more nutrient quality than females and juveniles. Significant inter-annual variation was detected for all the grit variables. There was also a change in gizzard mass and gut length between years. These changes in the grit variables and in the size of the gizzard mass and gut length may reflect changes in the quality of the food the ptarmigans were consuming between the years. It is possible that these changes in the food affect the population change, which was supported by the observed correlation between roundness of the grit and the population density. The population was highest one year after the grit had the highest value in roundness but high value in roundness is possibly a result of poor quality food. Poor quality food when the population peaked might have resulted in weaker birds and higher mortality, which consequently leads to decrease in the population.

Keywords: grit; gizzard; gut; rock ptarmigan; interannual variation; population change

Sammendrag

Fjellrype (*Lagopus muta*) ernærer seg på tungt fordøyelig kost som er kvernet ned i kråsen med hjelp av stein som fuglen svelger. Sammensetningen av stein i kråsen har tidligere blitt observert å forandre seg med kvaliteten av maten sammen med størrelsen av fordøyelses organer, kråsmasse og tarmlengde. Formålet med denne oppgaven var å: 1) undersøke stein karakteristikk (antall, vekt og morfologi), kråsmasse og tarmlengde på fjellrypen på Island; 2) teste om det var årlig variasjon på stein karakteristikk, kråsmasse og tarmlengde og 3) teste om det var forskjeller mellom kjønn og alder på fuglene. Videre, de mellom-årlige forandringene, hvis de finnes, ble sammenlignet med endringene i rype populasjonens tetthet. Rypene ble samlet under den første uken av oktober 2006-2013. Antall stein og deres vekt ble analysert for hver fugl sammen med den morfologiske parameter størrelsen, robusthet og rundhet. Stein ble funnet i 92% av fuglene og signifikant forskjell mellom fuglenes kjønn og alder ble påvist i noen av stein variablene og for kråsmassen og tarmlengden. De voksne hann fuglene ble observert å ha kortere tarm og de unge fuglene den lengste. Det er sannsynlig at voksne stegger er mer dominerende territorielt og har bedre tilgang til mat av høgere næringskvalitet enn hønene og ungfuglene. Signifikant årlig variasjon ble oppdaget for alle stein variablene. Det var også forandring i kråsmasse og tarmlengden mellom årene. Disse endringene i stein variablene, størrelsen på kråsen og tarmen kan tyde på at det forekom noen endringer i kvaliteten på maten som rypene ernæret seg på mellom årene. Det er mulig at disse endringene i maten påvirker populasjonsstørrelsen. Rundhetsgraden på stein ble observert til å være korrelert med populasjonstettheten. Populasjonen var høyest ett år etter at stein hadde den høyeste verdien i rundhetsgraden, men en høy verdi i rundhet er muligens et resultat av dårlig kvalitet på maten. Mat med dårlig kvalitet når populasjonen var på topp kan ha medført svakere fugler og høyere dødelighet som dermed fører til reduksjon i populasjonen.

Nøkkel ord: stein; krås; tarm; fjellrype; årlig variasjon; populasjon variasjon

1 Introduction

Grouse belonging to the genus *Lagopus* (family *Tetraonidae*) are distributed through much of the arctic, subarctic and north temperate regions in Europe, Asia and America, living in scrublands and open habitats (Forshaw & Parkes, 1991; Perrins & Middleton, 1985; Watson & Moss, 2008). They are herbivorous and particularly adapted to browse on coarse and fibrous plant parts (Moss & Hanssen, 1980; Watson & Moss, 2008). They consume mainly coarse diet in autumn and winter, a diet consisting largely of cellulose and lignin and low in digestibility, energy and nutrients (Moss, 1997; Murphy, 1996; Ricklefs, 1996). Through spring and summer the birds consume fresh growing plant products, and also insects when easily obtained. The spring and summer diet is more digestible and has a higher energy and nutrient content than the winter diet (Moss & Hanssen, 1980; Watson & Moss, 2008).

Herbivorous birds, have morphologically and physiologically adapted to variation in food availability by the development of their digestive systems (Battley & Piersma, 2005; Leopold, 1953; McLelland & King, 1984). The digestive system of the avian herbivore includes the bill, the esophagus, the crop (functions as a storage organ), the stomach (divided into two parts, the proventriculus or the glandular stomach and the gizzard or the muscle stomach), the gut consists of the duodenum, the small-intestine (digestion and nutrient absorption chamber), the caecum (bacterial fermentation chamber); the large-intestine and the cloaca (Figure 1) (Gasaway, 1976b; McLelland & King, 1984; Moss & Hanssen, 1980; Sjaastad, Hove, & Sand, 2003).

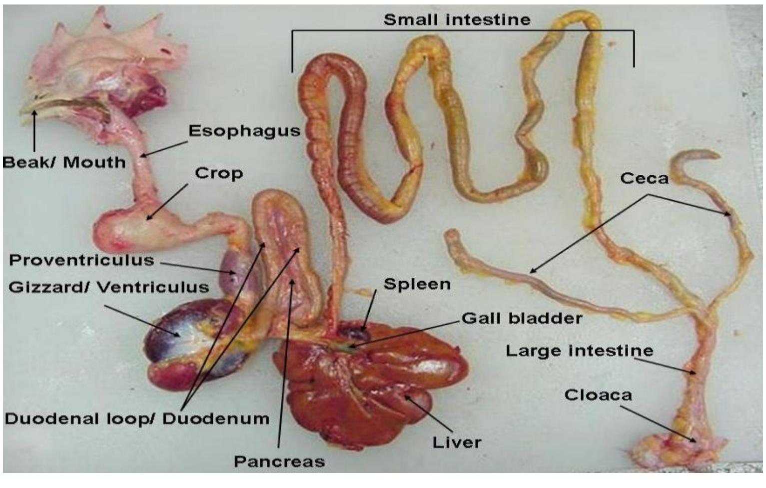

Figure 1. The avian digestive system (Jacob, 2015).

1.1 Chewing and churning

Mammalian herbivores feeding on digestively resistant plant items normally rely on teeth. They pre-process the food by reducing particle size through chewing and churning in the oral cavity with lateral grinding movement of the jaw before swallowing and digestion (Reilly, McBrayer, & White, 2001; Robbins, 1993; Sherwood, Klandorf, & Yancey, 2012; Sjaastad, et al., 2003). Unlike mammalian herbivores, avian herbivores lack any advanced physical pre-treatment abilities in their oral cavity. Therefore, they ingest the food items unprocessed into the esophagus and the stomach where the "chewing process" begins (Duke, 1986; McLelland & King, 1984; Reilly, et al., 2001; Sherwood, et al., 2012; Sjaastad, et al., 2003).

The size and shape of the stomach components varies among bird species, depending primarily on food type. Predatory birds, i.e., carnivorous and piscivorous birds, rely on chemical treatment of the food in the stomach and possess a large proventriculus and a small gizzard with a poorly developed muscle tunic (Hilton, Houston, Barton, Furness, & Ruxton, 1999; McLelland & King, 1984). Birds that feed on digestively resistant diet (i.e. herbivorous, granivorous and some insectivorous birds) rely more on mechanical treatment in the gizzard, i.e. "chewing and churning" movement of the gizzard muscle. These birds have developed a special mechanical churning mechanism "gastric mill" to grind down food particles (Enoki & Morimoto, 2000; Moore, 1998a, 1999; Svihus, 2011). Such birds have small proventriculus and a large asymmetrical gizzard consisting of two powerful muscle groups, the thick and the thin muscles (McLelland & King, 1984; Moore, 1998b).

1.1.1 Grit consumers

To meet the need for rapid ingestion and effective digestion of the food, avian species that have developed the "gastric mill" also deliberately ingest small stones (henceforth called grit), which are stored in the gizzard. The function of the grit is to assist in the mechanical grinding and size reduction of the food particles in the gizzard to facilitate the digestive process (Bennett, Hoff, & Etterson, 2011; Gionfriddo & Best, 1999; Hetland, Svihus, & Krogdahl, 2003; Moore, 1998c, 1999; Svihus, 2011).

The number of grit in gizzards varies greatly among species and between individuals (Gionfriddo & Best, 1996; Gionfriddo & Best, 1999). Studies using both wild and captive birds have shown that birds have different preferences regarding grit size, shape and surface texture (Best, 1995; Best & Gionfriddo, 1991; Best & Gionfriddo, 1994; Gionfriddo & Best, 1999; Stafford & Best, 1999).

Domestic chickens and other gallinaceous birds kept in captivity and fed highly processed and digestible food do not need grit to aid digestion (Amerah, Lentle, & Ravindran, 2007; Gionfriddo & Best, 1999; Hetland, Svihus, & Choct, 2005). In these cases the cost of carrying the grit with respect to both space and energy, surpasses the benefits. However, wild birds may practice a deliberate optimization digestive procedure where the cost of picking and storing nutrient and energy deficient material like grit, is outweighed by the assistance that the grit provides in utilizing the food (Alonso, 1985; Amat & Varo, 2008).

