NÍ-14003

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NÍ-14003 Garðabær, desember 2014

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Image on cover: Adult male rock ptarmigan, Northeast Iceland first week of October 2014. Photo Daniel Bergmann.

ISSN 1670-0120

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Skýrsla nr.	Dags, Mán, Ár	Dreifing
NI-14003	Desember 2014	Opin

Heiti skýrslu / Aðal- og undirtitill
Rock ptarmigan *(Lagopus muta)* health studies in Northeast Iceland 2013: morphology and body reserves

Upplag
20

Fjöldi síðna
42

Kort / Mælikvarði

Verknúmer 3128

Höfundar
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Unnið fyrir

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Útdráttur
A research project on the relationship between rock ptarmigan health and population change was started in Northeast Iceland in 2006. This is a progress report on the 2013 data collection, and on morphology and body reserves of the birds. The birds were collected in 6 days (28 September to 3 October). The sample analyzed was 101 birds (60 juveniles, 41 adults). Thirteen persons took part in the expedition and preparation, travel, field work, laboratory work and packing involved 99 man-days. Further laboratory work in Garðabær, drying tissues and organs and extracting their fat, entering and analyzing the data and doing the report involved 3 persons and 75 man-days. The ptarmigan has a sexual size dimorphism, males are larger than females. Structural size of the ptarmigan did not show any significant relation to age, indicating that the juvenile birds had reached full size. Body mass and mass of locomotor muscles was highly correlated with structural size. When controlling for structural size, age but not sex came out as significant in explaining body mass and mass of locomotor muscles, adults were heavier than juveniles. A body condition index calculated by regressing lean dry body mass on structural size showed that adult ptarmigan had larger reserves than juveniles. This index is a measure of protein reserves. The other main type of body reserves are fat deposits. Fat reserves did not show any relation with either structural size or age or sex of the birds. The two types of body reserves were correlated, birds with large fat stores also had large protein stores and vice versa. Measurements of size or mass of other body systems gave different patterns. The digestive system, except the gizzard, did not show a relation with structural size but was age related and juveniles had a larger digestive system than adults. This either reflects different energy requirements of the age groups or digestive efficiency. Tissues relating to the lymphoid system showed age relationship, the bursa fabricii was only found in juveniles and the spleen was larger in juveniles than adults. This reflects greater investment in the immune system by juveniles. The adrenal glands of the endocrine system did not show any relation to structural size or age or sex. Adult males had bigger testicles than juveniles and comb size was related to testicles size. This reflects the role of androgen hormones produced in the testis on secondary sexual ornaments like combs.

Lykilorð	Yfirfarið
Rock ptarmigan, morphology, body reserves, healt studies	MH

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1 INTRODUCTION

The rock ptarmigan (*Lagopus muta*) is a common and widespread breeding bird in Iceland. The population shows multi-annual cycles with peaks in numbers approximately every 10 years (Nielsen and Pétursson 1995). Similar cycles have been reported for rock ptarmigan populations in Alaska (Weeden and Theberge 1972), Greenland (Vibe 1967) and Scotland (Watson et al. 2000). It is not known what drives these cycles but predator-prey interactions have been suggested as an explanation for the rock ptarmigan cycle in Iceland (Nielsen 1999) and cyclic weather patterns in Scotland (Watson et al. 2000). Similar population cycles are known for various boreal and arctic herbivore populations, including mammals (Krebs et al. 2001), birds (Moss and Watson 2001) and invertebrates (Myers and Cory 2013). Many scientists believe that such cycles are driven by trophic interactions like plant-herbivore, predator-prey or pathogen-host interactions (Berryman 2002). Such interactions can be complicated (Turchin 2003). Experiments with red grouse (*Lagopus lagopus scoticus*) and nematode infections support the hypothesis that parasites can play an important role in driving population cycles (Hudson et al. 1998). Recent studies from both Scandinavia (Holmstad et al. 2004; 2005) and Scotland (Martínez-Padilla et al. 2014) on parasite-host interactions further strengthen the notion that parasites play a role in grouse cycles.

A study on the health of the rock ptarmigan was initiated in Iceland in 2006. The main question addressed is: what is the relation between the general condition of the birds and population change and do these indexes of health show a delayed density-dependent connection with ptarmigan numbers? The condition factors studied are: morphology, fat and protein reserves, parasite burden, stress levels, genetics, immunological defences and condition of the preen gland and the plumage. The study will cover 12 years (2006 through 2017). The purpose of this report is to describe the 2013 collection of birds, dissections and tissue analysis and do the first cursory analysis of data relating to morphology and energy reserves.

2 STUDY AREA, MATERIAL AND METHODS

2.1 Study area

The study area is centered near Lake Mývatn in Northeast Iceland. The field base and laboratory in 2013 was at the Lake Mývatn Nature Research Station at Skútustaðir (65°34’ N, 17°03’ W), and most of the birds were collected in the highlands east and north of Lake Mývatn (Fig.1).

2.2 Field crew

A total of 13 persons took part in the 2013 expedition. The hunters were Finnur L. Jóhannsson, Friðrik Jónasson, Guðmundur A. Guðmundsson, Haukur Haraldsson, Þorkell L. Þórarinsson and Þorvaldur Þ. Björnsson. Aðalsteinn Ö. Snæþórsson assisted hunters. Alexander Weiss, Aron Guðmundsson, Péter Villanyi and Ute Stenkewitz assisted hunters and worked in the laboratory. Karl Skírnisson and Ólafur K. Nielsen worked in the laboratory. Preparation in Reykjavík involved 2 man-days. Seven team members from Reykjavík arrived to Lake Mývatn on 27 September and three more the following day. Three team members were local people. Birds were collected during 6 days, 28 September to 3 October, involving in total 51 man-days in the field for hunters (31 days) and assistants (20 days) combined. The laboratory operated for 8 days, 29 September to 6 October, involving a total of 32 man-days in the lab. Packing samples, clearing the laboratory and cleaning the facilities was done on the 7th, involving 4 man-days. Travel to and from the study area for team members coming from Reykjavík involved some 10

