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ABSTRACT

We analysed food data for rock ptarmigan *Lagopus muta* collected during a 10 day period at the end of September and beginning of October 2006–2014 in northeast Iceland or for nine years. The total sample was 679 birds, including 455 juveniles and 224 adults; the annual range was 48–88 birds. To describe the importance of items consumed we used percentage by dry biomass (total 1399 g) and percentage by frequency of occurrence. A total of 80+ species were identified, the most important were *Betula nana* (27% biomass, 62% frequency), *Empetrum nigrum* (14%, 63%), *Dryas octopetala* (11%, 64%), and *Salix herbacea* (10%, 41%). Important plant parts consumed were berries, woody shoots with buds, buds, catkins, seeds and leaves. Difference in diet, both with respect to species and plant parts consumed, depended on year and altitude of collection site but not on ptarmigan sex, age or sex*age interaction. The only significant age difference observed was that juveniles consumed more seeds and less woody parts than did adult birds. *Betula* spp. dominated the diet in five years and *Salix* spp. in four years. *Betula* and *Vaccinium* spp. were most important at low and medium elevations but *Salix* spp. showed an opposite pattern. Berries (*E. nigrum* and *Vaccinium* spp.) were the dominant plant parts in the diet for six years and woody parts of *Salix* and *Betula* spp. in three years. Berries dominated in the diet at low to medium elevations and woody parts showed an opposite pattern.

INTRODUCTION

Herbivory is rare among birds and only 3% of living species use plants as their main energy source (Lopez-Calleja and Bozinovic 2000). Plants respond to herbivory by depositing large quantities of cellulose and lignin within their tissues, substances that are difficult both to grind and digest (Molles 2005). Plants also produce so-called secondary compounds like tannins, resins, alkaloids and phenols as part of their defences (Feeny 1970). These secondary compounds can interfere with physiological processes of the herbivore (Bryant and Kuropat 1980, Molles 2005). Plant-herbivore interaction is an arm race and herbivore adaptations include among others a way to overcome plant defences.

Grouse (subfamily Tetraoninae) are herbivorous birds found in nemoral to Arctic areas (Fig. 1). In

Fig. 1. Rock ptarmigan grazing in grassland (a), grass heath (b), birch schrub (c), heath (d). Photos by Þorfinnur Sigurgeirsson (a & b), and Daníel Bergmann (c & d). – *1. mynd. Rjúpur á beit í graslendi (a), grasmóa (b), birkikjarri (c), og (d) móa. Ljósm. Þorfinnur Sigurgeirsson (a og b) og Daníel Bergmann (c og d).*

Fig. 2. A flock of rock ptarmigan grazing in grass heath. Photo by Daníel Bergmann. – *2. mynd. Rjúpnahópur á beit í grasmóa. Ljósm. Daníel Bergmann.*

autumn and winter they typically feed on plants that are low in nutrients (protein, phosphorus and sodium) and high in indigestible components (fibres, tannins and resins). The spring and summer diet is more digestible and richer in nutrients than the winter diet (Watson and Moss 2008). Grouse have special physiological and morphological adaptations to assimilate food of low digestibility. They have very large caeca and belong to a group of herbivores referred to as "hind-gut fermenters" (Hume 1989, McWilliams 1999). Grouse also show reversible phenotypic plasticity in the size of the digestive tract in response to changes in diet characteristics. In autumn and winter, when feeding on a diet high in fibre and low in energy, the individual responds by growing a larger digestive system and this is reversed in spring and summer (Leopold 1953, Moss 1972, 1974, Gasaway 1976). Grouse also respond behaviourally to their food source, including what species and individual plants to feed from (Huempfner and Tester 1988), and what plant parts to consume (Moss 1968, Gardarsson and Moss 1970), and by ingesting gizzard stones (grit) for grinding to match the demands of the feed (Myrberget et al. 1975).

Several species of boreal and arctic herbivores – birds, mammals, moths – show multi-annual population cycles (Keith 1963, Myers and Cory 2013). Such cycles are thought to be driven by trophic interaction like herbivore-plant, predator-prey and parasite-host (Krebs et al. 2001, Berryman 2002). The rock ptarmigan (*Lagopus muta*) is the only wild gallinaceous bird in Iceland and the dominant wild vertebrate herbivore in xeric habitats (Gardarsson 1988)(Fig. 2). The population shows multi-annual cycles with peaks 10–12 years apart (Nielsen and Pétursson 1995). The demographics of the cycle are characterized by delayed density dependent winter mortality of juvenile birds (Gardarsson 1988, Magnússon et al. 2004). The gyrfalcon (*Falco rusticolus*) is very likely one of the drivers of the rock ptarmigan cycle in Iceland (Nielsen 1999, 2011), but other trophic relations may also be of importance.

Recent studies on health and population change of rock ptarmigan in Iceland (rock ptarmigan health project) have shown interannual changes in the size of the digestive tract and grit composition, suggesting that differing quality or composition of plants eaten affects rock ptarmigan cohorts (Guðmundsson 2015). Another source of rock ptarmigan health data suggesting a link with food is varying prevalence (range 5–48%) of diet derived oxalate crystals in kidneys (Sigurðardóttir and Nielsen 2015). We use crop data from the rock ptarmigan health project to address the following questions:

1. What plants species and parts are eaten?
2. Is there a difference in food habits among years, within the study area, or among age and sex groups?

The birds were collected in autumn 2006–2014 during a 10 day time period.

Based on earlier studies on rock ptarmigan food habits in Iceland (Gardarsson 1971) we expect the autumn diet to be dominated by *Salix herbacea* shoots and *Polygonum viviparum* bulbils and to a lesser extent berries, leaves and evergreen herbs. We expect also to observe both significant annual changes in diet composition and an age related difference. This prediction is supported by observations from the ptarmigan health project of significant interannual and age related differences in the size of the digestive tract (Guðmundsson 2015). This, according to Moss (1972, 1974, 1983), should reflect differences in the composition or characteristics of the food.

STUDY AREA AND METHODS

The study area was located in northeast Iceland, centred on Lake Mývatn (65°37'N, 17°00'W). This region is characterized by rolling hills rising from the coast to 300–400 metres above sea level (m a.s.l.) at Lake Mývatn. Extensive lava fields, 300–500 m a.s.l., 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 occur, the highest being Bláfjall 1,222 m a.s.l. Heath vegetation characterizes the xeric uplands, the dominant plants being dwarf shrubs such as *Betula nana* and four different species of *Salix*, also many species of the heather family (Ericaceae), various grasses, flowering plants, sedges, mosses and lichens.

The study of food habits of the rock ptarmigan covers the years 2006–2014. It is part of a long-term research program on health and population change of the rock ptarmigan in Iceland. The birds were shot during the last three days of September and the first seven days of October, in moorlands, lava fields and alpine areas west, east, and north of Lake Mývatn (Fig. 3). The size of the study area is approximately 2000 km^2. The birds were collected during this narrow time span each year in order to: (a) control for seasonal changes in anatomical features of the rock ptarmigan; and (b) sample the rock ptarmigan population at the start of winter as winter mortality determines population change (Gardarsson 1988). The birds were collected outside the hunting season under a license issued by the Icelandic Institute of Natural History. As the rock ptarmigan are free-flying wild birds, individuals could not be selected at random, but were collected by conventional walk-up hunting where the birds were shot sitting or flying when encountered. Each year the goal was to analyse 100 birds, 40 adults and 60 juveniles. The required number of adults was not achieved in the first 4 years but every year after that. More adult males than females were caught, the reason being that part of the population, mainly females, is migratory (Gardarsson 1971). Juveniles were shot in excess all years and individuals for analysis were selected at random from those but so that the sex ratio was 50:50. Each bird was tagged with a unique id immediately after capture, packed, cooled to 4°C and dissected within 3 days. Various parameters were recorded at the collection site including the geographic coordinates and elevation using a GPS unit.