Research of grit use among wild grouse has shown that the composition of the grit, number and size, in the gizzard of e.g. ptarmigan species (rock ptarmigan *Lagopus muta,* willow grouse *Lagopus lagopus* and white-tailed ptarmigan *Lagopus leucurus*) changes over the course of the year (May & Braun, 1973; Myrberget, Norris, & Norris, 1975; Norris, Norris, & Steen, 1975). This probably reflects seasonal changes in the digestibility of food. In spring and summer when the birds feed on fresh growing leaves and sprouts, which are highly digestible, more grit and smaller in size is found in the gizzard than in autumn and winter when the birds switch to a high fiber diet. (Myrberget, et al., 1975; Norris, et al., 1975). The grit was also observed to be larger during the winter than the summer and rounder if snow prevented access to grit implying longer retention time (Gionfriddo & Best, 1999; Myrberget, et al., 1975).

Ingestion of grit is also thought to aid supplementation of minerals that may be of limited availability in some natural environments. Especially calcium, which is an important source for egg laying hens, and for bone growth of juveniles (Gionfriddo & Best, 1996; May & Braun, 1973; Murphy, 1996; Svihus, 2011; Walton, 1984).

1.2 Phenotypic flexibility and digestive adjustments

Herbivorous birds experience considerable seasonal changes in the environmental condition, e.g. food availability and nutrient composition. Internal physiological demands may also change because of increased energetic requirements during reproduction, growth, thermoregulation and molt (Moss, 1997; Ricklefs, 1996; Robbins, 1993; Starck & Rahmaan, 2003; Whelan, Brown, Schmidt, Steele, & Willson, 2000). The digestive system among avian herbivore is not a fixed entity and a number of experimental studies have reported phenotypic flexibility in the digestive organs, i.e. reversible and repeatable changes in gizzard size and gut length (Battley & Piersma, 2005; Karasov, 1996; McWilliams & Karasov, 2001; Piersma & Drent, 2003; Starck, 2005). Feeding studies conducted by Moss (1989) and Starck and Rahmaan (2003) have showed that the gizzard size and the gut length increases in birds when feeding on a high-fiber diet with low energy content. The size of the gizzard and the gut length has been observed to decrease again when the birds switch to low-fiber diet with higher energy content. These phenotypic changes of the digestive organs allow dietary switches by increasing the efficiency of the digestion and permitting a higher feeding rate (Karasov, 1996).

1.2.1 Gizzard

As described above, the gizzard grinds the food with help of grit that makes the food more accessible for the digestive enzymes excreted by the proventriculus (Battley & Piersma, 2005; Gionfriddo & Best, 1999; Svihus, 2011). The food particles have to be ground to a certain size before they can leave the gizzard into the duodenum and the small-intestine through the small opening of the pyloric sphincter (Duke, 1992; Hetland, et al., 2003; Moore, 1999; Piersma, Koolhaas, & Dekinga, 1993; Svihus, 2011). The gizzard is known to respond particularly rapidly to changes in the diet, this is first of all a consequence of changes to the structure of the diet (Dekinga, Dietz, Koolhaas, & Piersma, 2001; Moss, 1989; Moss & Trenholm, 1987; Starck, 1999). Coarse food with high fiber content needs longer time in the gizzard than food low in fiber (Hetland, et al., 2005; Karasov, 1996; Svihus, 2011). Therefore, the gizzard needs to work harder when the bird is feeding on coarse food that consequently leads to increase in the gizzard size. When the food is low in energy and nutrients the bird needs more food to fulfill its energy requirements and the gizzard is enlarged to be able to both hold more food and grind more and coarser food (Svihus, 2011; van Gils, Piersma, Dekinga, & Dietz, 2003).

1.2.2 Gut

Studies on wild birds with large variations in their diet during the year show that both the small intestine and the caeca vary in size (Moss, 1983; Moss, 1989; Moss & Trenholm, 1987). The grinded and digested food is absorbed in the small-intestines but complex carbohydrate and fine particles that have not been digested and absorbed are transferred into the caceum (Son, Ragland, & Adeola, 2002; Watson & Moss, 2008). What is left, coarse and fibrous parts of the food bypass the caceum and go into the large intestine and through the cloaca. The cacecum acts as a fermentation chamber where the carbohydrates are broken down with the help of bacteria and absorbed by the bird (Gasaway, 1976a; Gasaway, 1976b; Watson & Moss, 2008).

When the fiber content of the food increases and energy and nutrient content is reduced, the time needed for digestion and absorption gets longer and also more food needs to be ingested, the phenotypic response to such changes in diet is the lengthening of the gut (Karasov, 1996; Whelan, Brown, & Moll, 2007; Whelan, et al., 2000).

1.2.3 Effects of plant defenses

Many plants toughen their tissues with large quantities of cellulose and lignin as a defensive shield against herbivores (Molles, 2005). As described above highly fibrous food is difficult to grind and digest. Herbivorous birds may use grit as a grinding tool in the gizzard to overcome these plant physical defenses (Gionfriddo & Best, 1999; Moore, 1999; Watson & Moss, 2008). The plant palatability frequently affects the grouse foraging selection pattern with seasonal changes in the fiber content and also with changes in the concentration of the so-called secondary compounds in plants (tannins, resins, alkaloids and phenols) (Bryant & Kuropat, 1980). Production of secondary compounds is associated with plant growth stage, but this association differs between and within plant species (Molles, 2005). There are different theories on the role of plant secondary compounds. Some studies claim that plant secondary compounds deter herbivores from feeding on them (Moss, 1991), whilst other studies claim that such compounds have evolved as a protection against solar UV-B radiation (Haukioja, 2005; Robbins, 1993; Selås, 2006; Sherwood, et al., 2012; Sinclair, Fryxell, & Caughley, 2006; Watson & Moss, 2008). It is known that some plant secondary chemicals inhibit herbivore digestion by binding to proteins and thus making them less digestible and they can also act as toxins (Bryant & Kuropat, 1980; Moss, 1974; Robbins, 1993; Sinclair, et al., 2006).

1.3 The Icelandic rock ptarmigan

The rock ptarmigan, hereafter ptarmigan, is the only grouse in Iceland and the dominant wild vertebrate herbivore in upland areas (Gardarsson & Moss, 1970). Their most important breeding grounds are low-lying heath lands, but generally ptarmigan leave these habitats in autumn and migrate to alpine wintering areas (Nielsen, 1996). During autumn and winter the bird feeds on coarse and low-digestible sprouts, buds and catkins of small woody shrubs such as dwarf birch (*Betula nana)*, dwarf willow (*Salix herbacea*), tea-leaved willow (*Salix phylicifolia*) and ever-green leaves of mountain avens (*Dryas octopetala*) (Gardarsson, 1988; Gardarsson & Moss, 1970) . During summer they feed on more digestible food such as new shoots of various plants, bulbils of the alpine bistort (*Polygonum viviparum*) and in late summer they also eat bilberries (*Vaccinium myrtillus)* and crowberries (*Empetrum nigrum*).

The ptarmigan is a popular game-bird in Iceland (Gardarsson, 1988) and since 1995 38,000 - 166,000 birds have been harvested annually (The Environment Agency of Iceland, 2015). The population has historically shown multi-annual cycles with a 10-12 year period (Gardarsson, 1988; Gudmundsson, 1960; Magnússon, Brynjarsdóttir, & Nielsen, 2005; Nielsen & Petursson, 1995). The main demographic factor involved with the cyclic changes is juvenile winter mortality which shows 2-4 year time lag with the population density (Brynjarsdóttir, Lund, Magnússon, & Nielsen, 2003; Magnússon, et al., 2005). In Iceland, the rock ptarmigan is the main prey of the gyrfalcon (*Falco rusticolus*), and its predation has been proposed to be one of the possible agents driving the population cycles of the ptarmigan (Nielsen, 1999).

Benjamínsson (1997) studied grit use of the Icelandic rock ptarmigan during autumn from 1984‒1996 and found a relationship between average grit number and ptarmigan population density. Both the number of grit and average grit weight changed in synchrony with the population index. During population peak years the number of grit was high but their average weight low but during years when the population was low the reverse was the case. He also showed that when grit number decreased grit size increased and stated that the grit with respect to morphology was rounder when grit number was high. From these results it has been suggested that the grit characteristics reflect the quality of the food that may influence the changes in the population number.

1.4 Objectives of this study

My study is part of a long-term research project on the relationship between health, body condition and population change of the rock ptarmigan in Iceland. The aim of my study is to investigate the grit, gizzard and gut of the rock ptarmigan to evaluate if the quality of the food could play a role in the population change. I will test if there is an inter-annual variation of grit, gizzard and gut and if there are differences between sex and age of the birds. Further, the inter-annual variations, if present, will be compared to density changes in the ptarmigan population.

2 Materials and methods

2.1 Study area

The study area is centered on Lake Mývatn (65°37’N, 17°00’W) in north-east Iceland (Figure 2). This area is characterized by rolling hills rising from the coast to 300-400 m a.s.l. at Lake Mývatn. Extensive lava fields are found east and north of the lake. Several river valleys border the area on the west side including Laxárdalur, Reykjadalur, Aðaldalur and Bárðardalur. Some isolated mountains and larger mountain ranges are found within the area, the highest being Mount Bláfjall 1222 m a.s.l.. Heath vegetation characterizes the uplands, the dominant plants being small shrubs such as dwarf birch and tea-leaved willow, also many species belonging to the heather family (*Ericaceae*), various grasses, sedges, mosses and lichens (Nielsen, 1999).