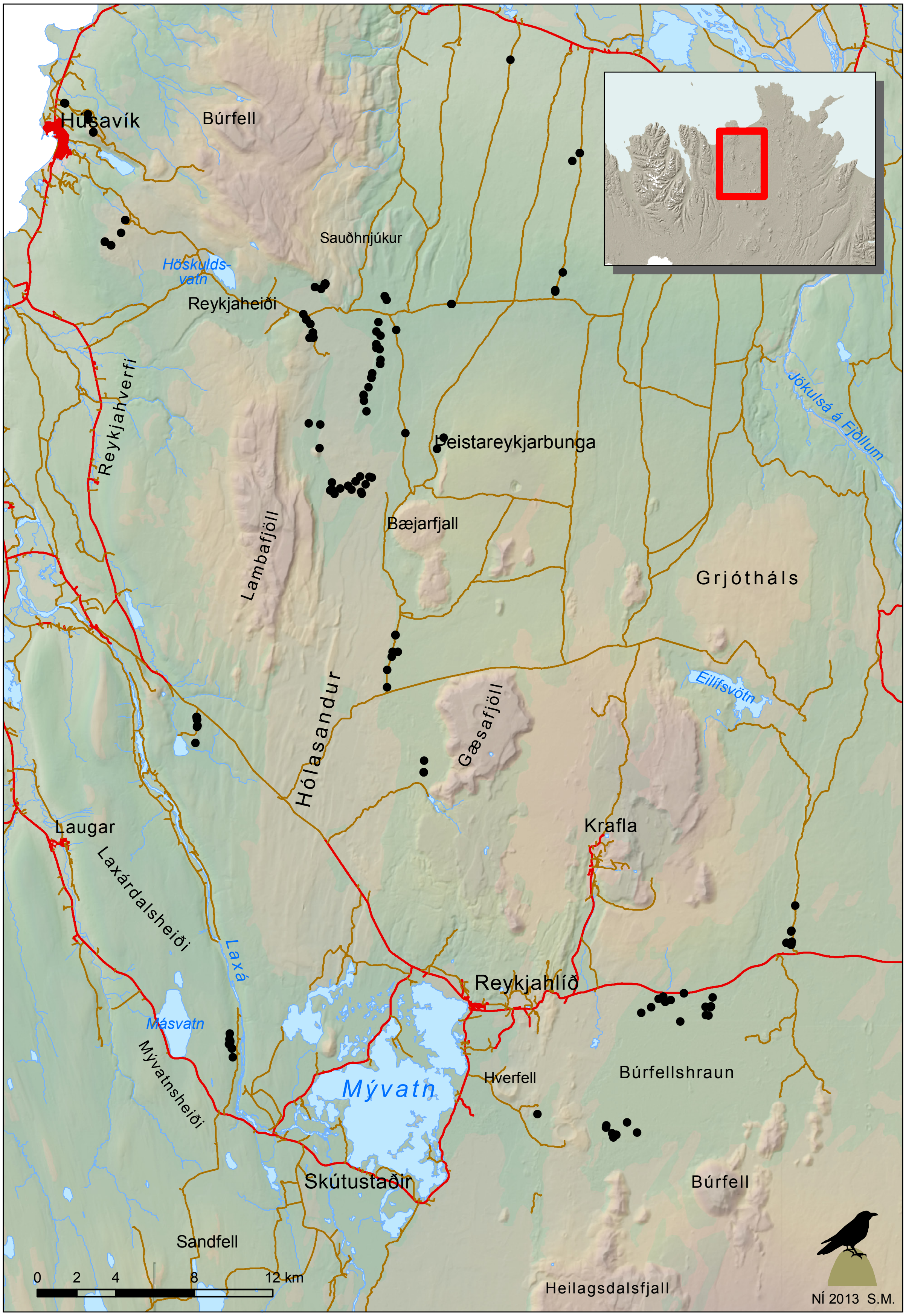

Fig. 1. The rock ptarmigan health study area in Northeast Iceland in 2013. Black dots are collection sites of ptarmigan. A dot can present more than one bird.

man-days. Total the expedition accounted for 99 man-days in preparation, travel, field work, laboratory work and packing.

2.3 Collecting of birds

The rock ptarmigan is a game bird in Iceland and since 1995 38–166 thousand birds have been harvested annually (Environment Agency of Iceland). For this project birds are collected out-of-season under a special permit issued by the Icelandic Institute of Natural History.

A total of 189 birds were collected in 2013, 187 were shot and two were found freshly dead after having flown into fences (Table 1). Here we will only describe methods relating directly to the topic of this report. The annual goal is to sample 100 birds for the health study, 40 adults and 60 juveniles. As juveniles dominate in the autumn population, and the hunters cannot distinguish between adults and juveniles on sight, there is always surplus hunting. The hunt was stopped when the desired number of adults had been reached. Immediately after collecting each bird was individually labelled to the leg with a unique identification number. The hunter or his assistant noted the id-number into a field book along with date and time, coordinates of the sampling site, height above sea level, flock size and number of birds caught from each flock. Coordinates and elevation was measured with a GPS device. A plug, made of absorbing paper, was stuffed down the bird's throat and the carcass then wrapped completely with several layers of absorbing paper and placed in a marked paper bag and the bag then sealed with staples. When at the car the packed birds were stored in Styrofoam boxes with cooling elements and kept at c. 4°C until being processed at the lab.

Table 1. Rock ptarmigan collected for health studies in Northeast Iceland 2013 according to collecting date, sex and age. **Ad** are adult birds, 15 months and older, **juv** are juvenile birds and approximately 3 months old.

Date	Sex	Ad	Juv	Total
28 September	Female	4	14	18
	Male	3	7	10
	Total	**7**	**21**	**28**
29 September	Female	3	22	25
	Male	8	21	29
	Total	**11**	**43**	**54**
30 September	Female	1	4	5
	Male	3	10	13
	Total	**4**	**14**	**18**
1 October	Female	4	16	20
	Male	6	19	25
	Total	**10**	**35**	**45**
2 October	Female	2	7	9
	Male	5	13	18
	Total	**7**	**20**	**27**
3 October	Female	1	8	9
	Male	2	6	8
	Total	**3**	**14**	**17**
	Grand total	**42**	**147**	**189**

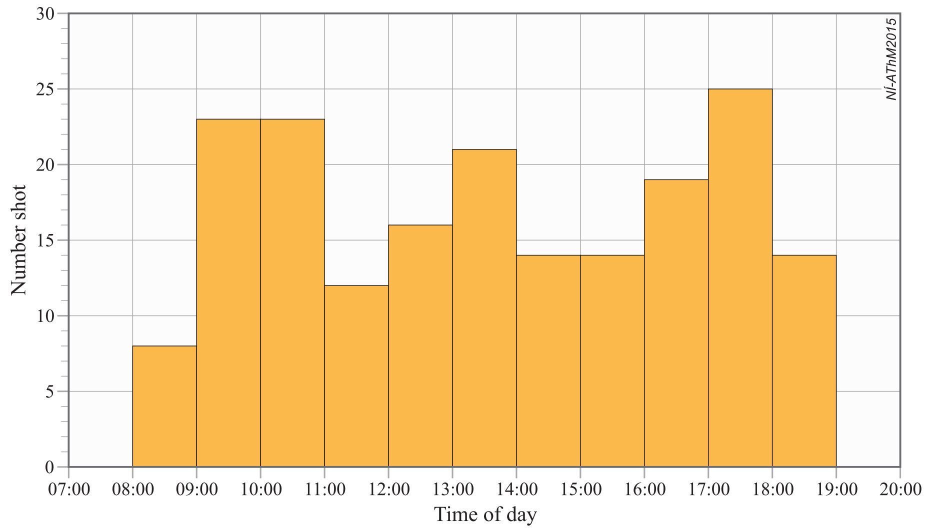

Fig. 2. Time of the day when rock ptarmigan were collected in Northeast Iceland 28 September to 3 October 2013.

The hunters worked in three teams. The number of birds shot each day was highly variable and ranged between 17 to 54 birds (Table 1). This was determined largely by weather but also the number of hunters taking part each day (4 to 6). On the two best days, 29 September and 1 October, a total of 99 birds (52% of total catch) were collected. Temperature was above freezing all hunting days except 28 September. Only one day was without precipitation, 29 September; it snowed a little on the 28th and other days it rained. It was windy on 28 and 29 September, max. gusts more than 10 m/sec, but much calmer the other days.

The hunting team set out around 08:00 each morning. By that time it was light enough to hunt but travel to the hunting areas took approximately 1 hour. The hunters usually stopped hunting at dusk (around 18:00) and arrived back at the field station between 19:30 and 20:30. Ptarmigans were shot between 08:40 and 18:57; most of the birds were shot in the early morning (09:00–11:00), at noon (13:00–14:00) and late in the afternoon (16:00–18:00) (Fig. 2).

2.4 Processing of birds at Lake Mývatn

The field laboratory was at the Mývatn Research Station. Processing of the birds started on 29 September and finished on 6 October (8 days). The birds were divided into two groups: (a) the sample for the health study (101 birds, 41 adults and 60 juveniles); and (b) other birds. The sample for the health study was prioritized in the processing and the necropsies were done on those birds during the first 7 days, other birds were processed on 6 October.

2.4.1 Birds for health studies

The processing of each bird took approximately 40 minutes. Two electronic scales were used to record mass, AND Fx-3000 (precision 0.01 g) and Mettler AJ100 (precision 0.0001 g). To measure size we used vernier calipers (accuracy 0.01 mm), measuring tape (accuracy 1 mm), steel ruler with a zero-stop (accuracy 1 mm) and steel ruler (accuracy 1 mm).

The body mass was measured and eight external morphometrics recorded: (a) wing length, measured on the folded wing with a zero-stop ruler from the carpal joint to the tip of the flattened and straightened wing; (b) head + bill, measured with vernier calipers from the hindmost point of the head to the tip of the bill, the bill was kept in a horizontal position in relation to the head; (c) tarsus length, measured with vernier calipers from the joint between tarsus and toes to the inter-tarsal joint, the toes were bent backward approximately 90° to the tarsus, the tibia was at the same angle; (d) tarsus + mid-toe, measured with a zero stop ruler, the inter-tarsal joint was pressed to the stop and the tarsus and the toes stretched out on the ruler and the distance read was the base of the central claw, to facilitate reading the claw was cut off at the base; (e) circumference, measured with a measuring tape placed round the body immediately behind the wings; (f) width across shoulders, the index finger and thumb of one hand were used to touch the shoulder joints (the humerus head) from the outside and the distance between the fingers was measured with calipers; (g) comb size, the comb was flattened and the length and width measured with a ruler; and (h) wing area, the outlines of the flattened wing were traced on a sheet of paper with the wing extended so that the leading edge formed as straight a line as possible in 90° angle from body axis (Pennycuick 1989). In November 2013 the outlines of the wings were analyzed at Icelandic Forest Research at Mógilsá using a scanner and the WinFOLIA Pro V.2008 software to calculate the wing area.