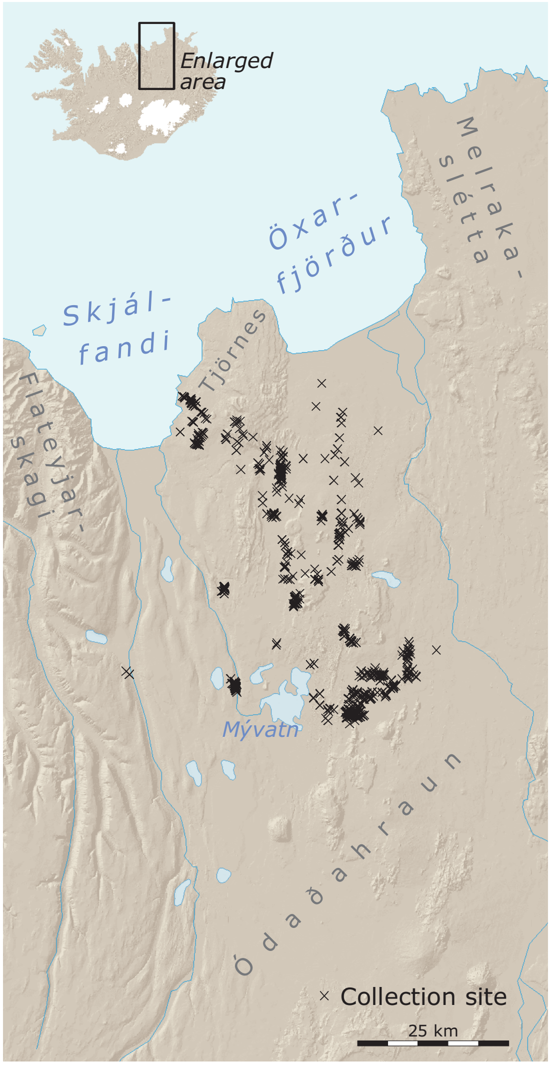

Fig. 3. Collection sites of rock ptarmigan (n =679) used for studies of food habits in north-east Iceland autumn 2006–2014. – *3. mynd. Rannsóknasvæðið á Norðausturlandi 2006–2014. Söfnunarstaðir rjúpna sem notaðar voru við rannsóknir á fæðu (n =679).*

During dissection, the birds were sexed based on the genital organs and aged using both the pigmentation of the primaries (Weeden and Watson 1967) and the presence or absence of the bursa of Fabricius. Two age classes were recognized: juveniles (about 3 months old); and adults (about 15 months or older). The crop was cut out of the bird and its content emptied into a marked plastic bag and frozen until analysis (Fig. 4).

We used crop contents to describe the food habits. The sampling unit was the individual rock ptarmigan. During analyses we separated the thawed vegetation according to species or a higher taxon and plant parts. References used for the identification of plants were *Flowering plants and ferns of Iceland* (Kristinsson 2010), *Norsk Flora* (Lid and Lid 1994), and *Flora of Iceland* (Löve 1983). For definition of parts of vascular plants we used Gardarsson (1971: page 124) who recognized 15 groups: (1) shoots; (2) reproductive shoots (strobili) of pteridophytes; (3) shoots with leaves; (4) woody shoots with buds (mostly current growth); (5) woody dwarf shoots with buds (current and older growth); (6) buds; (7) leaves; (8) flowers; (9) inflorescenses; (10) inflorescense buds; (11) fruits; (12) infructescenses; (13) viviparous bulbils, single and aggregate; (14) male catkins; and (15) roots (Fig. 5). After separation each sample was placed in an aluminium beaker marked with bird's id, taxonomic unit and plant part. The samples were weighed to the nearest 0.0001 g after 5 days in a drying oven at 50°C to derive the dry mass. Berries of *Empetrum nigrum* and *Vaccinium* spp. were crushed with a spoon before going into the oven. The same person (Chloé Depré) analysed part of the food data for 2007–2009 and all the data for 2011–2014. She also reviewed all earlier analysis done by Valentin Mader for the years 2006–2007, and Valerie Moos for the years 2008–2010. This was to ensure consistency in identification and quantification of data. Frequency of occurrence and percentage of dry mass was used to describe the importance of different plant species and plant parts in rock ptarmigan diet. Invertebrates were found in a few crops. They were identified to species but not used in any analysis of diet composition.

Fig. 4. The first steps in the process of dissecting a rock ptarmigan: (a) skin cut along the keel of the sternum; (b) skin moved, exposing the breast muscles and the crop; (c) crop loosened from connective tissues; and (d) crop cut open and content exposed. Photo by Svenja N.V. Auhage. – *4. mynd. Fyrstu skref við krufningu á rjúpu: (a) húð skorin og kili bringubeins fylgt; (b) hami flett frá bringu og þá sér í sarpinn framan bringu; (c) sarpur losaður; og (d) sarpur er opnaður og innihaldi safnað. Ljósm. Svenja N.V. Aughage.*

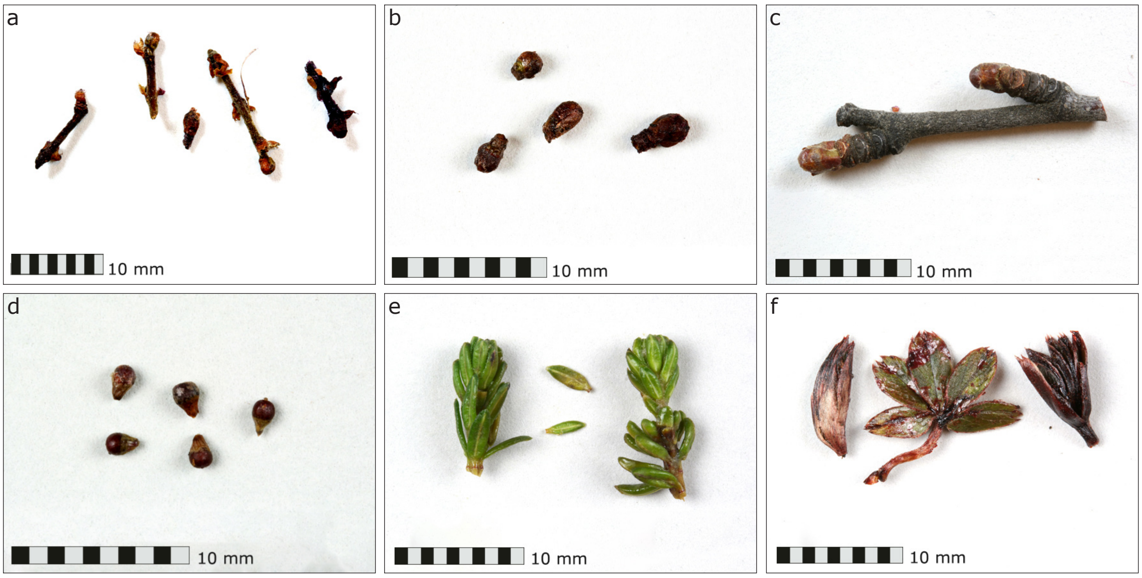

Fig. 5. Food for rock ptarmigan: (a) *Betula nana,* woody shoots with buds; (b) *Betula nana,* catkins; (c) *Betula pubescens,* woody dwarf shoots with buds; (d) *Polygonum viviparum,* bulbils; (e) *Empetrum nigrum,* shoot with leaves; and (f) *Alchemilla alpina,* leaves. Photos by Chloé Dépré. – *5. mynd. Nokkrar fæðugerðir rjúpu: (a) fjalldrapi, sprotar með brumi; (b) fjalldrapi, rekklar; (c) birki, dvergsprotar með brumi; (d) kornsúra, laukar; (e) krækiberjalyng, sprotar með laufi; og (f) ljónslappi, lauf. Ljósm. Chloé Dépré.*