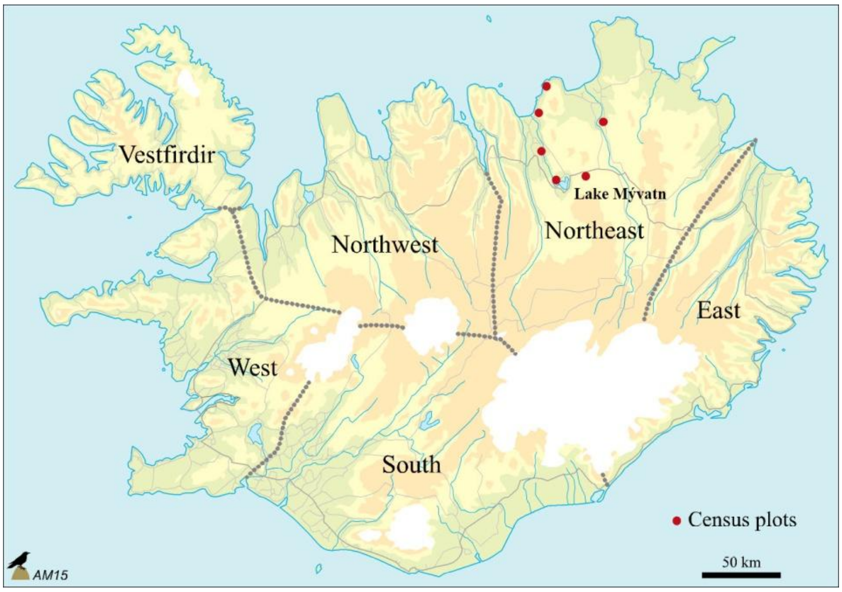

Figure 2. The study site by Lake Mývatn, Northeast Iceland, and the six ptarmigan census plots (red dots) used in this study.

2.2 Collection of rock ptarmigans

The ptarmigans were collected during the first week of October 2006-2013. The ptarmigans were collected out-of-hunting season under a special permit issued by the Icelandic Institute of Natural History (IINH). The first week of October was chosen as a reference point for two main reasons: (a) to control for seasonal changes in organ size (Moss, 1989; Starck, 2005; Starck, 1999, 2003; Starck & Rahmaan, 2003); and (b) sample the ptarmigan population at the start of the season when it’s fate is determined but winter survival determines population change (Gardarsson, 1988). As the ptarmigan are free-flying wild birds the individuals for the study could not be selected systematically but were shot sitting or flying when encountered and in areas where they gather at this season. The goal was to have 40 adults and 60 juveniles in the annual sample. The number of ptarmigans analyzed for grit each year by age and sex can be seen in Table 1.

Table 1. Number of ptarmigans analyzed for grit by year, age and sex, from 2006-2013 in NE-Iceland.

	Age	**Sex**	
Year		**Female**	**Male**
2006	Adult	11	15
	Juvenile	38	37
2007	Adult	5	14
	Juvenile	27	30
2008	Adult	12	12
	Juvenile	28	29
2009	Adult	5	12
	Juvenile	27	26
2010	Adult	11	23
	Juvenile	30	25
2011	Adult	13	22
	Juvenile	26	26
2012	Adult	8	31
	Juvenile	29	30
2013	Adult	13	24
	Juvenile	28	25

After capture the dead bird was immediately fitted around the leg with an identification tag. Then, to avoid blood contamination and contact with other dead ptarmigan, the carcass was completely wrapped with multiple layers of absorbing paper before being placed into a paper bag sealed with staples. The birds were cooled to 4 °C until being processed, which was usually within three days of collection.

2.3 Processing of birds

The birds were sexed by the loral stripe and size and color of the combs (Montgomerie & Holder, 2008). Age was determined by the pigmentation of the primaries (Weeden & Watson, 1967). Sex and age was verified by examination of the gonads and presence or absence of the bursa of Fabricius during dissection.

Anatomical terms are following Baumel (1979). The following morphometric measurements were taken during dissection at the laboratory at Lake Mývatn: (a) wing length, measured to the nearest mm with a ruler from the carpal joint to the tip of the flattened and straightened wing; (b) head + bill, measured to the nearest 0.01 mm with calipers, from the hindmost point of the head to the tip of the bill (positioned horizontally to the head); (c) sternum length, measured to the nearest 0.01 mm with calipers from the tip of the *spina externa* along the center line to the *margo caudalis*; and (d) sternum-coracoid length, measured to the nearest 0.01 mm with calipers from the center line of the *margo caudalis* to the cranial end of the *coracoideum*, which had been released from the shoulder articulation. All dissecting and measurements were done by the same individual (Ólafur K. Nielsen).

The gut was removed and measured according to Leopold (1953); first mesenteries were cut with scissors allowing the gut tube to be laid out on a table straight without loops or convulsions, but without undue stretching. Following measurements were taken with a tape to the nearest 0.5 cm: (a) small intestine from gizzard pyloric sphincter to junction of caeca; (b) caecum from junction with small intestine to tip (only one measured); and (c) large intestine from caeca junction to lip of vent including cloaca. The gizzard was packed into a plastic bag and kept frozen until later analyses.

2.4 Processing of the gizzard

The gizzard was cut open and the content separated from the organ. The gizzards were oven dried at 55°C (Memmert UFE-800 universal oven). Three gizzards were selected for daily monitoring of weight loss. The dry mass of the gizzard muscle was deemed constant when weight loss between days was less than 1%. When dry mass was reached, the gizzards were weighted and packed individually in filter paper (Bravilor Bonamat B20, 203/535). The packed samples were washed in petroleum ether (boiling point 40–60°C) in a Soxhlet to extract fat. After five cycles the samples were taken out of the Soxhlet unless they were still leaking fat, if so one or more cycles of washing were added to the process. Each cycle took ca. 30 minutes. When out of the Soxhlet, the samples were placed in the drying oven at 55°C for 18–20 hours and then the fat free dry weight (FFDW) of the gizzzard was measured. For a detailed description of Soxhlet methods see Piersma, Gudmundsson & Lilliendahl (1999).

2.5 Grit analysis

The gizzard content – a matrix of vegetation and grit – was weighed (precision 0.01 g). The matrix was put into an aluminum cup and dried in an oven at 55°C until a constant weight was reached (deemed dry when changes in weight were less than 1% between days). The dry matrix was weighed and then broken down using the fingers and the material placed into a 250 ml transparent plastic jar. The jar was filled 2/3 with water, closed with a lid and shaken vigorously by hand in order to separate grit from the vegetation. Grit and seeds sank to the bottom but most of the vegetation floated on top. The floating material was then poured into a plastic tray (35×22×5 cm) with water added, and searched for grit using a 1.3-fold magnifying glass. Any grit found was collected using tweezers and kept but the vegetation discarded. This was then repeated for the material sitting on the bottom of the jar. The grit from each bird was placed in an aluminum cup and dried overnight in the oven at 40°C. The next day each grit sample was sealed in a plastic bag for later analysis on grit morphology.

The grit morphology, i.e. size, roundness and ruggedness (Table 2), was analyzed at the Icelandic Institute of Earth Sciences, University of Iceland in Reykjavík. First, each sample (all grit found in one bird) was placed in a glass cylinder and washed in an ultrasound bath (120 kHz) for 30 minutes at 40°C. Then, each sample was dried and weighed to the nearest 1 mg. Each grit sample was photographed with a digital camera (Sony, DCR-TRV20E) using a stereoscope (Olympus SZ-CTV) and CCD-colour video camera module (XC-999P DC 12V) (Figure 3). The grit was placed on a microscopic glass slide prior to photographing and arranged in such a way that they were all visible in the display screen of the camera. The grit was aligned so as not to touch each other. Each grit was arranged approximately flat-lying on the glass slide so that the camera "saw" the maximum projection plane of the grit. This plane includes the long and intermediate axes of that grit. Large samples (> 100 grit) were split and subsets photographed separately, yielding a batch of images. The background and lighting were arranged to give the best contrast. The same zoom metering on the camera lens was used for the whole session. To derive the scale, a picture was taken of a ruler using the same magnification as for the grit images. This was repeated at the end of the session as a safety measure.

Table 2. Description of the grit parameter used in the analysis for rock ptarmigan in NE-Iceland 2006-2013.

Grit parameter	**Description**
Grit number	Number of grit in a gizzard
Grit total weight	Weight of all grit in a gizzard (g)
Grit mean weight	The average weight of grit particles in a gizzard (grit total weight (g)/grit number)
Grit mean size	The average equivalent diameter of grit in a gizzard (mm)
Grit mean roundness	Value describing the average roundness of the grit in gizzard
Grit mean ruggedness	Value describing the average ruggedness of the grit in gizzard

Each grit image was transferred to a computer and processed in Adobe Photoshop CS2 to prepare them for the morphometry program Morphocop (Eiríksson, Sigurgeirsson, & Hoelstad, 1994). This involved changing the mode of each picture to a gray scale. The image resolution was set at 300 pixels and image size as 8×6 cm. The original background was removed using the "magic wand tool" and the silhouette of each grit was used to obtain a black grit on a white background (Figure 3). The program Morphocop analysis the black and white image files in batches for each sampled bird and outputs ten size and shape parameters for each grit as well as the mean and the standard deviation for each parameter for that bird.