The bird was skinned and the crop removed. The crop content was isolated and weighed and preserved frozen in a sealed plastic bag. The following body parts, tissues, organs and glands were collected and weighed: (a) right pectoralis major; (b) right pectoralis minor; (c) right leg (minus the tarsus and toes); (d) heart; (e) liver; (f) gizzard; (g) spleen; (h) adrenal glands; (i) testes; (j) ovaries; and (k) bursa Fabricii. All these parts except the spleen, the adrenal glands, the testes, the ovaries and the bursa, were frozen in sealed plastic bags pending further analysis at the laboratory in Garðabær. During the necropsy the following internal measurements were taken: (a) sternum length, measured with vernier calipers from tip of *Spina externa* along center line to *Margo caudalis*; (b) sternum keel height, measured with a ruler pressed against the sternum keel and aligned along the base of the keel, the height from base to top of keel was read at the rostral end; (c) sternum width, measured with a tape from the base of the keel to the tip of the lateral notch, the tape followed the curvature of the sternum; and (d) sternum-coracoid length, measured with vernier calipers from the center line of *Margo caudalis* to the cranial end of the *Coracoideum*, the *Coracoideum* was first cut free from the shoulder joint. Anatomical terms are according to Baumel (1979).

“Structural size” refers to the supporting tissues of the body form, primarily the skeleton. Six size variables were selected to present structural size, they were: head + bill, wing length, tarsus length, tarsus + mid-toe, sternum length and sternum-coracoid length. We used factor 1 from a Principle component analysis (PCA) on those 6 variables to reflect structural size (see part [1] in Appendix 1). So whenever we refer to body size or structural size in the text it is the factor 1 of the PCA.

The entrails were removed and measured according to Leopold (1953); first mesenteries were cut with scissors allowing the intestines 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 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 entrails were collected and preserved frozen.

2.4.2 Other birds

Juvenile birds dominated the catch (78%; Table 1). To get the required number of adult birds (the goal was 40 adults but 41 was analysed) a total of 88 extra birds were collected. These extra birds were all weighed and four external morphometrics were measured as described above: (a) wing length; (b) head + bill; (c) tarsus length; and (d) tarsus + mid-toe. Also, the crop was removed and weighed. Processing each bird took little less than 10 minutes. Twenty birds were frozen in sealed plastic bags and are reserved as stock at the IINH for future reference if necessary. The rest, 68 birds, were discarded, consumed or distributed among the participants.

2.5 Processing of tissues at the laboratory in Garðabær

The frozen samples were transported to the Icelandic Institute of Natural History in Garðabær on 9 October 2013 and kept in a storage freezer at -18°C. During 10 October to 27 November the pectoralis major, pectoralis minor, heart, leg and liver of each bird were thawed, put into an aluminum tray of known mass (Fig. 3) and placed in a drying oven at 55°C (Memmert UFE-800 universal oven). Three samples of each body part were selected for daily monitoring of weight loss. The pieces were kept in the oven until a constant mass was reached; mass was considered constant when the weight loss between days was less than 1%. Thawed gizzards were cut open and emptied before drying in the oven. The gizzard content was weighed separately and oven dried. When dry mass was reached, all tissue samples were weighted along with the tray and then packed in filter paper (Bravilor Bonamat B20, 203/535). The packed samples were washed in petroleum ether with boiling point 40–60°C in a Soxhlet to extract fat. After a minimum of five cycles the samples were taken out of the Soxhlet unless they were still leaking fat (the solvent coloured yellow), if so one or more cycles of washing were added to the process. Each cycle took c. 30 minutes. When out of the Soxhlet the samples were placed in the drying oven at 55°C for 18–20 hours before being weighed to derive lean dry mass (for a detailed description of Soxhlet methods see Piersma et al. 1999). Two scales were used to measure mass an AND Fx-3000 (precision 0.01 g) and an AND HR-120 (precision 0.0001 g).

Three people took part in the laboratory work: Guðmundur A. Guðmundsson operated the Soxhlet, Alexander Weiss weighed, dried and packed the tissues and organs and entered all the data into Microsoft Excel spreadsheets. Ólafur K. Nielsen helped with weighing the samples, monitored the drying process and analyzed the data files and wrote the report. The laboratory work involved 40 man-days and data entering and checking, analyzing and report 35 man-days.

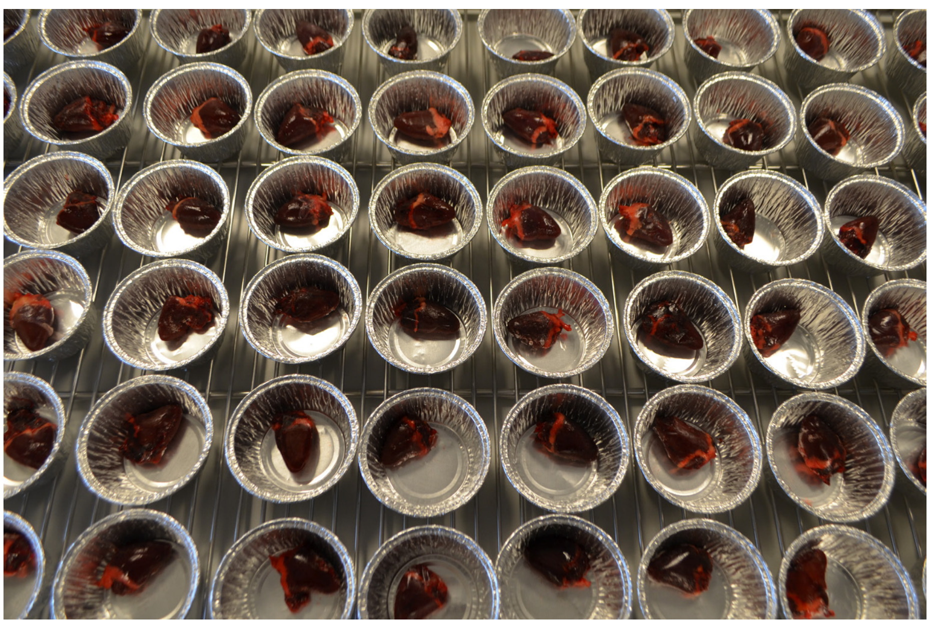

Fig. 3. Dissected rock ptarmigan hearts ready for the drying oven. Photo. Sebastian Wierzba.

2.6 Fat and protein reserves

Total body fat and lean dry body mass were calculated using functions derived from whole carcass analysis done in 2006 on rock ptarmigans from the study area in northeast Iceland (unpublished data). The function for total fat (TF) is:

$$TF = 0.8135 + 3.7476 \times FL + 1.4334 \times FPM + 6.3327 \times FH + 2.2939 \times FPI$$

FL is fat content of legs in g, FPM is fat content of the two pectoralis major in g, FH is fat content of heart in g, and FPI is fat content of the two pectoralis minor in g.

The function for lean dry body mass (LDBM) is:

$$LDBM = 12.5275 + 1.7042 \times LDMPM + 3.0068 \times LDML + 5.5307 \times LDMH$$

Where LDMPM is lean dry mass of both pectoralis major, LDML is the lean dry mass of both legs, and LDMH is the lean dry mass of the heart.

As we only analyzed one pair of pectoralis muscles and one leg in 2013 we multiplied those measurements with 2 before entering the values into the functions.

Lean dry body mass was used as an index of protein reserves. This was done by regressing LDBM on body size and using the residuals as the index. The justification being that LDBM is dependent on body size and needs to be controlled for so different size individuals can be compared.

2.7 Grit analysis

The gizzard content – a matrix of vegetation and grit – was removed and 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 lamp (Lightcraft). 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 of each bird were collected into 9 cm Petri dish, counted and placed in an aluminum cup and dried overnight in the oven. The next day each collection was weighed and sealed in a plastic bag for later analysis on grain morphology.

2.8 Statistical analysis

Statistical analysis of the data was done using the software STATISTICA 12 (StatSoft 2013). The variables were first inspected graphically. General linear models were used to study how the variables related to age and sex of birds. Prior the dependent variable was tested for normality and for homogeneity of variance among groups. Non-parametric tests were used in lieu of General linear models where variance was non-homogenous among groups. The software Flocker Version 1.1 (28.10.2007) was used to calculate statistics for flock size and compare flock size and distribution of flock size among age groups.