For the analysis we lumped the 80+ plant species recorded into six groups and the 15 plant part categories defined into five groups. The six species groups were: (a) *Betula* spp. (2 species); (b) *Salix* spp. (4 species); (c) *Vaccinium* spp. (2 species); (d) *E. nigrum;* (e) *Dryas octopetala;* and (f) other species (70+ species). The five plant part categories were: (a) woody parts, i.e. catkins, buds and shoots of *Betula* spp. and *Salix* spp.; (b) leaves; (c) berries; (d) seeds (infructescenses); and (e) other parts. For the individual bird we calculated for each food category its importance as a proportion of the total dry biomass for that bird. The different items sum up to 1 for the individual and the data points in such data sets are not statistically independent (Aitchinson 1986). Therefore we used composition analysis where the data points were made independent by calculating a ratio of proportions using one group as the denominator and then log-transforming the ratios to normalize the data (Aebisher et al. 1993). This gives n-1 groups for analysis. But first we replaced 0 proportions with a number lower than any observed (we used 0.00001).

We did a multivariate analysis of variance (MANOVA) on the log-ratios to check for the possible effects of rock ptarmigan age, sex, age*sex, sampling year and altitude of sampling site on food selection. Age, sex and year were modelled as categorical explanatory variables and altitude as a continuous variable. This was done separately for plant species and plant parts. We used a univariate analysis of variance to investigate the relative differences in abundance of individual food categories using as dependent variables arcsine-transformed proportions of plant taxa and plant parts. We tested for those explanatory variables that came out as significant in the MANOVA, namely years and altitude for species groups and years, altitude and bird's age for plant parts. Altitudinal distribution according to years and age groups was studied using respectively a Median test and a Mann-Whitney U test. All analysis was done using the data analysis software system STATISTICA (version 12, www.statsoft.com). Statistical significance was declared at $\alpha<0.05$.

RESULTS

We analysed a total of 679 rock ptarmigan crops that contained food, including 224 adults (145 males and 79 females) and 455 juveniles (227 males and 228 females). The mean annual sample was 75 birds (range 48–88) (Table 1). The birds were collected in the same general area all years, but there was significant interannual difference with respect to altitude (Median Test, Chi-Square=66.338, df=8, p<0.001). In some years, like 2006, the birds were found lower down in the hills but in others, like 2007, higher up (Fig. 6).

Table 1. Age, sex and collection date of rock ptarmigan analysed for food composition in northeast Iceland autumn 2006–2014. – *1. tafla. Aldur, kyn og söfnunartími rjúpna á Norðausturlandi 2006–2014 sem notaðar voru við rannsóknir á fæðu.*

Collection period –	**Adults – *Fullorðnir***		**Juveniles – *Ungfuglar***		**Total**
Söfnunartímabil	**Males – *kk***	**Females – *kvk***	**Males – *kk***	**Females – *kvk***	***Samtals***
2–5 Oct. 2006	8	4	21	15	48
1–4 Oct. 2007	4	3	33	31	71
2–5 Oct. 2008	11	10	20	24	65
1–7 Oct. 2009	12	6	26	29	73
1–6 Oct. 2010	18	11	28	26	83
1–6 Oct. 2011	24	13	24	25	86
30 Sep. – 6 Oct. 2012	23	6	25	25	79
28 Sep. –3 Oct. 2013	23	11	26	26	86
30 Sep. – 5 Oct. 2014	22	15	24	27	88
Grand total – *Samtals*	145	79	227	228	679

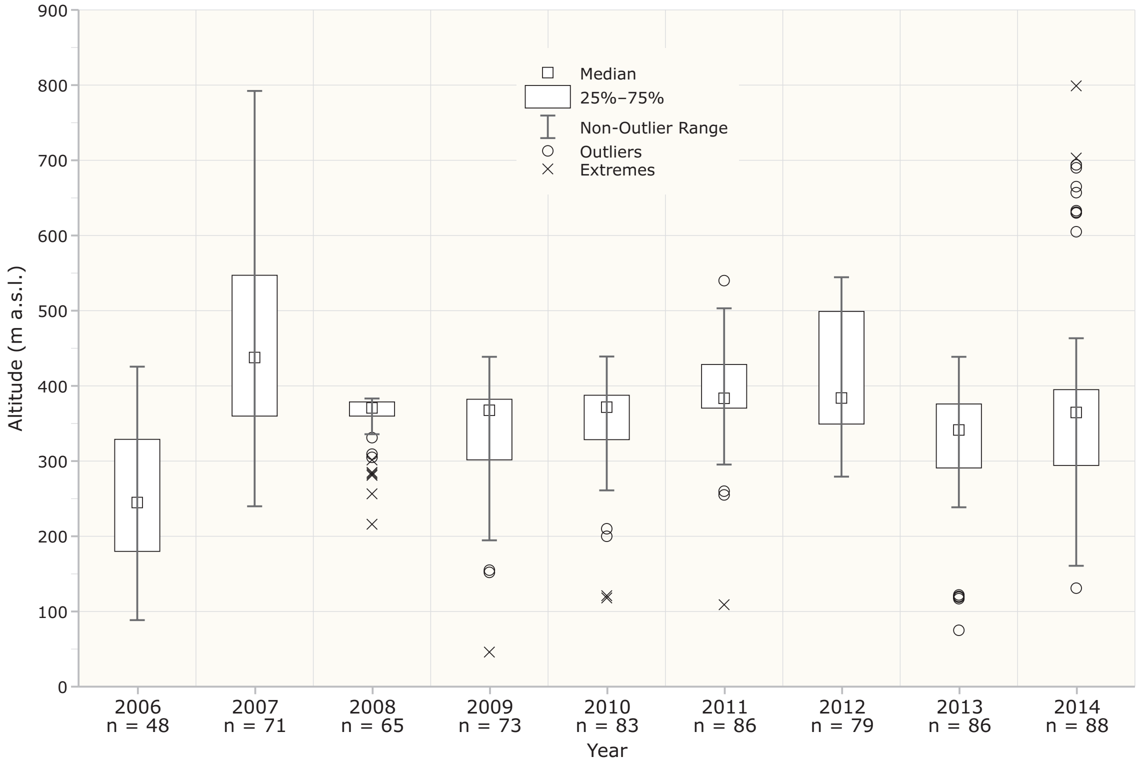

Fig. 6. Altitudinal distribution of collection sites for rock ptarmigan (n =679) used for studies of food habits in north-east Iceland autumn 2006–2014. – *6. mynd. Hæðardreifing fyrir söfnunarstaði rjúpna (n =679) á Norðausturlandi 2006–2014 sem notaðar voru við rannsóknir á fæðu.*

The altitude range was 46–799 m a.s.l., but most of the birds (54.3%) were collected between 300 and 400 m a.s.l. The two age groups, adults versus juveniles, did not show any difference with respect to altitude of collection site (Mann-Whitney U Test, U=48626, Z=0.6977, p=0.485).