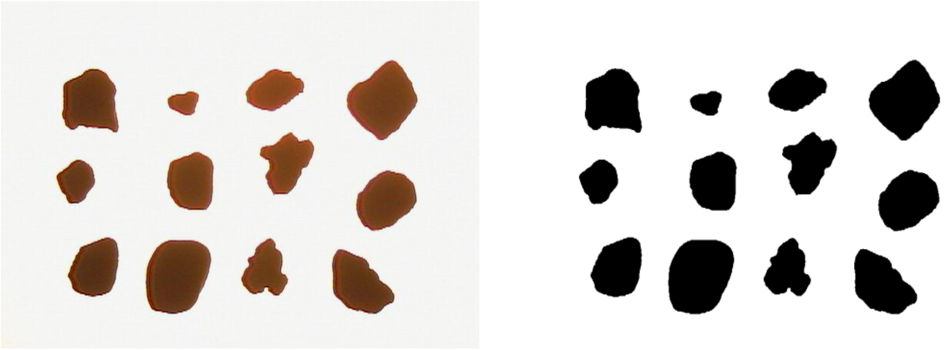

Figure 3. Images of rock ptarmigan grit for analysis in the software Morphocop. Left, an image from the digital camera; right, an image after processing and ready for further analysis.

The Morphocop parameters used in this study were: (1) Area; (2) Ruggedness; and (3) Roundness. The area was used to calculate the "equivalent diameter", an another measure of size, using the formula: $\sqrt{area * 4/\pi}$. Ruggedness and roundness are dimensionless measures of the ruggedness and circularity of the outline of the grit silhouette as observed in the maximum projection plane (mpp), for definition of these parameters see Schwartz (1980). The ruggedness gives the value 1 for grit with straight edges (such as for triangles and squares) and 0 value for highly rugged edges (Figure 4). Roundness values close to zero represent very elongated grit or grit with jagged edges but values of 1 corresponds to perfectly round or circular grit (Figure 4) (Eiríksson, et al., 1994).

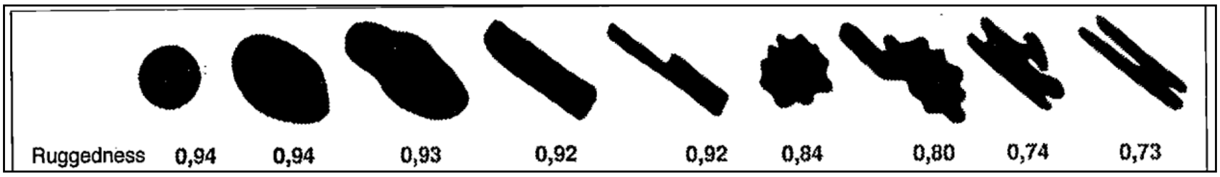

Figure 4. Forms and the measured ruggedness of grit with Morphocop analyzes (Eiríksson, et al., 1994).

2.6 Ptarmigan population status

Each spring territorial ptarmigan cocks were counted on six plots within the general study area (Figure 2). These plots are a part of a long-term monitoring program for the ptarmigan in Iceland and birds have been counted there since 1981 by Ólafur K. Nielsen and associates. The combined size of these plots is 26.8 km^2 (range 2.4–8.0 km^2). Each plot was censused once during May (mean date 20 May, SD = 5.49, range 7 May – 6 June). The census was usually conducted by two observers in the late afternoon (time 17:00–24:00) or the early morning hours (time 05:00–10:00). Position of territorial cocks was plotted on a map as was the location of all kills. “Kills” are the remains of a ptarmigan dead and eaten after arrival on census plot in spring. Total number of cocks in spring was taken as the sum of the number of territorial cocks alive and killed. The ptarmigan index used for this study was the annual mean density of cocks on the six plots. For a detailed description of census plots and methods see (Nielsen, 1996).

2.7 Statistical Method

All statistical analyses and graphs were done with the software R (R Core Team, 2013). The quality and properties of the data was investigated by: (1) using boxplots and Cleveland dotplots to filter out any typing mistakes and to identify outliers; (2) check for normality in the frequency distribution of the response variables using histograms; and (3) the homogeneity of variance was tested using the Levene’s test (Faraway, 2005; Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

For the grit number and grit total weight I used generalized linear models (GLM) techniques (glm function in R) to model the effects of age and sex of the birds and year. For grit number the GLM was based on the negative binomial distributions with a log link function. The GLM for grit total weight was based on the gamma distribution with a log link function (Faraway, 2005; Zuur, et al., 2009). For the grit mean weight I used multiple linear regression models (LM), using the lm function in R, to model the effects of age and sex of the birds and year. The grit mean weight was log transformed prior to analysis to fulfill the assumption of normality and homoscedasticity. For the grit mean size, grit mean roundness and grit mean ruggedness, I used LM to model the effects of age and sex of the birds and year.

The gizzard mass index was calculated by correcting the gizzard weight with body size. The body size was found using principle component analysis (PCA) with the four size variables: wing length, head+bill, sternum length and sternum-coracoid length. The Factor 1 from the PCA was used as an index of structural body size. Factor 1 explained 79% of the variance in the original variables. Loadings: wing = 0.861; head + bill = 0.845; sternum = 0.920; sternum-coracoid = 0.934). All references to body size in the thesis refer to the Factor 1 of the PCA. Gizzard weight was significantly correlated with body size ($r = 0.30$, $n = 610$, $p < 0.001$) but not gut length ($r = 0.02$, $n = 586$, $p = 0.647$). Therefore, the gizzard mass index was used instead in the statistical analysis. The gizzard mass index and gut length was analyzed using a LM to model the effects of age, sex and year. Two-way interactions of age, sex and year was included in all models.

I selected the most parsimonious models using a backwards selection procedure with statistical significance ($p < 0.05$) as a selection criterion. Using year as a multiple nominal explanatory variables with eight levels involved and two levels involved for age and two for sex, I used “drop1-function” for my backward selection procedure to examine for the main effects in the model selection (Zuur, et al., 2009). The assumptions for the statistical tests were analyzed by plotting: (1) residuals against the fitted values to check for homoscedasticity (2) Q-Q plots to assess if the residuals follow the normal distribution; and (3) Cook‘s distance to assess the model for influential observations, value >1 (Faraway, 2005; Quinn & Keough, 2002; Zuur, et al., 2009).

During the analyses of grit number, grit total weight and grit mean weight I excluded bird with identification-number LM-09-166 which had one grit with weight of 0.0009 g. The prevalence of grit was known for 755 birds. Grit total weight was known for 690 birds and grit number for 680 birds. Two samples in 2007 (birds with identification-number LM-07-145 and LM-07-146) and four samples in 2010 (LM-10-058, 071, 074 and 078) were mixed together and those birds did not have a measure of the grit. Seven samples from 2012 (LM-12-001, 005, 055, 071, 195, 198 and 213) were mixed prior to grit analysis and were therefore excluded. Of the total number of gizzards collected, grit was not found in 8% of the gizzards. This 8% were not included in the statistical analyses of gizzard mass index. For the analyses of the grit roundness I excluded bird with identification-number LM-08-035 for nonsensical value. In the analyses for grit ruggedness I removed a significant two-way interaction between year and age ($F_{7,655} = 5.87$, $p = 0.044$) as the difference of the change between years was very much alike for both ages. This simplifies the interpretation of the results.

3 Results

3.1 Grit prevalence in ptarmigan gizzard

Grit was found in 692 birds or in 92% (90 - 94%, 95% CI) of 755 birds checked. The chi-square test showed that there was neither sex ($\chi^2 = 0.005$, df = 1, p = 0.945) nor age dependent difference ($\chi^2 = 0.481$, df = 1, p = 0.488) in grit prevalence, but the year effect was statistically significant ($\chi^2 = 14.365$, df = 7, p = 0.045). The prevalence of grit in birds among years ranged between 86 and 98%. The prevalence was above 92% in 2006, 2007 and 2008, it then declined in 2009 and 2010 to a low of 86% in 2011, increased in 2012 to 98%, and then declined to less than 90% in 2013 (Figure 5).

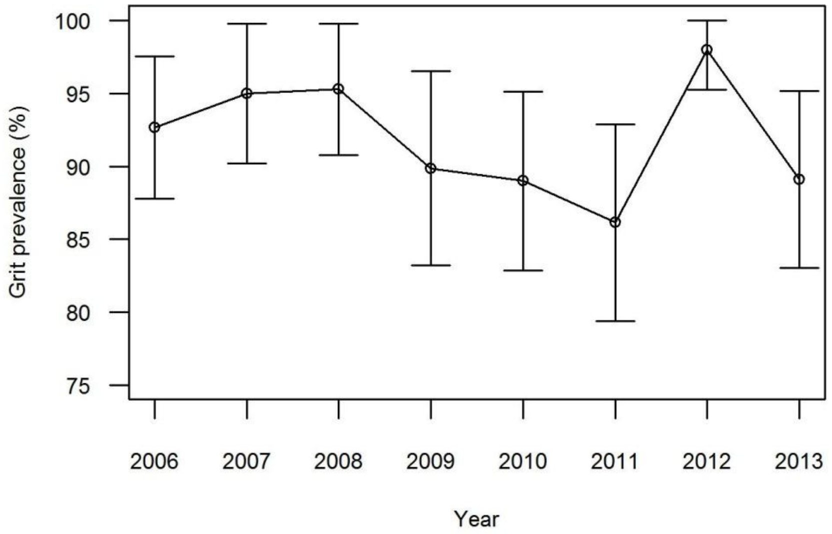

Figure 5. Prevalence (with 95% confidence interval) of rock ptarmigans with grit in gizzard collected in north-east Iceland in early October 2006 – 2013.