Results of statistical tests are in Appendix 1 and are referred to in text below with a number in brackets.

3 RESULTS

3.1 Group size

The largest group observed numbered 11 birds, but most frequently single birds were encountered by the hunters (Fig. 4). Mean group size for the total sample was 2.10 birds (95% confidence limits 1.81–2.51). There was no significant difference in either mean group size [2] (number in brackets refer to numbered parts of Appendix 1) or in distribution of group sizes [3] among

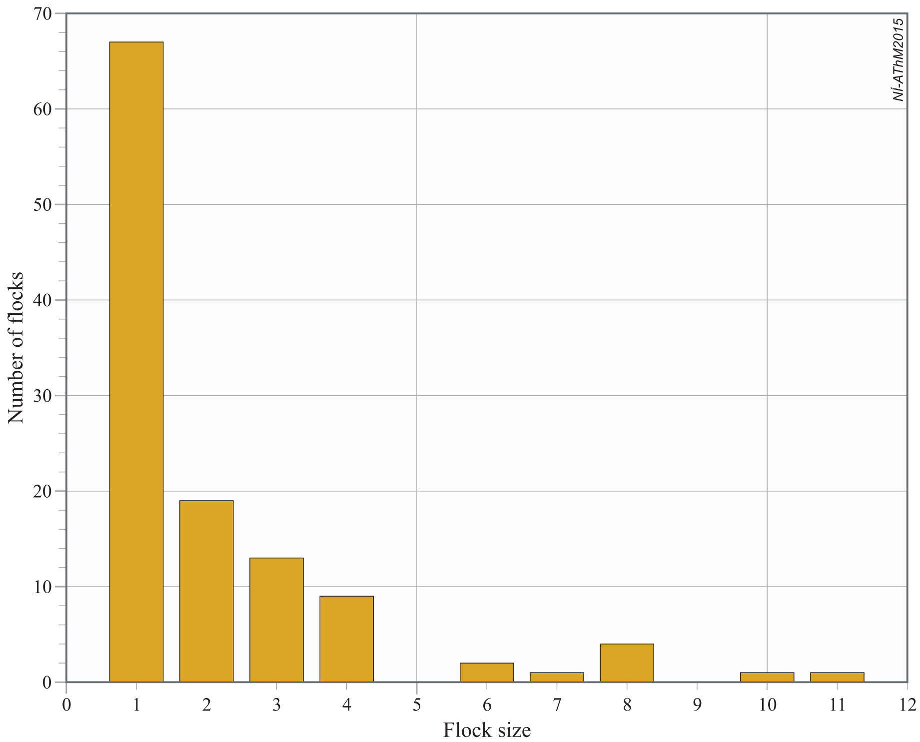

Fig. 4. The frequency distribution of group size of rock ptarmigan collected in Northeast Iceland 28 September to 3 October 2013. Birds were collected from 117 groups. Single birds are included in the data set.

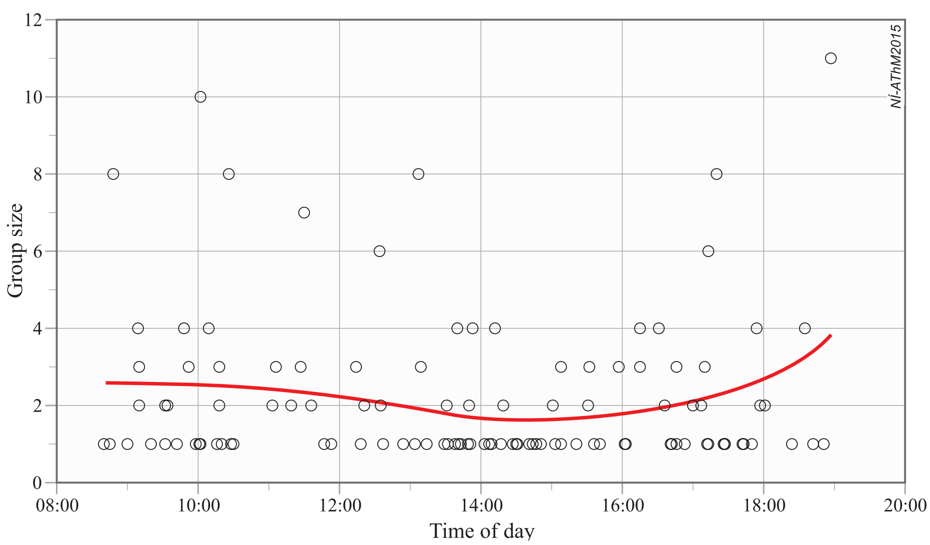

Fig. 5. Group size versus time of the day when encountered for rock ptarmigan collected in Northeast Iceland 28 September to 3 October 2013. Birds were collected from 117 groups. Single birds are included in the data set. The fitted line is calculated using distance weighted least squares.

age groups. There was a tendency for larger groups (> 5 birds) to be encountered early in the morning and late in the afternoon (Fig. 5). Note that these statistics are not an unbiased description of flock size within the study area. They only describe flock size for birds collected. We do not have information for flock size where no birds were collected.

3.2 Morphometrics and structural size

The rock ptarmigan showed sexual size dimorphism, males were larger than females for all 11 size parameters examined (Table 2). This difference was always significant [4]. There was also an age component in size; juveniles had shorter wings, smaller heads and tighter circumferences. The interaction effect sex × age was significant in three cases: juvenile males had shorter wings and smaller wing areas than adult males, but juvenile and adult females did not differ in this respect; and adult females had a higher sternum keel than juvenile females, but adult and juvenile males did not differ in this respect.

Structural size (the PCA factor 1) showed a clear relationship with sex, males were bigger than females, but no age relationship [1].

3.3 Body mass

Two values were used to describe body mass, first intact carcass (gross body mass) and second carcass minus crop content (net body mass) (Table 3). Crop content was newly ingested food stored in the crop. The average difference between the two body weights was 1.0%. Both parameters showed the same relation with age and sex, males were heavier than females and adults heavier than juveniles [5].

Table 2. Structural size parameters for rock ptarmigan collected for health studies in Northeast Iceland 28 September to 3 October 2013. **Ad** are adult birds, 15 months and older, **juv** are juvenile birds and approximately 3 months old. **N** is sample size and **SE** is standard error of the mean.

Parameter	Units	Sex & age	Mean	N	SE	Min	Max
Head + bill	mm	Female ad	52.46	15	0.380	49.94	54.96
		Female juv	51.86	55	0.139	49.25	54.07
		Male ad	54.88	26	0.228	52.24	57.57
		Male juv	54.38	68	0.123	51.87	56.58
		All groups	**53.44**	**164**	**0.131**	**49.25**	**57.57**
Wing length	mm	Female ad	187.9	15	1.05	182	195
		Female juv	189.0	70	0.45	177	195
		Male ad	201.9	27	0.54	197	207
		Male juv	196.7	75	0.42	184	203
		All groups	**193.9**	**187**	**0.45**	**177**	**207**
Wing area	cm^2	Female ad	220.3	15	3.29	203.0	240.5
		Female juv	225.4	30	1.81	207.2	255.3
		Male ad	242.3	26	1.98	220.1	260.5
		Male juv	235.1	30	1.79	219.4	259.3
		All Groups	**231.9**	**101**	**1.29**	**203.0**	**260.5**
Width across shoulders	mm	Female ad	59.1	15	1.13	51	68
		Female juv	57.7	30	0.39	54	63
		Male ad	61.8	25	0.43	57	66
		Male juv	61.6	29	0.49	55	67
		All Groups	**60.1**	**99**	**0.33**	**51**	**68**

Table 2. Continued.