Crop content other than vegetation

We found grit in seven crops (prevalence 1.0%). In eight birds (seven juveniles and one adult) we found invertebrates (prevalence for juveniles 1.5%, for adults 0.4%), including the arachnids *Mitopus morio* (in two birds) and *Pardosa palustris,* the coccoid *Artorthezia cataphracta,* the coleopterans *Phratora polaris* and *Otiorhynchus nodosus,* and two lepidopteran larvae including *Rheumaptera hastate* and an unidentified species. Invertebrates were a minuscule part of the diet; one bird had consumed two *P. polaris* but the others only single animals.

Number of plant species in rock ptarmigan diet

We identified a total of 68 plant species and further 12 species were identified to genus only. This gives a minimum of 80 recorded species (Appendix 1). The four most prevalent plant species were *D. octopetala* (64%), *E. nigrum* (63%), *B. nana* (62%) and *S. herbacea* (41%). The prevalence of the two *Vaccinium* species (*V. uliginosum* and *V. myrtillus*) was 63%. The most frequent *Vaccinium* parts in diet were berries and distinction between the two species was not possible. The prevalence of *Salix* spp., *S. arctica, S. lanata* and *S. phylicifolia* was 45%. Other frequently occurring species or taxa were *P. viviparum* 28%, *Armeria maritima* 23%, *Carex* spp. (including *C. capitata*) 19%, and *Thymus praecox* (12%). The prevalence of other species was less than 10%.

Changes in plant species composition in rock ptarmigan diet

The five main food groups, *Betula* spp., *Salix* spp., *E. nigrum, D. octopetala* and *Vaccinium* spp., representing 10 species, formed the bulk of the rock ptarmigan diet in all years (mean 92% of dry biomass, range 78–99%). There was a significant difference in species composition of food with respect to year (Wilks' lambda=0.538, F=11.051, df=40, p<0.001) and altitude (Wilks' lambda=0.892, F=15.948, df=5, p<0.001), but not with respect to bird age (Wilks' lambda=0.993, F=0.910, df=5, p=0.474), sex (Wilks' lambda=0.994, F=0.865, df=5, p=0.474) or sex*age interaction (Wilks' lambda=0.999, F=0.180, df=5, p=0.970). All plant taxa showed significant changes in relative importance between years (Table 2, Fig. 7). *Betula* spp. was the dominant food item in 5 years (2008–2011 and 2013) and *Salix* spp. in 4 years (2006, 2007, 2012 and 2014) (Table 3). The importance in diet of 4 plant groups,

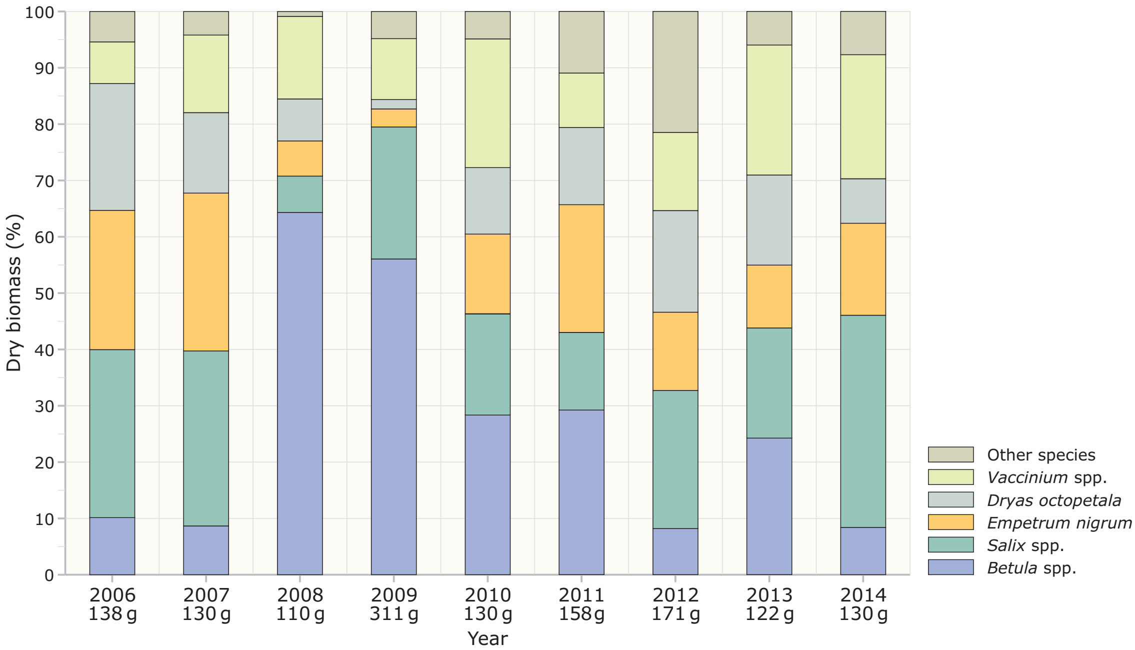

Fig. 7. Annual changes in the importance (% dry biomass) of six plant taxon in the food of the rock ptarmigan in north-east Iceland autumn 2006–2014. – *7. mynd. Breytingar á milli ára á vægi einstakra plöntutegunda eða tegundahópa í haustfæðu rjúpu á Norðausturlandi 2006–2014.*

Table 2. F and p values from an ANOVA of relative differences in abundance of plant taxa and plant parts in rock ptarmigan diet in northeast Iceland autumn 2006–2014. The explanatory variables are altitude of sampling site (m a.s.l.), year and bird age (adult versus juvenile). – *2. tafla. F- og p-gildi fervikagreiningar á hlutfallslegu magni plöntutegunda og tegundahópa og plöntuhluta í haustfæðu rjúpu á Norðausturlandi 2006–2014. Skýribreytur eru hæð söfnunarstaðar yfir sjó (m y.s.), söfnunarár og aldur fugla (1. árs fuglar =juv; ársgamlir og eldri fuglar =ad).*

Species groups ***Tegundir***	**F**	**p**	**Plant parts** ***Plöntuhlutar***	**F**	**p**
***Betula* spp.**			**Berries**		
m a.s.l.	13.427	<0.001	m a.s.l.	19.901	<0.001
Years	49.149	<0.001	Years	4.852	<0.001
Dryas octopetala			Age	0.289	0.591
m a.s.l.	0.276	0.600	**Seeds**		
Years	8.411	<0.001	m a.s.l.	1.504	0.220
Empetrum nigrum			Years	26.922	<0.001
m a.s.l.	0.375	0.540	Age	17.341	<0.001
Years	11.504	<0.001	**Leaves**		
Salix spp.			m a.s.l.	0.055	0.814
m a.s.l.	53.954	<0.001	Years	12.328	<0.001
Years	5.738	<0.001	Age	0.916	0.339
Vaccinium spp.			**Woody parts**		
m a.s.l.	37.988	<0.001	m a.s.l.	29.117	<0.001
Years	6.232	<0.001	Years	5.882	<0.001
Other species			Age	4.868	0.028
m a.s.l.	9.540	0.002	**Other plant parts**		
Years	9.921	<0.001	m a.s.l.	11.581	0.001
			Years	10.198	<0.001
			Age	0.030	0.862

Note: Effects tested in the ANOVA are those that showed significant results in a MANOVA, altitude and year for plant species, and altitude, year and bird age for plant parts. – *Þau hrif sem voru prófuð í fervikagreiningunni (ANOVA) eru þau sem gáfu marktæka niðurstöðu í fjölbreytu dreifnigreiningunni (MANOVA). Það voru hæð yfir sjó og söfnunarár fyrir plöntutegundir og tegundahópa, og hæð yfir sjó, söfnunarár og aldur fugla fyrir plöntu hluta.*

Betula spp., *Vaccinium* spp., *Salix* spp. and "other species", showed a significant relationship with altitude of sampling site (Table 2). *Betula* spp. and *Vaccinium* spp. were most important at low and medium elevations and disappeared from diet at high elevations, *Salix* spp. showed an opposite pattern (Fig. 8). "Other species", a consortium of some 70 species, peaked at relatively high elevations (Fig. 8).