3.2 Grit number

The mean grit number was 31.1 (28.1 – 34.1, 95% CI), the distribution was right skewed (range: 0 – 348) with a median of 18. The GLM showed a significant difference in grit number between years ($F_{7,670} = 5.78$, $p < 0.001$), bird sex ($F_{1,670} = 12.75$, $p < 0.001$) and bird age ($F_{1,}670 = 7.16$, $p < 0.001$). The model including year, sex and age as explanatory variables only explained 8% of the variation in grit number. Grit number was high in 2006, declined in 2007 and 2008, then increased in 2009 and 2010, declined in 2011 and increased again in 2012 and was at same level in 2013. Males had 8 more grits on average than females, and juveniles had 7 more than adults (Figure 6).

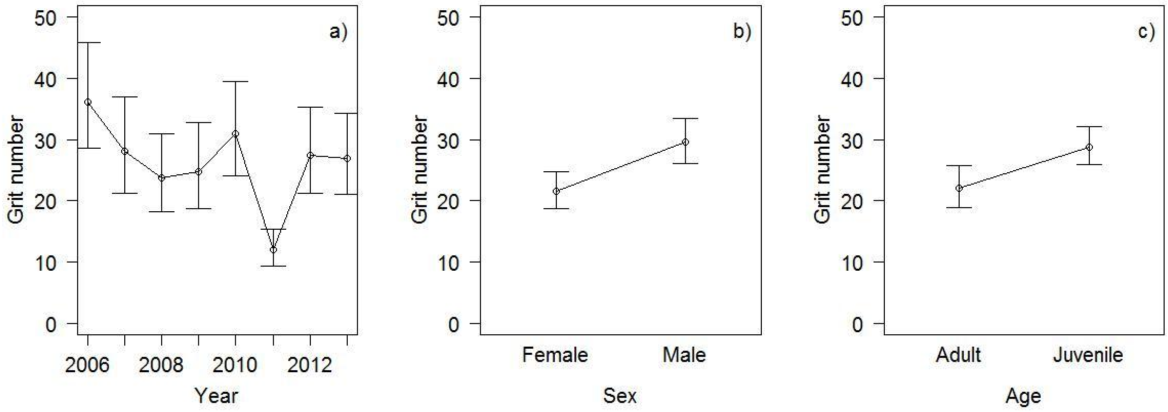

Figure 6. Mean grit number (with 95% confidence interval) in gizzards of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. a) Mean grit number by year, averaged over sex and age; b) mean grit number by sex, averaged over years and age; and c) mean grit number by age, averaged over years and sex.

3.3 Grit total weight

The frequency distribution of grit total weight was right skewed with a long tail and values ranging from 0.002 to 3.170 g. The mean was 0.368 g (0.335 - 0.401, 95% CI) and the median 0.219 g. The results of the GLM showed that the grit total weight was significantly related to year ($F_{7,681}$ = 4.08, $p < 0.001$), and sex of the birds ($F_{1,681}$ = 10.51, $p < 0.001$), but not age. The fitted model explained 6% of the variation in grit total weight. The grit total weight showed the same changes between years as grit numbers. Males had on average 36% greater grit total weight than females (Figure 7).

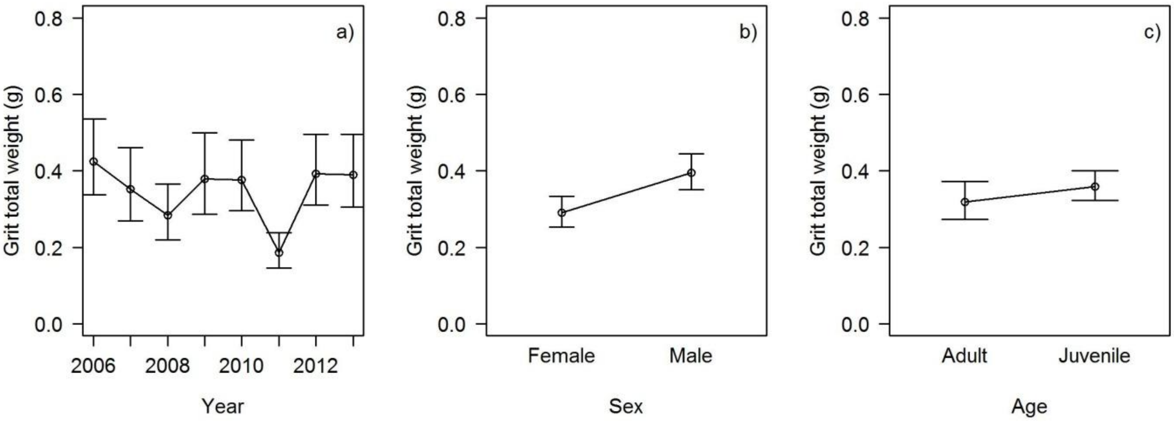

Figure 7. Grit total weight (with 95% confidence interval) in gizzards of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. a) Mean grit total weight by year, averaged over sex and

age, b) mean grit total weight by sex, averaged over years and age and c) mean grit total weight by age, average over years and sex.

3.4 Grit mean weight

The frequency distribution of grit mean weight was right skewed and values ranging from 0.001 to 0.064 g, with mean of 0.013 g (0.012 - 0.013, 95% CI) and median of 0.012 g. The LM showed there was a significant difference in the grit mean weight between years ($F_{7,\ 671}$ = 4.88, $p < 0.001$), and bird age ($F_{1,\ 671}$ = 4.81, $p = 0.029$) but not between the birds sex. The fitted model explained 5% of the variation in the average grit weight. The annual pattern of change for the grit mean weight differed from the pattern for grit number and grit total weight. The grit mean weight increased from 2006 to 2012, except for a dip in 2010, and declined again in 2013. Adult birds had on average 7% greater mean grit weight than juveniles (Figure 8).

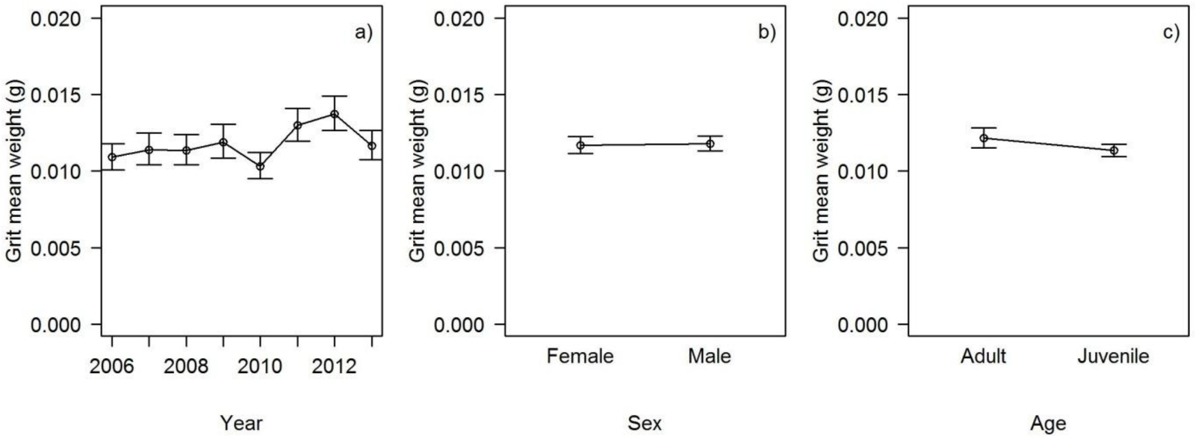

Figure 8. Grit mean weight (with 95% confidence interval) in gizzards of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. a) Grit mean weight by year, averaged over sex and age; b) grit mean weight by sex, averaged over years and age; and c) grit mean weight by age, averaged over years and sex.

3.5 Grit mean size

The mean grit size (diameter mm) had a normal frequency distribution with values ranging from 1.03 to 3.87 mm with mean of 2.27 (2.25 – 2.30, 95% CI). The mean grit size was significantly related to year ($F_{7,672}$ = 13.45, $p < 0.001$) but not to sex and age of the birds. The model explained 12% of the variation in mean grit size. The mean grit size showed similar pattern of change as the mean grit weight, it increased 2006 to 2009, declined in 2010, increased in 2011, then declined slightly in 2012 followed by a decline in 2013 (Figure 9).