Parameter	Units	Sex & age	Mean	N	SE	Min	Max
Circumference	mm	Female ad	237.0	15	1.94	225	250
		Female juv	234.0	30	1.21	220	250
		Male ad	247.8	24	1.43	235	265
		Male juv	243.8	29	1.13	230	255
		All groups	**240.7**	**98**	**0.87**	**220**	**265**
Tarsus length	mm	Female ad	32.54	15	0.218	30.46	33.82
		Female juv	32.66	68	0.108	30.06	34.10
		Male ad	33.61	27	0.180	32.05	36.02
		Male juv	33.38	73	0.111	31.64	36.67
		All groups	**33.08**	**183**	**0.074**	**30.06**	**36.67**
Tarsus + mid-toe	mm	Female ad	63.4	15	0.52	59	66
		Female juv	63.1	65	0.19	60	66
		Male ad	64.7	26	0.27	62	68
		Male juv	64.2	72	0.21	60	70
		All groups	**63.8**	**178**	**0.13**	**59**	**70**
Sternum length	mm	Female ad	83.39	15	0.552	79.93	87.78
		Female juv	82.89	30	0.251	79.54	85.50
		Male ad	87.31	26	0.350	84.63	92.10
		Male juv	87.32	30	0.336	81.61	91.27
		All groups	**85.42**	**101**	**0.273**	**79.54**	**92.10**
Sternum coracoid length	mm	Female ad	107.86	14	0.649	104.55	112.05
		Female juv	107.49	30	0.301	104.62	110.94
		Male ad	112.28	26	0.432	108.84	117.99
		Male juv	112.44	29	0.393	106.25	116.13
		All groups	**110.25**	**99**	**0.314**	**104.55**	**117.99**
Sternum width	mm	Female ad	43.0	15	0.35	40	45
		Female juv	43.2	30	0.24	40	46
		Male ad	44.3	25	0.27	41	48
		Male juv	43.9	30	0.26	41	48
		All groups	**43.7**	**100**	**0.14**	**40**	**48**
Sternum height	mm	Female ad	23.9	15	0.25	23	26
		Female juv	23.1	30	0.21	21	25
		Male ad	24.6	26	0.21	23	27
		Male juv	24.7	30	0.19	23	27
		All groups	**24.1**	**101**	**0.12**	**21**	**27**

Table 3. Body mass, crop content mass, comb size and mass of spleen, bursa, adrenal glands and testicles of rock ptarmigan collected for health studies in Northeast Iceland 28 September to 3 October 2013. **Ad** are adult birds, 15 months and older, **juv** are juvenile birds and approximately 3 months old. All mass values are wet mass. **N** is sample size and **SE** is standard error of the mean.

Parameter	Units	Sex & age	Mean	N	SE	Min	Max
Gross body mass	g	Female ad	499.2	15	8.10	440	551
		Female juv	476.3	71	4.04	371	550
		Male ad	542.0	27	5.88	487	590
		Male juv	519.5	76	3.78	430	587
		All groups	**504.9**	**189**	**2.96**	**371**	**590**

Table 3. Continued.

Parameter	Units	Sex & age	Mean	N	SE	Min	Max
Net body mass	g	Female ad	492.9	15	7.59	436	551
		Female juv	472.5	71	4.00	362	535
		Male ad	535.1	27	5.46	487	586
		Male juv	514.2	76	3.55	430	583
		All groups	**499.8**	**189**	**2.85**	**362**	**586**
Crop content fresh mass	g	Female ad	6.31	15	2.425	0.00	36.45
		Female juv	3.85	71	0.448	0.00	15.05
		Male ad	6.86	27	1.276	0.00	24.48
		Male juv	5.30	76	0.646	0.00	22.62
		All groups	**5.06**	**189**	**0.410**	**0.00**	**36.45**
Comb length	mm	Female ad	16.1	14	0.29	14	18
		Female juv	15.2	59	0.15	12	18
		Male ad	18.8	26	0.27	16	22
		Male juv	17.2	72	0.11	15	19
		All groups	**16.7**	**171**	**0.13**	**12**	**22**
Comb width	mm	Female ad	5.6	14	0.17	5	7
		Female juv	4.8	59	0.09	3	6
		Male ad	7.5	26	0.20	5	9
		Male juv	6.3	72	0.08	5	8
		All groups	**5.9**	**171**	**0.09**	**3**	**9**
Comb area	mm^2	Female ad	89.6	14	3.32	75.0	119
		Female juv	73.5	59	1.68	36.0	108
		Male ad	142.2	26	4.82	85.0	189
		Male juv	108.7	72	1.75	75.0	144
		All groups	**100.1**	**171**	**2.17**	**36.0**	**189**
Bursa mass	g	Female juv	0.2337	30	0.0113	0.1235	0.3537
		Male juv	0.3171	30	0.0183	0.0488	0.4902
		All groups	**0.2754**	**60**	**0.0120**	**0.0488**	**0.4902**
Spleen mass	g	Female ad	0.0633	15	0.0041	0.0423	0.0916
		Female juv	0.0753	30	0.0060	0.0382	0.1981
		Male ad	0.0597	26	0.0035	0.0287	0.1014
		Male juv	0.0743	30	0.0062	0.0079	0.2176
		All groups	**0.0692**	**101**	**0.0028**	**0.0079**	**0.2176**
Adrenal mass	g	Female ad	0.0430	15	0.0042	0.0172	0.0760
		Female juv	0.0420	30	0.0016	0.0288	0.0630
		Male ad	0.0491	26	0.0017	0.0287	0.0709
		Male juv	0.0471	29	0.0017	0.0321	0.0657
		All groups	**0.0455**	**100**	**0.0011**	**0.0172**	**0.0760**
Testis mass	g	Male ad	0.0526	26	0.0022	0.0340	0.0872
		Male juv	0.0321	29	0.0013	0.0181	0.0447
		All groups	**0.0418**	**55**	**0.0019**	**0.0181**	**0.0872**
Ovary	g	Female ad	0.0994	15	0.0073	0.0587	0.1550
		Female juv	0.0840	29	0.0122	0.0155	0.3537
		All groups	**0.0892**	**44**	**0.0084**	**0.0155**	**0.3537**

3.4 Digestive system: gizzard, gut and liver

Mean lean dry (FFDM) gizzard mass was 3.97 g (Table 4). Gizzard mass was correlated with structural size [6]. Controlling for structural size in the General linear model showed that juvenile ptarmigan had heavier gizzards than adult birds [7].

The gut was measured in three parts: small intestine; rectum; and caecum (Table 5). The length of the small intestine and the caecum was positively correlated, but the length of the rectum was neither correlated with length of small intestine nor length of caecum [8]. The three parts were added to derive gut length (as only one caecum was measured this value was multiplied with 2). There was no correlation between structural size and gut length [9]. Sex did not show any relation to gut length but age did [10], juveniles had longer guts than adults.

Mean fresh mass of liver was 11.69 g but FFDM was 3.06 g (Table 4). Liver mass did not show any relation to structural size [11] nor was there an age or sex related difference [12].

Table 4. Wet mass (WM), fat-free dry mass (FFDM) and fat mass of some organs and tissues of rock ptarmigan collected for health studies in Northeast Iceland, 28 September to 3 October 2013. **Ad** are adult birds, 15 months and older, **juv** are juvenile birds and approximately 3 months old. **N** is sample size and **SE** is standard error of the mean.

Pectoralis major (one)

Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	Water % Means	SE	Range
Female ad	15	53.43	1.125	47.34-63.75	15.15	0.330	13.47-18.40	0.63	0.078	0.25-1.40	70.5	0.168	69.0-71.2
Female juv	30	51.49	0.609	43.87-60.06	14.53	0.167	12.47-16.45	0.65	0.059	0.20-1.44	70.5	0.143	68.8-72.0
Male ad	26	58.96	0.776	52.55-66.75	16.74	0.231	14.79-19.34	0.52	0.035	0.23-1.09	70.7	0.116	69.6-71.7
Male juv	30	57.68	0.760	49.00-68.08	16.36	0.227	13.86-18.79	0.58	0.035	0.32-1.14	70.7	0.138	68.4-71.9
All groups	101	55.54	0.496	43.87-68.08	15.73	0.145	12.47-19.34	0.59	0.025	0.20-1.44	70.6	0.070	68.4-72.0

Pectoralis minor (one)

Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	Water % – Means	SE	Range
Female ad	15	12.99	0.297	10.88-14.51	3.50	0.070	3.05-3.87	0.17	0.013	0.12-0.30	71.7	0.196	69.7-72.5
Female juv	30	11.78	0.159	10.09-13.62	3.12	0.041	2.65-3.58	0.16	0.008	0.07-0.25	72.2	0.103	71.0-73.4
Male ad	26	14.00	0.188	12.24-15.97	3.79	0.052	3.25-4.36	0.18	0.009	0.11-0.28	71.7	0.116	70.2-72.6
Male juv	30	13.04	0.206	10.39-15.52	3.47	0.056	2.80-4.04	0.17	0.008	0.09-0.27	72.1	0.090	71.0-72.9
All groups	101	12.90	0.130	10.09-15.97	3.45	0.036	2.65-4.36	0.17	0.005	0.07-0.30	71.9	0.062	69.7-73.4

Leg (one)

Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	Water % – Means	SE	Range
Female ad	15	23.82	0.415	21.14-26.08	7.44	0.174	6.56-8.53	0.38	0.038	0.15-0.64	67.2	0.372	64.8-69.1
Female juv	30	21.77	0.257	19.11-24.67	6.80	0.124	5.44-8.42	0.35	0.028	0.10-0.76	67.2	0.361	63.5-70.8
Male ad	26	26.39	0.399	22.76-31.19	8.17	0.139	6.90-9.83	0.29	0.015	0.19-0.53	68.0	0.175	66.0-69.6
Male juv	30	24.80	0.343	21.21-29.38	7.72	0.117	6.49-8.82	0.31	0.019	0.13-0.63	67.7	0.227	64.6-69.8
All groups	101	24.16	0.247	19.11-31.19	7.52	0.084	5.44-9.83	0.32	0.012	0.10-0.76	67.5	0.146	63.5-70.8

Table 4. Continued.