Changes in plant part composition in rock ptarmigan diet

The importance of the different plant parts in rock ptarmigan diet varied among species. Off *Betula* spp. mainly seeds and catkins were eaten, *Salix* spp. mainly buds and twigs with buds, *E. nigrum* and *Vaccinium* spp. mainly berries, and *D. octopetala* only leaves (Table 4). There was a significant difference in plant parts consumed with respect to rock ptarmigan age (Wilks' lambda=0.982, F=3.305, df=4, p=0.017), collection year (Wilks' lambda=0.518, F=14.943, df=32, p<0.001) and altitude of sampling site (Wilks' lambda=0.952, F=8.376, df=4, p<0.001), but not with sex (Wilks' lambda=0.992, F=1.308, df=4, p=0.266) or age*sex interaction (Wilks' lambda=0.999, F=0.217, df=4, p=0.929). Juveniles consumed more seeds and less woody parts than adults (Table 2). The importance of all plant parts differed significantly among years (Table 2, Fig. 9). Berries were the most important item in six years (2006, 2007, 2010, 2011, 2013 and 2014) and woody parts in three years (2008, 2009 and 2012) (Table 3). The importance of berries in the diet was highest at low altitudes and declined fast above 500 m a.s.l., woody parts showed an opposite pattern and peaked in importance at the highest sampling sites and the importance of "other" plant parts peaked at relatively high elevations (Fig. 8).

Table 3. Annual changes in the importance of plant species or plant species groups and plant parts in rock ptarmigan diet in northeast Iceland autumn 2006–2014. Importance is calculated as proportions by dry biomass. SE is standard error of the mean. – *3. tafla. Breytingar á milli ára á vægi plöntutegunda og tegundahópa og plöntuhluta í fæðu rjúpu á Norðausturlandi 2006–2014. Vægi einstakra þátta er reiknað sem hlutfall þurrefnis. SE er staðalskekkja meðaltals.*

	2006	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**All grps**
n=	**48**	**71**	**65**	**73**	**83**	**86**	**79**	**86**	**88**	**679**
Plant species or species groups										
***Betula* spp.**										
Mean % ± SE	12±3	7±2	59±3	54±3	27±3	15±3	8±2	22±3	6±2	23±1
Min – max %	0–80	0–59	0–100	0–100	0–100	0–99	0–81	0–93	0–84	0–100
***Salix* spp.**										
Mean % ± SE	18±3	32±4	9±2	12±2	16±3	17±3	27±3	12±2	34±4	20±1
Min – max %	0–77	0–100	0–62	0–66	0–86	0–95	0–100	0–91	0–100	0–100
***Vaccinium* spp.**										
Mean % ± SE	11±3	13±3	16±3	23±3	28±3	12±3	9±2	27±4	27±4	19±1
Min – max %	0–75	0–100	0–87	0–94	0–100	0–100	0–66	0–100	0–100	0–100
Empetrum nigrum										
Mean % ± SE	26±4	29±4	6±1	4±1	14±2	27±3	17±2	13±2	14±3	16±1
Min – max %	0–100	0–100	0–61	0–44	0–73	0–98	0–96	0–100	0–100	0–100
Dryas octopetala										
Mean % ± SE	23±4	13±2	9±2	2±1	10±2	18±3	21±3	17±2	12±3	14±1
Min – max %	0–97	0–87	0–96	0–41	0–98	0–100	0–100	0–88	0–100	0–100
Other species										
Mean % ± SE	10±3	6±1	0.9±0.2	5±1	5±1	11±2	18±3	9±2	8±1	8±1
Min – max %	0–100	0–49	0–8	0–63	0–56	0–100	0–94	0–88	0–70	0–100
Plant parts										
Fruits										
Mean % ± SE	39±4	42±4	22±3	27±3	40±3	38±3	22±3	37±4	40±4	34±1
Min – max %	0–100	0–100	0–89	0–94	0–100	0–100	0–85	0–100	0–100	0–100
Woody parts										
Mean % ± SE	19±3	35±4	36±3	39±3	29±3	26±3	33±3	16±2	37±4	30±1
Min – max %	0–76	0–99	1–95	1–100	0–88	0–99	0–100	0–93	0–99	0–100
Leaves										
Mean % ± SE	27± 4	17±2	9±2	2±1	16±2	20±3	27±3	24±3	16±3	18±1
Min – max %	0–99	0–94	0–96	0–41	0–98	0–100	0–100	0–88	0–100	0–100
Infructescenses										
Mean % ± SE	11±3	4±1	33±3	31±3	15±2	8±2	9±2	18±3	3±1	14±1
Min – max %	0–76	0–54	0–95	0–91	0–89	0–100	0–79	0–87	0–75	0–100
Other parts										
Mean % ± SE	4±2	3±1	0.2±0.1	0.3±0.1	0.5±0.2	7±2	8±2	4±1	3±1	3.5±0.4
Min – max %	0–88	0–63	0–4	0–5	0–16	0–84	0–81	0–99	0–35	0–99