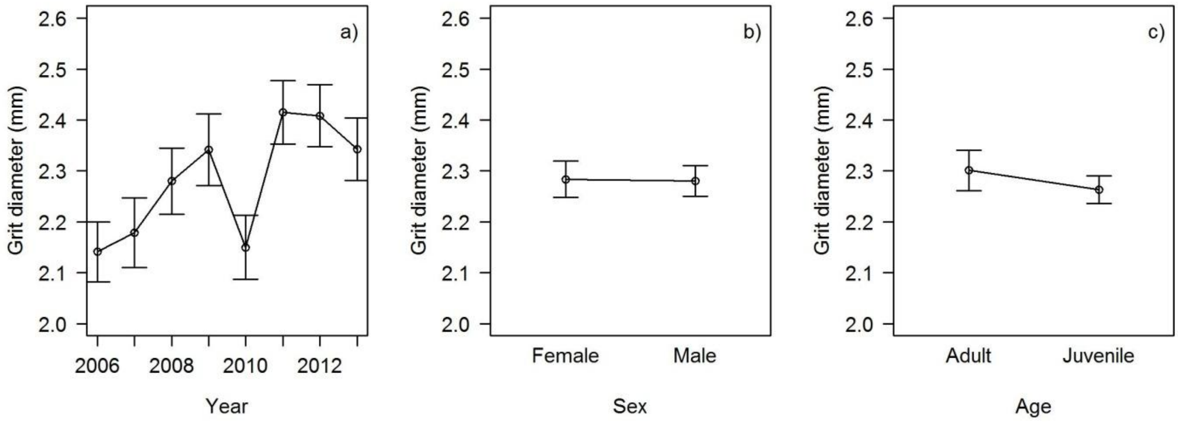

Figure 9. Mean grit size (with 95% confidence interval) in gizzard of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. a) Mean grit size by year, averaged over sex and age; b) mean grit size by sex, averaged over years and age; and c) mean grit size by age, averaged over years and sex.

3.6 Grit mean roundness

The grit mean roundness had a normal distribution and values ranged from 0.10 to 0.62, with mean of 0.38 (0.37 – 0.39, 95% CI). The model showed that the grit mean roundness was significantly related to year ($F_{7,670}$ = 13.79, $p < 0.001$), but not to sex and age of the birds. The fitted model explained 13% of the variation in grit roundness. The grit roundness declined in 2007, increased in 2008 and 2009, then declined in 2010 and 2011, then increased again in 2012 and 2013 (Figure 10).

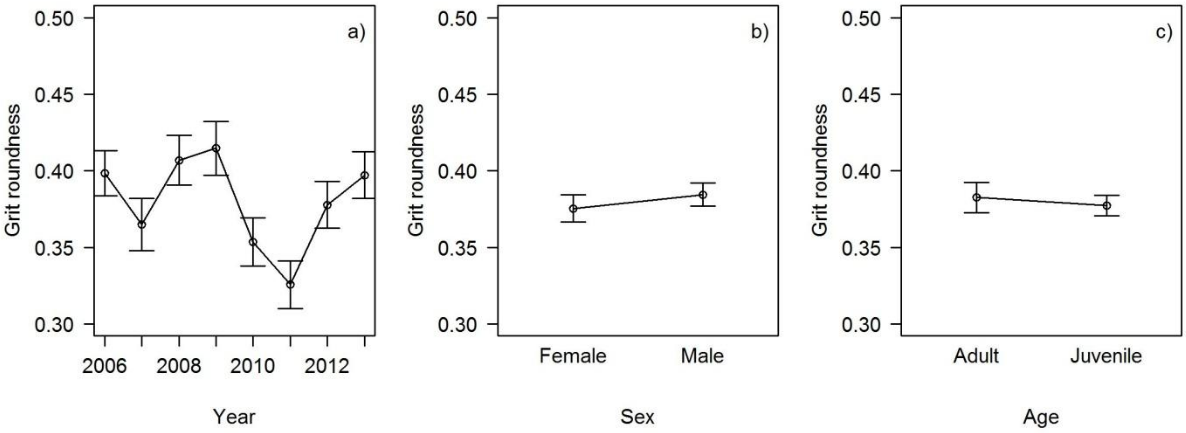

Figure 10. Grit mean roundness (with 95% confidence interval) in gizzards of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. a) Mean grit roundness by year, averaged over sex and age, b) mean grit roundness by sex, averaged over years and age and c) mean grit roundness by age, averaged over years and sex.

3.7 Grit mean ruggedness

The grit mean ruggedness had a normal distribution and ranged from 0.31 to 0.85, with mean of 0.59 (0.58 – 0.60, 95% CI). According to the model there was a significant difference in grit mean ruggedness between years ($F_{7,669}$ = 14.00, p < 0.001), and also a significant sex related difference ($F_{1,669}$ = 6.96, p = 0.009), but was no age related difference. The fitted model explained 14% of the variation in grit ruggedness. The grit ruggedness showed similar annual changes as grit roundness. The grit was most rugged in 2011 and the least rugged in 2009. Males had 3% less rugged grit then females (Figure 11).

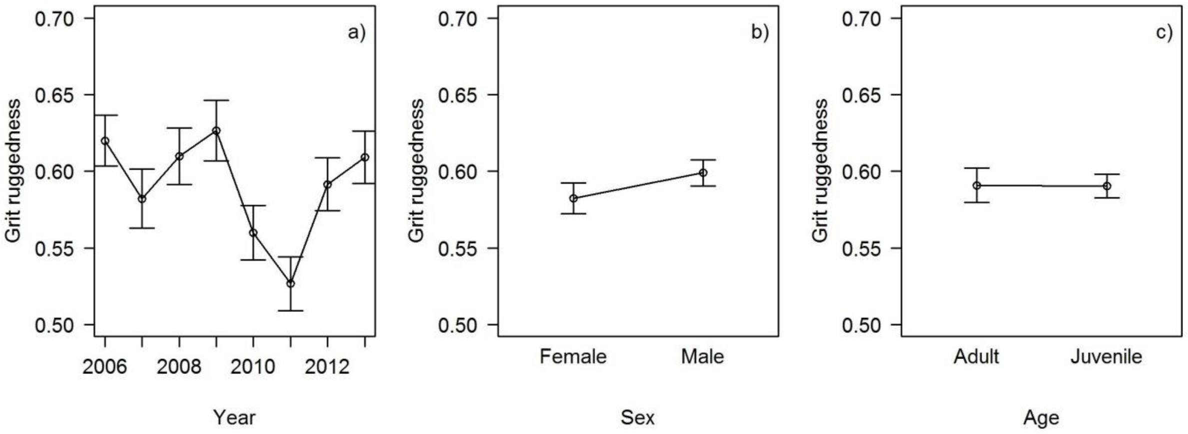

Figure 11. Grit mean ruggedness (with 95% confidence interval) in gizzards of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. a) Mean grit ruggedness by year, averaged over sex and age, b) mean grit ruggedness by sex, averaged over years and age and c) mean grit ruggedness by age, average over years and sex.

3.8.1 Gizzard mass index

Gizzard mass index followed a normal distribution with values ranging from 2.55 to 5.37 g, with mean of 3.84 g (3.81 – 3.87, 95% CI). The model showed significant interactions between year and sex ($F_{6,596}$ = 3.26, p = 0.004) and age and sex ($F_{1,596}$ = 5.11, p = 0.024). The fitted model explained 20% of the variation in the gizzard mass index. The interaction between year and sex showed that the inter-annual pattern in gizzard mass index depended on the bird’s sex. The gizzard mass index show an increasing pattern for both sexes over the years of the study, for both sexes there was a decline in the gizzard mass index in 2010 and for males also in 2014; the female gizzard mass index was in general greater and less variable the male index, and the males had clear peaks in the gizzard mass index in 2009 and 2012 (Figure 12).

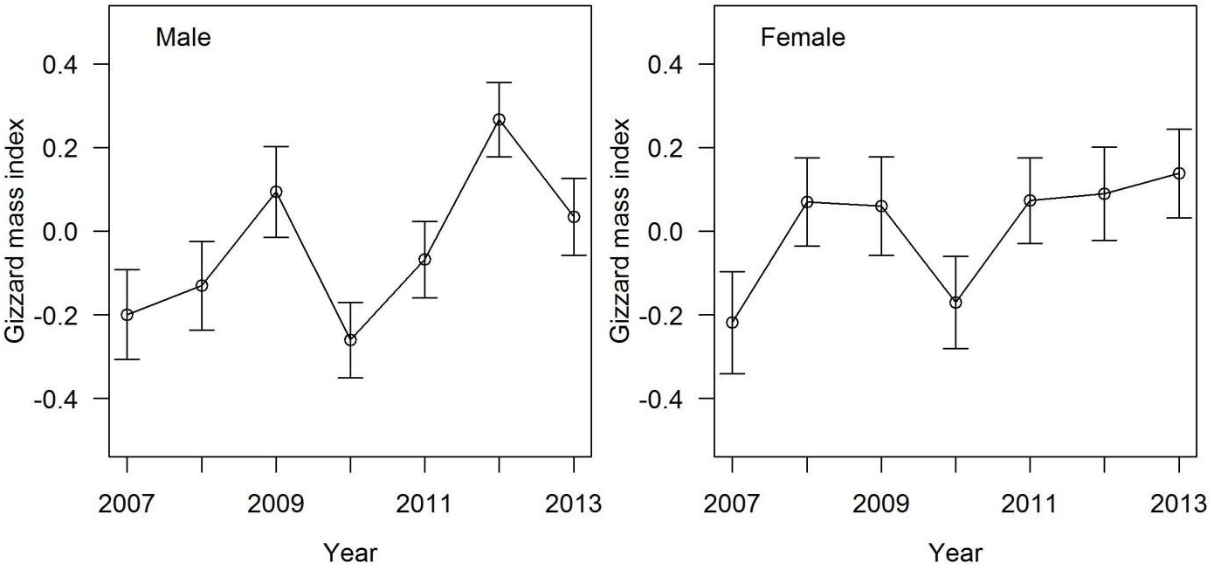

Figure 12. Mean value (with 95% confidence limit) of the gizzard mass index (gizzard FFDW corrected for body size) for rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. The sexes are shown separately because of significant age versus year interaction.