Heart

Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	Water % – Means	SE	Range
Female ad	15	10.72	0.203	9.52-11.8	2.54	0.056	2.26-2.95	0.30	0.027	0.16-0.50	73.5	0.230	72.0-75.1
Female juv	30	10.12	0.123	8.68-11.8	2.37	0.042	1.97-3.03	0.34	0.017	0.18-0.56	73.2	0.256	69.5-75.6
Male ad	26	11.38	0.196	9.57-14.0	2.72	0.060	2.17-3.31	0.28	0.019	0.16-0.60	73.6	0.228	71.7-76.4
Male juv	30	11.27	0.146	9.69-13.0	2.67	0.042	2.27-3.21	0.38	0.022	0.19-0.69	73.0	0.177	70.5-74.6
All groups	101	10.88	0.097	8.68-14.0	2.57	0.028	1.97-3.31	0.33	0.011	0.16-0.69	73.3	0.116	69.5-76.4

Gizzard

Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	Water % – Means	SE	Range
Female ad	15	13.56	0.322	10.05-15.11	3.78	0.092	2.78-4.23	0.17	0.027	0.06-0.44	70.9	0.414	66.7-73.1
Female juv	30	14.12	0.277	10.63-16.62	4.00	0.086	3.16-4.94	0.19	0.021	0.05-0.44	70.3	0.368	66.7-73.5
Male ad	26	14.19	0.276	11.58-16.48	3.92	0.071	3.15-4.62	0.12	0.007	0.06-0.20	71.5	0.203	67.9-73.2
Male juv	30	14.46	0.258	11.76-19.46	4.06	0.069	3.30-5.23	0.15	0.011	0.05-0.35	70.8	0.252	67.5-73.1
All groups	101	14.15	0.142	10.05-19.46	3.97	0.040	2.78-5.23	0.16	0.009	0.05-0.44	70.8	0.159	66.7-73.5

Liver

Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	Water % – Means	SE	Range
Female ad	15	11.42	0.575	8.22-15.88	2.94	0.145	1.99-3.80	0.14	0.012	0.09-0.27	73.0	0.404	70.1-75.8
Female juv	30	12.04	0.466	8.60-16.88	3.16	0.123	2.32-4.58	0.15	0.013	0.06-0.38	72.5	0.277	68.0-75.0
Male ad	26	11.15	0.469	8.62-17.74	2.95	0.113	2.28-4.51	0.11	0.011	0.04-0.31	72.5	0.208	70.5-74.6
Male juv	30	11.94	0.339	8.82-18.78	3.11	0.082	2.31-4.63	0.14	0.008	0.06-0.22	72.7	0.239	70.1-74.9
All groups	101	11.69	0.226	8.22-18.78	3.06	0.057	1.99-4.63	0.13	0.006	0.04-0.38	72.6	0.134	68.0-75.8

Table 5. Measurements of the gastrointestinal tract including the small intestines (duodenum, jejunum and ileum), rectum, one cecum and total gut length of rock ptarmigan collected for health studies in Northeast Iceland 28 September to 3 October 2013. Total gut length is the combined length of small intestines plus rectum plus 2 × cecum length. **Ad** are adult birds, 15 months and older, **juv** are juvenile birds and approximately 3 months old. **N** is sample size and **SE** is standard error of the mean.

Parameter	Units	Sex & age	Mean	N	SE	Min	Max
Small intestines length	cm	Female ad	91.9	14	1.19	84.0	100.0
		Female juv	94.6	28	1.00	86.0	110.0
		Male ad	89.3	26	0.63	84.0	99.0
		Male juv	95.9	29	1.09	87.0	106.0
		All groups	**93.2**	**97**	**0.56**	**84.0**	**110.0**
Rectum length	cm	Female ad	11.7	15	0.23	10.0	13.0
		Female juv	12.7	29	1.30	10.0	49.0
		Male ad	12.5	26	1.05	10.0	38.5
		Male juv	11.4	30	0.12	10.0	12.5
		All groups	**12.1**	**100**	**0.47**	**10.0**	**49.0**
Cecum length (only one measured)	cm	Female ad	40.0	15	0.60	35.0	45.0
		Female juv	42.1	29	1.15	12.0	46.5
		Male ad	38.8	26	1.19	11.5	44.0
		Male juv	43.1	30	0.58	35.0	50.5
		All groups	**41.2**	**100**	**0.52**	**11.5**	**50.5**
Total gut length	cm	Female ad	183.6	14	2.01	168.5	195.0
		Female juv	191.8	29	1.63	172.0	209.0
		Male ad	179.4	26	1.43	160.5	192.0
		Male juv	193.6	30	1.96	168.5	213.0
		All groups	**187.9**	**99**	**1.07**	**160.5**	**213.0**

3.5 Vegetative content of crop and gizzard and grit

The mean fresh mass of the crop content was 5.06 g (Table 3). Some crops were empty but the heaviest crop contained 36.45 g of vegetation. Crop content mass did not show any relation to either sex or age of birds (Fig. 6) [13]. There was no obvious diurnal pattern with respect to crop content (Fig. 7).

Gizzard content was separated into two parts, vegetation and grit (Table 6). A priori one would expect that gizzard size (here mass) should show a significant relationship with vegetative content and grit numbers or mass. This was the case for the vegetative content but not for either grit number or mass [14]. So heavier (= bigger) gizzards contained more vegetation than lighter (= smaller) but this was not so for the grit. The vegetative content showed no relation with either age or sex of the birds [15]. This lack of relationship was still apparent when gizzard mass was added to the analysis to control for gizzard size [16].

Ten (10%) of the birds did not have any grit. Mean number of grit per bird was 33.1 (Table 6). Grit number and mass were highly correlated [17]. There was a relation between sex groups, males had more grit than females [18] and higher grit mass [18]. There was also a significant positive relationship between water content of gizzard vegetation and grit mass [19].

3.6 The lymphatic system: bursa and spleen

Two lymphoid tissues were measured, the bursa of Fabricius and the spleen. The bursa is only found in juveniles. Mean fresh bursa mass was 0.275 g (Table 3). The bursa mass was not significantly correlated with the structural size index [20] but the p-value was low ($p = 0.094$) so structural size was included in a General linear model to compare the two sexes. The linear model gave a significant sex related difference in bursa size; males had heavier bursas than females [21]. Mean fresh mass of spleen was 0.069 g (Table 3). It was not correlated with the structural size [22]. Spleen mass was significantly related to the age of the birds, adults had smaller spleens [23]. There was no correlation between bursa mass and spleen mass [24].

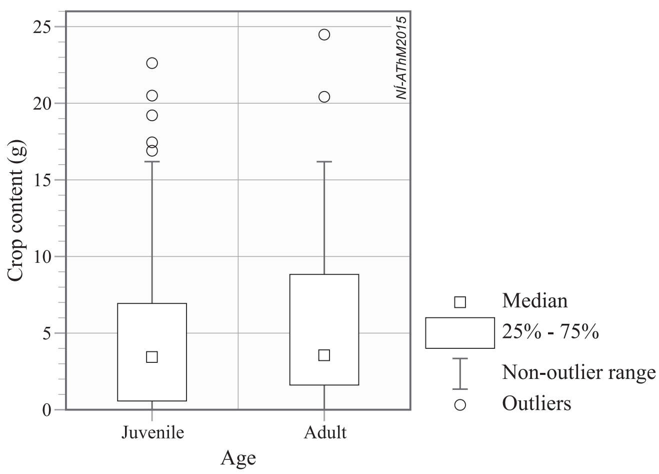

Fig. 6. A box plot for fresh mass (g) of crop content of rock ptarmigan collected in Northeast Iceland 28 September to 3 October 2013.