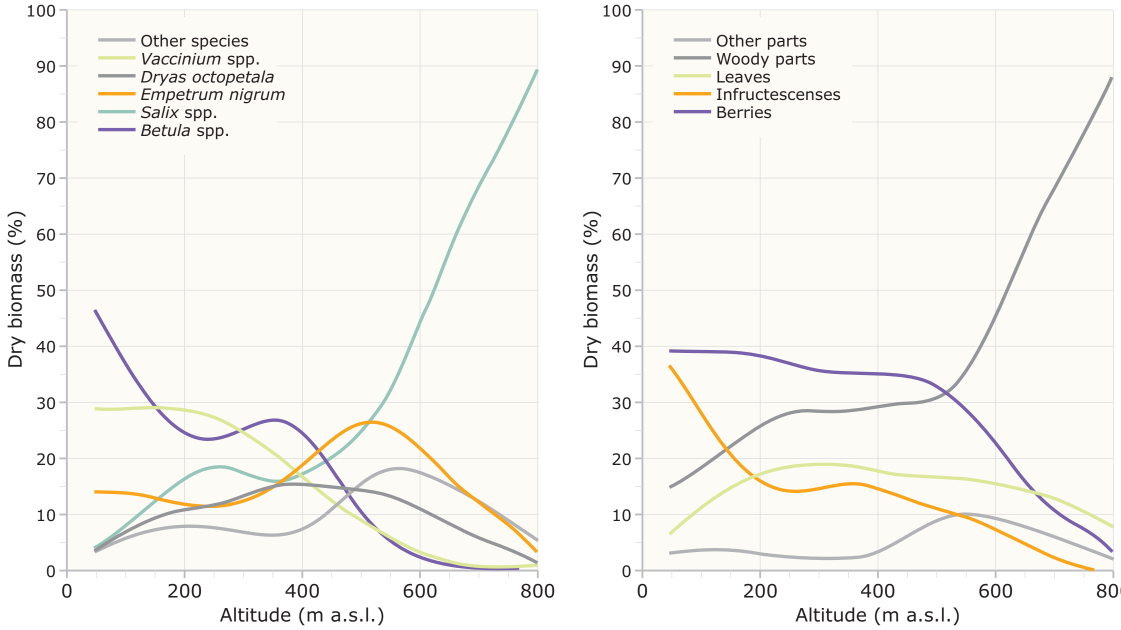

Fig. 8. Changes in the importance (% dry biomass) of six plant taxon and five plant parts in rock ptarmigan diet in northeast Iceland 2006–2014 according to altitude of sampling site. The trajectories were calculated using distance weighted least squares based on analysis of 679 ptarmigan crops. – *8. mynd. Breytingar á vægi (% þurrefni) sex plöntutegunda eða tegundahópa og fimm plöntuhluta í haustfæðu rjúpu á Norðausturlandi 2006–2014 eftir hæð yfir sjó. Ferlarnir eru reiknaðir samkvæmt aðferðinni um vigtuð minnstu fervik og byggja á fæðugreiningum úr 679 rjúpnasörpum.*

Table 4. Comparison of plant parts consumed (% dry biomass based on overall contribution of items) for five main plant groups (nine species) in rock ptarmigan diet (n = 679 crops), northeast Iceland autumn 2006–2014. – *4. tafla. Samanburður á vægi einstakra plöntuhluta (% þurrefni) fimm mikilvægustu plöntutegunda eða plöntuhópa í haustfæðu rjúpu á Norðausturlandi 2006–2014. Vægi er reiknað sem hlutfall af samanlögðu þurrefni fyrir hverja tegund eða tegundahóp.*

	***Betula* spp.**	***Dryas octopetala***	***Salix* spp.**	***Empetrum nigrum***	***Vaccinium* spp.**
Seeds	50.8	0.0	0.0	0.0	0.0
Catkins	42.5	0.0	7.2	0.0	0.0
Leaves	0.4	100.0	1.8	0.2	1.7
Buds	2.7	0.0	13.8	0.0	0.0
Shoots with buds	3.6	0.0	76.3	0.0	1.4
Shoots	0.0	0.0	0.1	0.0	0.0
Shoots with leaves	0.1	0.0	0.8	2.7	0.9
Fruits	0.0	0.0	0.0	97.1	95.9
All groups	100.0	100.0	100.0	100.0	100.0
Dry biomass (g)	408.9	160.6	319.7	200.3	203.5

Note: *Betula* spp. are *B. nana* and *B. pubescens, Salix* spp. are *S. herbacea, S. lanata, S. phylicifolia* and *S. arctica*, and *Vaccinium* spp. are *V. uliginosum* and *V. myrtillus*. The catkins developed the previous summer and will expand and blossom the following spring. – *Betula* spp. eru *B. nana* og *B. pubescens, Salix* spp. eru *S. herbacea, S. lanata, S. phylicifolia* og *S. arctica*, og *Vaccinium* spp. eru *V. uligionosum* og *V. myrtillus.* Reklar (e. catkins) hafa þroskast fyrr um sumarið og blómstra næsta vor.

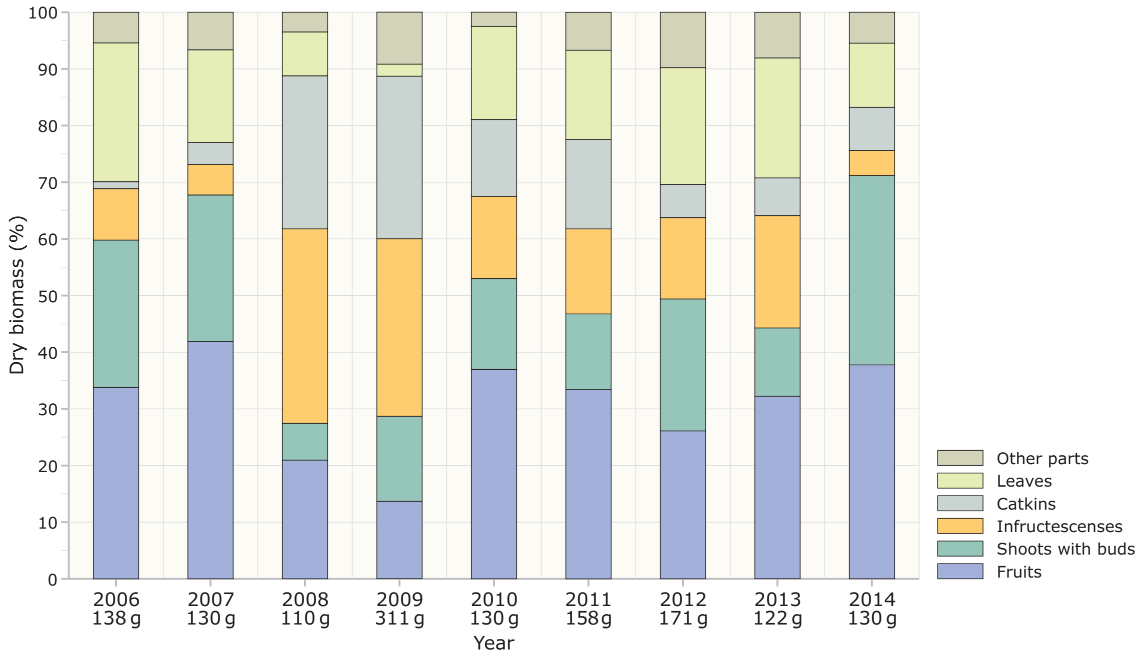

Fig. 9. Annual changes in the importance (% dry biomass) of different plant parts in the food of the rock ptarmigan in north-east Iceland autumn 2006–2014. – *9. mynd. Breytingar á milli ára á vægi (% þurrefni) mismunandi plöntuhluta í haustfæðu rjúpunnar á Norðausturlandi 2006–2014.*

DISCUSSION

Autumn is an important period in the life cycle of the rock ptarmigan, it is the transition time from summer to winter and spans approximately two months (from mid-August to mid-October). The broods have broken up, the birds are growing their winter plumage, forming flocks, displaying, and rearranging their social structures as they move to winter habitats (Weeden 1969). In Iceland, juvenile winter survival determines population change (Gardarsson 1988, Magnússon et al. 2004). Recent studies indicate that the condition of the birds in fall has predictive power for winter survival. This includes factors like body condition and the amount of resources that the birds allocate to immunological defences, as expressed in the size of the spleen. These indices track population change (Stenkewitz et al. 2015). This suggests that the general conditions experienced by the juveniles during their first 3 months of life are vital to their survival. One of these factors is the food and the observed changes in the size of the digestive tract strengthens our belief that this connection between "quality" of the food and future survival is of major importance (Moss 1972, 1974, 1983, Guðmundsson 2015).