The interaction between age and sex showed that there was a greater difference in the gizzard mass index when comparing juvenile and adult males than juvenile and adult females. Also, it showed that the gizzard mass index was similar for juvenile males and females, but adult females had a greater gizzard mass index than adult males (Figure 13).

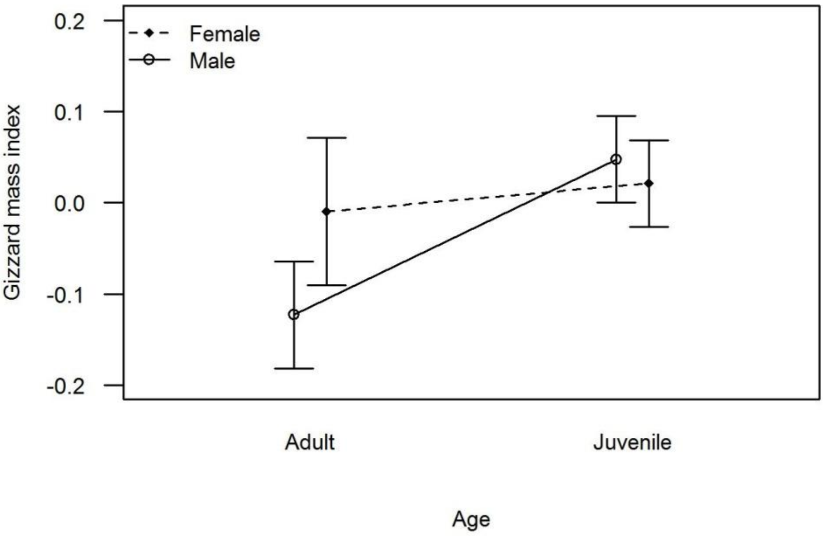

Figure 13. Mean value (with 95% confidence limit) of the gizzard mass index corrected for body size) of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. Mean values by sex and age.

3.9.1 Gut mean length

The gut mean length was normally distributed with values ranging from 143.0 to 213.5 cm, mean of 186 cm (185 – 187, 95% CI). There was no correlation between body size and gut length ($r = 0.02$, $n = 586$, $p = 0.647$) and therefore correction for body size was not done. The model for the gut length showed that it was significantly related to year ($F_{6,608} = 42.63$, $p < 0.001$) and with interactions between age and sex ($F_{1,608} = 5.23$, $p = 0.023$). The fitted model explained 40% of the variation in gut length. The gut length increased in 2008 and 2009, declined in 2010 and increased again in 2011 and 2012, and then declined in 2013. The interaction between age and sex showed that adult birds had shorter gut lengths than juveniles and adult females had longer guts then adult males but juvenile females shorter gut then juvenile males (Figure 14).

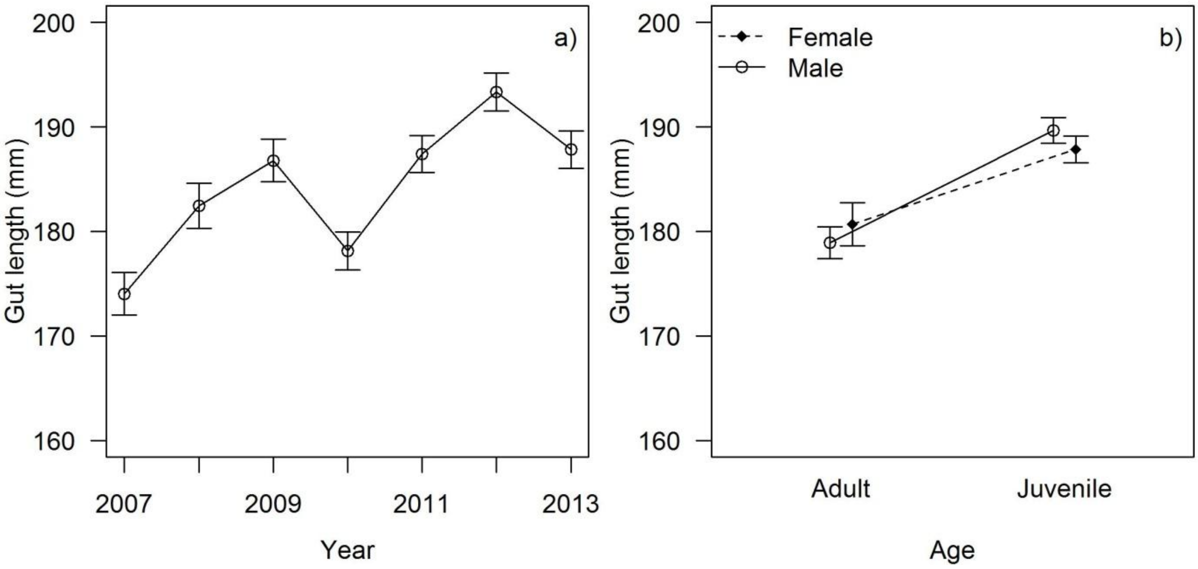

Figure 14. Mean gut length (with 95% confidence limit) of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013. a) Mean gut length by year, averaged over sex and age; and b) mean gut length by sex and age, averaged over years.

3.10 Correlations between grit and digestive variables

The grit number was highly correlated with grit total weight but showed a weak negative correlation with grit mean weight and mean grit size. The grit number showed a weak positive correlation with grit ruggedness and grit roundness. For grit total weight there was a weak positive correlation with grit mean weight, grit mean ruggedness and grit mean roundness but there was no correlation with grit mean size. There was strong positive correlation between grit mean weight and grit mean size and between grit mean ruggedness and grit mean roundness (Table 3).

The gizzard mass index was weakly correlated with grit total weight, grit size and grit mean weight and grit roundness but not with grit number and grit ruggedness. The gut length was weakly positively correlated with gizzard mass index and with grit size. The vegetation dry mass was weakly negatively correlated with grit number, grit total weight, grit ruggedness and grit roundness. There was a weak positive correlation between vegetation dry mass and gizzard mass index and between vegetation dry mass and gut length (Table 3).

Table 3. Pearson's correlation between the variables collected from the rock ptarmigan sampled in north-east Iceland in early October, data from 2007 – 2013, bold numbers is significant (p = 0.05).

Variable names	Grit total weight	Grit number	Grit size	Grit mean weight	Grit roundness	Grit ruggedness	Gizzard mass index	Gut length
Grit number	**0.93**							
Grit size	0.07	**-0.11**						
Grit mean weight	**0.12**	**-0.08**	**0.84**					
Grit roundness	**0.32**	**0.26**	0.04	0.06				
Grit ruggedness	**0.3**	**0.24**	0.02	0.05	**0.92**			
Gizzard mass index	**0.12**	0.06	**0.21**	**0.14**	**0.1**	0.07		
Gut length	0.04	0.04	**0.13**	0.08	0.03	0.02	**0.39**	
Vegetation dry weight	**-0.24**	**-0.21**	-0.03	-0.05	**-0.16**	**-0.19**	**0.27**	**0.16**

3.10 Ptarmigan population number

The sum of all territorial cocks counted on the six census plots is taken as the index of population abundance from the spring counts. The abundance index show decline in rock ptarmigan numbers 2007 increases in numbers 2008 and 2009 to a peak in 2010, decline in numbers 2011 and 2012, then increases in numbers 2013 (Figure 15).

The grit roundness was significantly and positively correlated with the population index with -1 lag. That means that if roundness had high value then the population index had a high value the following year (Figure 15). Grit mean weight and grit mean size showed negative correlation with the density index with lag of one year, this was however not significant (Table 4).

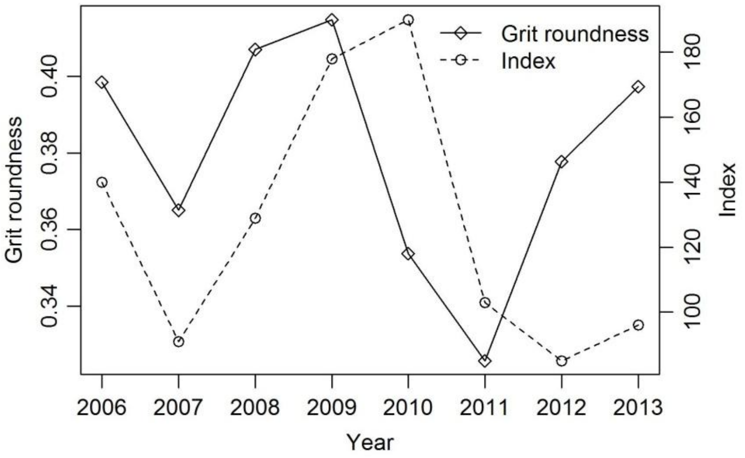

Figure 15. Mean grit roundness compared with population density index of rock ptarmigans collected in north-east Iceland in early October 2006 – 2013.