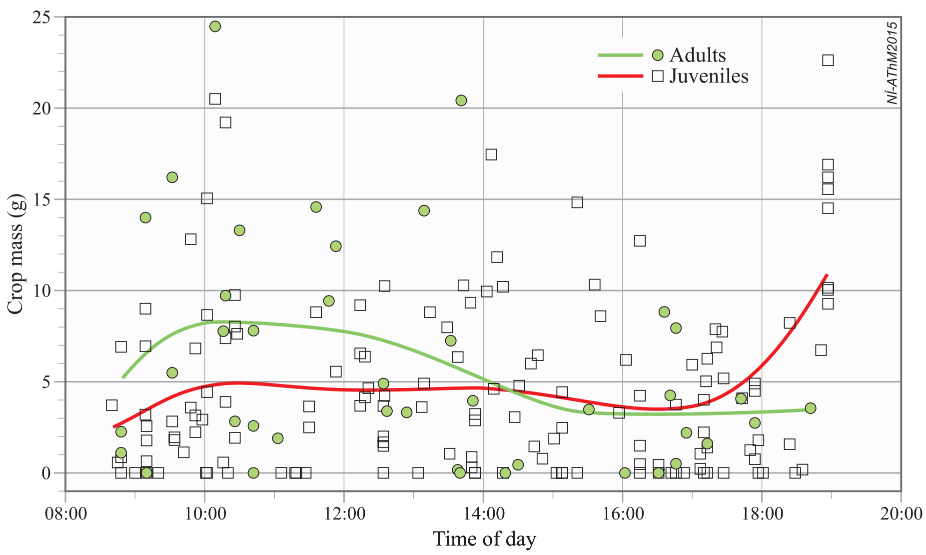

Fig. 7. Fresh mass (g) of crop content versus time of the day when collected for rock ptarmigan in Northeast Iceland 28 September to 3 October 2013. The fitted lines are calculated using distance weighted least squares.

Table 6. Gizzard content – vegetation and grit stones – of rock ptarmigan collected for health studies in Northeast Iceland 28 September to 3 October 2013. **Ad** are adult birds, 15 months and older, **juv** are juvenile birds and approximately 3 months old. **N** is sample size and **SE** is standard error of the mean.

Parameter	Unit	SexAge	Means	N	SE	Min	Max
Gizzard vegetation dry mass	g	Female ad	2.12	15	0.113	0.96	2.63
		Female juv	2.33	30	0.084	1.25	3.22
		Male ad	2.34	26	0.081	1.25	3.19
		Male juv	2.29	30	0.071	1.65	3.40
		All groups	**2.29**	**101**	**0.042**	**0.96**	**3.40**
Grit stones	g	Female ad	0.3547	13	0.1262	0.0192	1.6476
		Female juv	0.1948	28	0.0366	0.0034	0.7101
		Male ad	0.5296	24	0.1365	0.0045	2.2797
		Male juv	0.5833	25	0.1221	0.0028	2.7683
		All groups	**0.4151**	**90**	**0.0560**	**0.0028**	**2.7683**
Grit stones	number	Female ad	29.1	13	8.26	1	88
		Female juv	16.6	28	3.86	1	104
		Male ad	35.2	24	8.07	1	147
		Male juv	51.8	25	13.84	1	354
		All groups	**33.1**	**90**	**4.86**	**1**	**354**

3.7 Comb size, adrenal glands and testes

Both sexes have combs. Two measurements were taken of combs, height and length (Table 3). These two variables multiplied give comb area. Comb area was significantly correlated with structural size [25]. Comb area was compared among sex and age groups while controlling for structural size [26]. Males had significantly larger combs than hens and adults larger than juveniles.

Testis mass was not correlated with structural size [27]. Mean fresh mass of testis was 0.0418 g (Table 3) and significantly different between age groups, adult males had heavier testis than juvenile males [28].

Mean fresh mass of adrenal glands was 0.0455 g (Table 3). Mass of adrenal glands was positively correlated with structural size [29]. There was no age or sex related difference in adrenal gland mass [30].

Testis mass was correlated with both comb area and mass of adrenal glands. Comb area and mass of adrenal glands were not correlated but the p-value was low ($p = 0.067$) and close to the rejection limits ($p = 0.050$) [31].

3.8 Mass and fat content of organs and tissues

Wet mass, fat free dry mass, fat content and percentage water was measured for 6 different tissues and organs: pectoralis major (right); pectoralis minor (right); leg (right); heart; gizzard; and liver (Table 4).

The pattern for the FFDM of the gizzard and the liver has been described above. For the other organs and tissues the same pattern prevailed when controlling for structural size: adults were significantly heavier than juveniles except for heart mass. There was no relation with sex or an interaction effect [32].

Water content of tissues varied (Table 4). It was lowest for leg, mean for all groups 67.5%, and highest for heart, 73.3%. The variables were compared with respect to age and sex of birds and age × sex interactions. Age came out as significant twice, for the pectoralis minor where juveniles had higher water content than adults, and for the gizzard where adults had a higher water content [33].

Fat mass was usually well under a gram for the different organs and tissues measured (Table 4). Most fat was in the pectoralis major (mean for all groups 0.59 g) and the least fat in the liver (0.13 g). Fat content did not show any relation to structural size except for fat in the pectoralis major [34]. Juvenile birds had more fat in gizzard and heart than adults but for other organs or tissues there was no sex or age related variation in fat content [35].

3.9 Body reserves

We use two values as an index of fat and protein reserves. Firstly total calculated fat reserves (Fig. 8), and secondly the residuals from regressing calculated lean dry body mass on body size as an index of protein reserves (Fig. 9) [36]. Total fat deposits did not differ among age or sex groups [37]. Calculated total mean fat deposits were 7.82 g (range 4.40–13.54, SE=0.198) which is only 1.56% of net body mass. The protein index differed significantly among age groups [38]; adults were in better condition than juvenile birds. Fat reserves and protein reserves were correlated [39].

4 DISCUSSIONS

Our study on rock ptarmigan health and population change is set up as a mensurative experiment where we measure in a controlled way parasite-host interaction over a 12 year period (2006–2017) and test predictions relating to such trophic interaction. Doing a manipulative experiment in a system like ours where we are dealing with free-flying and far ranging wild birds is hard to carry out. Our project has already provided new information including 7 parasite species new to science (Skirnisson and Thorarinsdottir 2007; Mironov et al. 2010; Bochkov and Skirnisson 2011), 3 new host records (Skirnisson et al. 2012), and discovered a disease, mange, previously unknown for rock ptarmigan or grouse in general but quite prevalent in the study population.

We choose Northeast Iceland for our research for two reasons. This is the rock ptarmigan heartland in Iceland with extensive breeding and wintering habitats and large number of birds compared with other parts of the country (Guðmundsson 1960). Also, rock ptarmigan have been studied in this region since 1981 (Nielsen 1999) and these studies will continue during the tenure of our project (2006-2017) and contribute to it. This includes information on population size, demographics and gyrfalcon (*Falco rusticolus*) predation.