The rock ptarmigan population studied in northeast Iceland was catholic in food habits, taking at least 80 species of plants in autumn, but only some 10 species dominated diet and the birds were selective with respect to what parts of the plants they consumed. Similar patterns, where few items dominated the autumn diet, have been observed for rock ptarmigan in other areas (Gelting 1937, Watson 1964, Weeden 1969, Pulliainen 1970, Unander et al. 1985, Emison and White 1988). What determines what species are being used for food? Three things can be mentioned in this context (Emison and White 1988). The first item is what is available. Our observed changes in diet composition along the altitudinal gradient on the study area show this. Pulliainen (1970) stressed the same with respect to local distribution of *Betula tortuosa* a preferred food plant of rock ptarmigan in Finland. The second item has to do with food selection as rock ptarmigan are known to select the highest quality food, species and plant parts, among what is available (Moss 1968, Gardarsson and Moss 1970). The third item are constraints imposed by competition from closely related species such as willow grouse (*Lagopus lagopus*), white-tailed ptarmigan (*Lagopus leucura*) and the sharp-tailed grouse (*Tympanuchus phasianellus*). In areas where these species co-occur they diverge in food habits and the rock ptarmigan specializes in buds, catkins and twigs of *Betula* spp. and when feeding on *Salix* spp. taking parts not used much by the other grouse. This difference in food habits is reflected in bill size, size of the digestive system and gastrolite composition (Weeden 1969, Moss 1974, Thomas 1984). Insular rock ptarmigan populations that have not been exposed to interspecific competition from other grouse for thousands of generations should be more catholic in their food selection than continental populations and one would expect this to be expressed in the anatomy or proportions of the digestive system. High importance of *Salix* spp. in the diet of Icelandic rock ptarmigan as compared with Alaskan birds has been taken as an example of this competitive release (Moss 1974).

Our data does not conform fully to Gardarsson's (1988: 325–328) generalized picture of the diet of the Icelandic rock ptarmigan. Compared with our results *P. viviparum* bulbils and miscellaneous leaves and flowers are over-presented by Gardarsson, and *Betula* spp., *Salix* spp. other than *S. herbacea*, berries and *D. octopetala* are under-presented. The importance of *B. nana* seeds deserves special comment; Gardarsson (1971) listed them as locally important food item in July and August. We found them of major importance in autumn but large between years differences. *Betula* seeds have to our knowledge not been reported as rock ptarmigan food in other studies.

We found significant annual difference in autumn food composition. This could have implications for the population dynamics of our birds. Other researchers on rock ptarmigan food habits have not addressed the year effect in their studies. The strongest effects we found were changes in the importance of *Betula* spp., in particular the seeds of *B. nana*. What determines these annual differences in food selection? Varying importance of some items like berries and seeds may reflect variations in seed and berry production. We do not have any quantitative data on seed production of *B. nana* or production of berries by *E. nigrum* or *Vaccinium* spp. in our study area but we know that this varies greatly between years (for other region see Holm 1994, Selås 2000, Krebs et al. 2009). Observed changes in the browse of woody parts might reflect different intensity of defences mounted by the plants. We do not have any information relating to annual changes in plant defences against herbivores but we recognize this as a potentially important field of studies and hope to be able to use material collected in this project to address such questions.

We did not observe any difference with respect to sex or age in what plant species where selected by the rock ptarmigan as food. Similar observations were made by Pulliainen (1970) and Weeden (1969) for rock ptarmigan. It is only during their first months of life in summer that juveniles distinguish themselves from the adults in food selection (Gardarsson 1971, Weeden 1969). The only age related difference we found had to do with juveniles taking more seeds and less woody parts than adults. This lack of contrast between the age classes is of interest with respect to age related difference in the size of the digestive system but juveniles in our study population had longer guts and caeca and bigger gizzards than adults (Guðmundsson 2015). Moss (1972, 1974) concluded that the size of the digestive system reflects characteristics of the diet. Why is this difference between the two age classes in the size of the digestive tract if the adults and juveniles are more or less eating the same species of plants and if anything the juveniles ingesting less woody parts that are supposedly harder to digest? Could this have anything to do with age and experience of the birds as such, that adults having gone at least once through this cycle of seasonal changes in diet and therefore better able to cope with the harder to digest food items dominating the autumn and winter diet? Moss (1974) has shown that there is a relation between gut size and diet composition of wild caught rock ptarmigan. This will be a logical next thing to study for our data set.

CONCLUSIONS

Our study population utilized a large array of plant species for rock ptarmigan food in autumn but among those selected only some few formed the bulk of the diet, this included *Betula* spp. (buds, catkins, twigs, seeds), *Salix* spp. (buds, twigs, catkins), *D. octopetala* (leaves), *E. nigrum* (berries) and *Vaccinium* spp. (berries). There was a large within region difference in food, more *Salix* spp. was eaten at higher altitudes and more *Betula* spp. and *Vaccinium* spp. at lower altitudes. There was no difference among age and sex groups with respect to species browsed but some tendency for juveniles to take less woody parts and more seeds than adults. There was a large annual difference in food selection exemplified mainly in highly variable importance of *Betula* spp.

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SAMANTEKT Á ÍSLENSKU

Við greindum fæðu rjúpna *Lagopus muta* sem safnað var á 10 daga tímabili frá því seint í september og fram í byrjun október 2006–2014 á Norðausturlandi. Sýnið var 679 rjúpur (48–88 fuglar á ári) og þar af voru 455 ungar og 224 fullorðnar. Til að meta vægi einstakra fæðuþátta var stuðst við annars vegar % af heildarþurrvigt og hins vegar % tíðni miðað við fjölda rjúpna. Samtals voru greindar rúmlega 80 tegundir plantna í fæðunni. Þýðingarmestu tegundirnar voru birki *Betula nana* (27% miðað við þurrvigt, 62% miðað við tíðni), krækiberjalyng *Empetrum nigrum* (14% þurrvigt, 63% tíðni), holtasóley *Dryas octopetala* (11% þurrvigt, 64% tíðni), og grasvíðir *Salix herbacea* (10% þurrvigt, 41% tíðni). Algengustu plöntuhlutar í fæðu voru ber, sprotar smárunna, brum, reklar, fræ og lauf. Munur í fæðu rjúpna bæði með tilliti til plöntutegunda og plöntuhluta sýndi marktæk tengsl við söfnunarár og hæð söfnunarstaðar yfir sjó, en ekki við aldur eða kyn fuglanna eða samvirkni þáttanna (aldur*kyn). Birki og fjalldrapi *Betula* spp. voru ríkjandi fæðuþáttur í 5 ár af 9 og víðitegundir *Salix* spp. í fjögur ár af níu. Birki, fjalldrapi og bláber *Vaccinium* spp. vógu mest í fæðu fugla sem safnað neðarlega til í meðallagi hátt yfir sjó en víðitegundir voru mikilvægastar hjá fuglum sem safnað var tiltölulega hátt yfir sjó. Ber, bæði krækiber *Empetrum nigrum* og bláber, voru ríkjandi plöntuhlutar í haustfæðu í sex ár af níu, en trjákenndir hlutar líkt og sprotar, brum og reklar víðitegunda, birkis og fjalldrapa þrjú ár af níu. Ber voru ríkjandi í fæðu fugla sem safnað var neðarlega til í meðallagi hátt yfir sjó, en þessu var öfugt farið með trjákennda plöntuhluta. Eini marktæki þátturinn tengdur aldri fuglanna var að ungfuglar samanborið við fullorðna fugla átu meira af fræjum og minna af trjákenndum hlutum.