Table 4. Correlation coefficients between the grit variables, digestive organs and the population density index with lags of -1, 0, 1, and 2 years. Bold numbers are significant (p = 0.05).

Variable names	lag -1	lag 0	lag 1	lag 2
Grit prevalence	0.10	-0.35	-0.47	0.35
Grit number	-0.04	0.30	-0.04	-0.45
Grit size	0.08	-0.43	-0.38	0.30
Grit roundness	**0.70**	0.21	-0.62	-0.66
Grit ruggedness	0.6	0.16	-0.56	-0.64
Grit total weight	0.04	0.22	-0.22	-0.48
Grit mean weight	-0.2	-0.61	-0.23	0.58
Gizzard mass index male	0.03	-0.33	-0.49	0.02
Gizzard mass index female	0.18	-0.26	-0.5	-0.24
Gut length	-0.12	-0.27	-0.34	-0.02

4 Discussion

4.1 Coupling of the grit variables, gizzard and gut

When the grit number decreased the grit total weight also decreased, but the average size of the grit increased. This is in consistent with the results from Benjamínsson (1997), Myrberget et al. (1975), Norris et al. (1975), Alonso (1985) and Gionfriddo and Best (1995) which also observed inverse relationships between grit number and grit size. This coupling between the grit variables may indicates that the birds aim for a certain volume of grit rather than certain number of grit. When the bird has larger grit in the gizzard it needs less grit. It is also possible that less and larger grit are more efficient in grinding coarse food than small as many studies have shown (Gionfriddo & Best, 1999). Further, when the average grit size and the mean weight per grit particles increased, the gizzard mass index and the gut length also increased. This is consistent with results from other studies that have showed that large grit stimulate gizzard development (Gionfriddo & Best, 1999; Svihus, 2011).

The grit ruggedness and roundness were highly correlated and both variables were correlated with grit number and grit total weight. As the number and weight of grit increased the grit became more round shaped and with smoother edges. This is consistent with results from Benjamínsson (1997) but not with results from Norris et.al. (1975) and Myrberget et al. (1975) who observed that when the grit number was low the mean size was high and the grit was more rounded then smaller grit. The grit used by ptarmigan in Iceland is probably very different from grit used by ptarmigan in other countries. The volcanic activity in Iceland makes grit originating from ash available to the ptarmigan. The grit in the Icelandic ptarmigan has been observed to consist mostly of ash and basalt (Jón Eiríksson, personal communication). The ash has very different nature than basalt and breaks easily apart and does not become round with wear as the basalt does. This may explain the different result from Iceland.

4.2 Changes between years – effect of food quality?

4.2.1 Grit

Changes in the number and size of the grit have been linked to variations in the diet quality and environmental condition. According to Gionfriddo and Best (1999) larger grit particles may increase the gizzards efficiency in mechanically breaking down coarse fibrous foods. The grit size has been observed to be related to diet quality and according to Gionfriddo (1995) may be an important factor influencing grit number. Larger grit leads to less grit and vice versa. My result showed significant changes in grit size and grit mean weight between years. Grit size was increasing from 2006 to 2009 with a drop in 2010 and then increased again. The grit mean weight showed similar pattern with a drop in 2010. This indicates that the ptarmigan was feeding on higher quality food in 2010 than the other years. The grit roundness and ruggedness was rather low in 2010 (but similar in 2007 and 2012) which also supports that the bird was feeding on high quality food as Gionfriddo and Best (1999) have observed that the grit becomes more rounded when birds feed on low quality food which indicated that the grit is retained for longer time in the gizzard.

Others have suggested that changes in grit may be related to snow cover (Myrberget, et al., 1975; Norris, et al., 1975). I did not find any evidence of that in this study. For example the low grit number in 2011 cannot by a result of snow cover as the mean temperature in September was above average and no snow on the ground (The Icelandic Meteorological Office, 2011). These changes in grit may be related more to food quality rather than snow covering.

4.2.2 Gizzard and gut

The changes in gizzard index and gut length between years were very similar (especially for the males), with peaks in 2009 and 2012 and lows in 2007 and 2010 The gizzard is known to respond quickly to changes in diet by increase or decrease in size. The volume of the gizzard have been found to increase, up to 100% of its original size, when structural components such as hulls, wood shavings or large cereal particles are added to the diet (Svihus, 2011). The gut has also been shown to change in size with changing diet, i.e. it is longer in birds feeding on coarse material than in birds feeding on soft and more easily digestible material (Moss, 1983; Moss, 1989). My results indicate that the ptarmigan were feeding on coarser food of lower nutrient quality when the gizzard mass index was the highest and the gut the longest which was in the years 2009 and 2012. The gizzard mass and gut length were increasing from 2007 to 2012 except a drop in 2010 which may indicate for that particular year the ptarmigan were feeding on more digestible food of better nutrients, then compared to the other years. The reason for this increasing pattern from 2007 to 2012 may be that the birds had switched earlier to winter diet or that the autumn diet had more plant defenses such as higher content of fiber or secondary-compounds.

4.3 Differences between sex and age

Food habits studies have indicated that both territorial and aggressive behavior is related to food availability. Strong, territorial and aggressive individuals may gain access to more food with higher quality than submissive individuals (Newton, 1998; Robbins, 1993). One may postulate that weaker or socially less dominant individuals attempt to develop compensatory mechanisms to alleviate their access to less or inferior food. These compensatory mechanisms may be conscious (migration) (Newton, 1998) or more unconscious (modification of digestive system). Moss (1983) reviewed few studies on grouse and found that in general the adult males had shorter guts than females and juvenile males and that juvenile females had the longest gut length. This is consistent with the result from this study were adult males had the shortest guts but the juvenile females and males had very similar gut lengths. The shorter guts and lower gizzard mass in adult birds than in juveniles indicate that adult birds feed on more digestible food than juveniles. It could also be possible that adults have a better adopted gut flora to more efficiently extract energy out of the coarse food.

4.4 Population changes

The population of the ptarmigan did show changes in numbers from 2006 to 2013. These changes do not resemble the 10-12 year cycles previously observed. The mechanism behind cyclic fluctuation in population abundance of the grouse and the northern microtine rodents (*Lemmus lemmus* and *Microtus agrestis*), hares (*Lepus americanus* and *L.timidus*) and grouse is of wide ecological interest (Berryman, 2002; Stenseth, 1999; Watson, Moss, & Rae, 1998). What drives these cycles in species number is uncertain. Many scientist believe that the mechanism involves interactions between trophic levels such as herbivore-plant, predator-prey or parasite-host, or intra-population processes such as maternal effect and kinship (Krebs, 1985; Moss & Watson, 2001). The main demographic cause of periodic fluctuations in grouse numbers is generally thought to be because of the variation in the recruitment of young birds into the breeding population (Moss & Watson, 2001). According to Moss et al. (2001) there is some evidence that grouse breeding success and density vary with the quality and quantity of their diet. However, there is little that indicates that cyclic variations in weather may drive grouse cycles (Watson, et al., 1998; Watson, Moss, & Rothery, 2000).

My results showed significant correlation between roundness and population density. The population was highest one year after the peak in grit roundness and lowest one year after the grit had the lowest value in roundness. If high roundness of grit means that the grit is retained for longer time in the gizzard because it takes longer time to grind the low quality food the bird is feeding on. It could also be that more grit or physical roughness of the food wears the grit down rather than the retention time. Then it is possible that the birds are not as well prepared for the winter, because of the poor quality of the food, and mortality increases and the population starts consequently to decrease, which it did two years later.

There was not a significant correlation between the population index and the grit mean size or the grit mean weight. The correlation was observed to be negative with the density index (no lag). It is possible that if more years were included in the study then this would become significant.

The gizzard mass and the gut length were lowest in 2010 the same year that the population density was the highest. The small gizzard and gut indicate as described above that the ptarmigan was feeding on food with high quality in 2010. If this is the case then the birds should have been well prepared for winter and the population should not have decreased but as was shown in the results there was no significant correlation with the density index.

This study only covers eight years and the population has previously shown 10-12 year cycles. Therefore, more years are needed to get clearer picture on the relationship between the population density and the inter-annual variation of the grit, gizzard and gut.

5 Conclusion

The main findings of this study were that grit consumption seems to be a common behavior among Icelandic rock ptarmigan during the 1st week of October. Of all individuals studied 92% had grit in their gizzard with no sex and age dependency. Also, that the grit variables: number; weight; and size and also the gizzard mass index and gut length were significantly different between years. This inter-annual variation in the grit variables seems to be coupled, as well as changes in gizzard mass and gut length. The digestive system of the ptarmigan seems to be phenotypically flexible in response to the quality and the quantity of the food in order to obtain the essential nutrients to maintain the energy need. Grit use and the quantity of grit in the gizzard probably change with the level of the plant cellulose disintegration in the gizzard and are directly related to the feeding habits of the birds. The corollary of this – although my studies do not include relevant diet data – is that the quantity and quality of available food are directly reflected in the characteristics of the grit, and the gizzard size and gut length. The changes in grit roundness and how they relate to population change indicates that there is a relationship between ptarmigan food quality in autumn and changes in the population density.

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