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Appendix 1. Plant species and parts recorded in the food of the rock ptarmigan in northeast Iceland autumn 2006–2014. Also given is the frequency of occurrence and importance as per cent dry biomass calculated based on overall contribution of species. A total of 679 crops were analysed and the total dry biomass of the food was 1399 g. – *1. viðauki. Plöntutegundir og plöntuhlutar sem greindir voru í haustfæðu rjúpu á Norðausturlandi 2006–2014. Vægi er gefið miðað við % tíðni og % þurrvigt. Fæða 679 rjúpna var greind og þurrvigt hennar var samtals 1399 g.*

Family or higher taxon ***Ætt eða hærri flokkunareining***	**Species** ***Tegund***	**Parts** ***Plöntuhluti***	**% by frequency** ***% tíðni***	**% by dry biomass** ***% þurrvigt***
Fungi	*Fungi* spp.	Fr	0.6	<0.1
Bryophyta	*Bryophyta* spp.	L	4.1	<0.1
Lichen	*Cladonia rangiferina*	S	1.3	<0.1
Vascular plants				
Lycopodiaceae	*Lycopodium annotinum*	RS	0.2	<0.1
Selaginellaceae	*Selaginella selaginoides*	RS	8.7	0.3
Equisetaceae	*Equisetum hyemale*	RS	0.2	<0.1
	Equisetum variegatum	RS	0.6	<0.1
	Equisetum spp.	RS	1.3	<0.1
Cupressaceae	*Juniperus communis*	Fr	0.2	<0.1
Salicaceae	*Salix arctica*	Sb	0.6	<0.1
	Salix herbacea	B, C, L, S, Sb, Sl	41.3	9.6
	Salix lanata	B, C, Sb	1.5	1.0
	Salix phylicifolia	B, C, L, Sb, Sl	10.0	5.2
	Salix spp.	B, C, L, S, Sb, Sl	35.1	7.1
Betulaceae	*Betula nana*	B, C, IFr, L, S, Sb, Sl	62.2	26.8
	Betula pubescens	B, C, IFr, Sb	9.1	2.3
	Betula spp.	IFr, Sb	0.7	<0.1
Polygonaceae	*Rumex acetosa*	L	0.2	<0.1
	Rumex acetosella	IFr	0.6	0.4
	Rumex sp.	L	0.2	<0.1
	Oxyria digyna	IFr, L	1.2	<0.1
	Polygonum viviparum	bl, L	27.5	1.2
Plumbaginaceae	*Armeria maritima*	L	22.8	0.5
Caryophyllaceae	*Sagina* sp.	L	0.2	<0.1
	Minuartia sp.	L	0.2	<0.1
	Arenaria norvegica	L	0.2	<0.1
	Cerastium alpinum	Fl, Fr, L	6.5	0.2
	Cerastium cerastoides	Fr, L	0.3	<0.1
	Cerastium sp.	Fl, Fr, IFr, L	3.0	0.1
	Silene acaulis	L	0.2	<0.1
Ranunculaceae	*Thalictrum alpinum*	L	4.0	<0.1
	Ranunculus acris	L	0.2	<0.1
	Ranunculus pygmaeus	L	0.2	<0.1
	Ranunculus spp.	L	0.2	<0.1
Brassicaceae	*Arabidopsis petraea*	Fl, Fr, L	0.9	<0.1
	Cardamine nymanii	L	0.2	<0.1
	Arabis alpina	L	0.6	<0.1
	Capsella bursa-pastoris	Fr	0.2	<0.1
Saxifragaceae	*Saxifraga cespitosa*	L	0.4	<0.1
	Saxifraga oppositifolia	L	4.1	0.1

Family or higher taxon ***Ætt eða hærri flokkunareining***	**Species** ***Tegund***	**Parts** ***Plöntuhluti***	**% by frequency** ***% tíðni***	**% by dry biomass** ***% þurrvigt***
	Saxifraga spp.	L	0.4	<0.1
Rosaceae	*Dryas octopetala*	L	64.1	11.5
	Sibbaldia procumbens	L	2.2	<0.1
	Potentilla crantzii	L	0.2	<0.1
	Alchemilla alpina	L	4.3	0.1
	Alchemilla spp.	IFr, L	0.3	<0.1
Violaceae	*Viola palustris*	L	0.2	<0.1
Onagraceae	*Epilobium anagallidifolium*	L	0.2	<0.1
Pyrolaceae	*Pyrola minor*	L	0.2	<0.1
Ericaceae	*Loiseleuria procumbens*	IFr, L	1.5	<0.1
	Harrimanella hypnoides	Fr, L	7.7	0.1
	Arctostaphylos uva-ursi	Fr	1.2	0.2
	Calluna vulgaris	Fr, L	3.4	<0.1
	Vaccinium myrtillus	L, S, Sb, Sl	8.2	0.4
	Vaccinium uliginosum	L, Sl	15.4	0.3
	Vaccinium sp.	Fl, Fr, L	58.7	13.9
	Empetrum nigrum	Fr, L, Sl	63.2	14.3
Rubiaceae	*Galium normanii*	Fl, IFr, L	7.7	0.1
	Galium verum	IFr, L	2.1	<0.1
Boraginaceae	*Myosotis arvensis*	L	0.2	<0.1
	Myosotis sp.	Fl	0.3	<0.1
Lamiaceae	*Thymus praecox*	L	12.0	0.3
Scrophulariaceae	*Veronica alpina*	L	1.0	<0.1
	Veronica sp.	L	1.0	<0.1
	Euphrasia frigida	IFr	0.2	<0.1
	Rhinanthus minor	Fr	0.2	<0.1
	Bartsia alpina	Fr, L	9.3	0.4
Asteraceae	*Taraxacum* sp.	L	0.9	<0.1
	Hieracium sp.	L	0.2	<0.1
Tofieldiaceae	*Tofieldia pusilla*	IFl, IFr	7.7	0.1
Juncaceae	*Juncus trifidus*	IFr	0.2	<0.1
	Juncus spp.	IFr, Fl	1.0	<0.1
	Luzula spp.	IFr, IFl	0.7	<0.1
Cyperaceae	*Kobresia myosuroides*	L, IFr	1.0	<0.1
	Carex capitata	IFr	2.4	<0.1
	Carex spp.	IFr	17.8	2.7
Poaceae	*Poa pratensis*	IFr, L	0.3	<0.1
	Poa spp.	IFr, L	0.7	<0.1
	Festuca spp.	L	0.2	<0.1
	Poaceae spp.	IFr, L	3.4	<0.1
	Plantae spp.	B, Fr, IFr, IFl, L, S, SI	12.4	0.2

Abbreviations for plant parts: S = shoots; RS = reproductive shoots (strobili) of petridophytes; Sl = shoots with leaves; Sb = woody shoots with buds (mostly current growth); B = buds; L = leaves; Fl = flowers; IFl = inflorescences; Fr = fruits; IFr = infructescences; bl = viviparous bulbils, single and aggregate; C = male catkins. – Skammstafanir fyrir plöntuhluta: S = sprotar; RS = gróöx byrkninga; Sl = sprotar með laufi; Sb = viðarkenndir sprotar með brumi; B = brum; L = lauf; Fl = blóm; IFL = blómskipanir; bl = æxlilaukar, stakir eða í knippum; C = karlkyns reklar.

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