We choose the first week of October as our reference point for two main reasons. Firstly, to control for seasonal changes in condition and organ size as these factors show a strong seasonal component for many species of birds (Starck 1999; Piersma and Drent 2003) including grouse (Moss 1983). Secondly, to sample the ptarmigan population at the start of the season when its fate is decided but survival rates during fall and winter determine population change of the ptarmigan in Iceland (Magnússon et al. 2004). As we are dealing with free-flying wild birds we cannot select the individuals for our study at random but have to contend with conventional walk-up hunting where the birds are shot sitting or flying when encountered and in areas where they gather at this season. The annual goal is to sample 100 birds, 60 juveniles and 40 adults, for the health study. The hunters cannot distinguish between the two age classes on sight and as

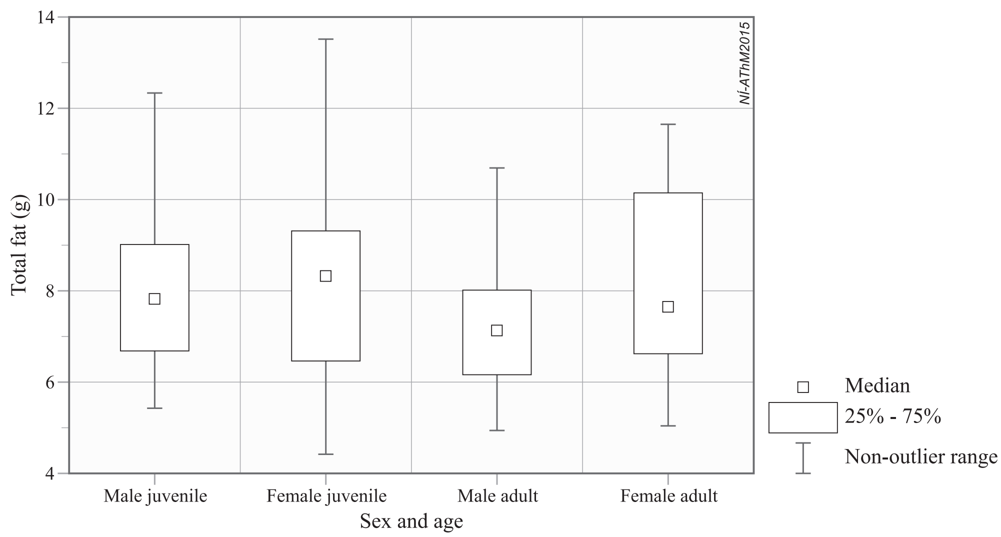

Fig. 8. A box plot for total calculated fat reserves (g) of rock ptarmigan collected in Northeast Iceland 28 September to 3 October 2013. Fat reserves were calculated using a function relating fat content of legs, pectoralis major, pectoralis minor and heart to total fat. Forty-one adult birds were 15 months or older and 60 juvenile birds were approximately 3 months old.

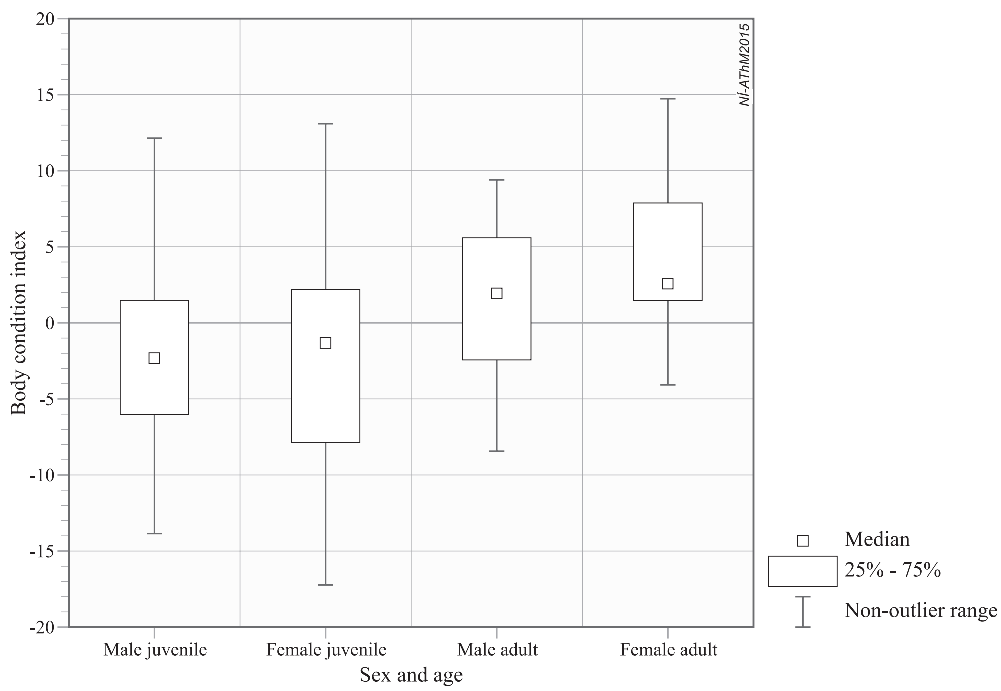

Fig. 9. A box plot for body condition index of rock ptarmigan collected in Northeast Iceland 28 September to 3 October 2013. The values are the residuals from regressing lean dry body mass (LDBM) on body size. Body size was taken as the factor 1 from a Principal component analysis of 6 structural size variables. LDBM was calculated using a function relating it to lean dry mass of pectoralis major, legs and heart. Forty-one adult birds were 15 months or older and 60 juvenile birds were approximately 3 months old.

the age ratio in the rock ptarmigan population on the study area in autumn has ranged between 71 and 83% since 2006 (Nielsen 2014) there is always surplus of juveniles in the catch. The annual goal is to have equal sex ratio in the sample analysed and this is easily achieved for juveniles but not for adults. Part of the ptarmigan population in Northeast Iceland, particularly females, is migratory (Icelandic Institute of Natural History, unpublished ringing and recovery data), and that is the reason males dominate in the sample of adult birds.

The ptarmigan population on our study area is censused in spring and we have used information from 6 census areas to derive a population index. There were peaks in 1986, 1998 and 2010. In 2003 and 2004 no rock ptarmigan hunting was allowed in Iceland and this was followed by a sharp increase in numbers felt in all parts of the country in spring 2004 and 2005. The demographics behind this increase during the non-hunting years were different from what takes place during the "natural" peaks. Our health studies have as of now covered the increase and peak phase of the ptarmigan cycle. The decline that started in 2011 was interrupted by an increase in numbers in spring 2013; this took place both on the study area and in other parts of Iceland. This was unexpected and in many ways is reminiscent of the situation during the non-hunting years. Ptarmigan harvest has been greatly reduced since 2005 and is down from 69 days to 9 days in both 2011 and 2012, further all commerce with ptarmigan and ptarmigan products is prohibited. The reduced harvest levels may be interacting with the natural population cycle.

It took the hunters 7 week days and 42 hunter man-days to collect the desired sample (40 adults and 60 juveniles) in 2012 and 6 week days and 31 hunter-days in 2013. Seven days is the maximum that the hunters from Reykjavík have up to now been able to stay at the site. We are obviously operating close to the limit of our endurance and need to be prepared to increase the collecting effort. This is probably best done by adding more hunters to the team rather than trying to extend the trip with the current crew. The same group of hunters has collected birds for the project since 2006.

We used 6 variables to describe structural size using factor 1 from a Principle component analysis. Structural size was primarily related to sex, males were bigger than females, in both 2012 and 2013. All of those variables except wing length refer to linear measurements of bones. Wing length includes the bones of the manus but most of the interval is primary feathers and feathers are prone to abrasion. Abrasion should not be a problem in autumn as the feathers are freshly grown but the problem should rather be incomplete growth. The wings of some adult and juveniles birds still had primaries growing, for adults these were the two outermost primaries, number 10 or 9, but for juveniles' always the 3rd outermost primary, number 8. This could affect the wing length measurement as primary number 8 is the longest primary on the folded wing and defines one of the two points used for the measurement. This is probably the reason that wing length showed a relation with age, juveniles had shorter wings than adults, the situation was the same in 2012 (Nielsen et al. 2013) and it is a question whether it should be included in the definition of structural size.

Total body mass and the mass of the pectoralis muscles, the leg and the heart were highly correlated with structural size and reflect the apparent sexual size dimorphism of the species. When we compared these mass values among age and sex groups while controlling for structural size sex became non-significant and the main explanatory variable was age, juveniles being lighter than adults. According to this the juvenile birds had reached adult size for all structural variables except wing length at the beginning of October but total body mass and mass of the locomotor musculature and heart was lighter than for adults.

Organs of the digestive system – the gizzard, the gut and the liver – behaved differently compared with the locomotor muscles and the heart in both 2013 and 2012 (Nielsen et al. 2013). These organs, except for the gizzard, did not show any relation with body size. Liver mass did not differ among age and sex groups. Gut length on the other hand showed a clear relation with age but not sex, juveniles had longer guts than adults. Juveniles had significantly larger gizzards than adults in 2013 but not in 2012. These results show that juveniles are allocating more of their resources to the digestive system than adults, this could reflect higher metabolic rate of juvenile birds compared with adults or difference in digestive abilities or different age related energetic needs.

This contrast between juveniles and adults was also apparent for the two endocrine tissues measured. The *Bursa fabricii* is only found in juveniles but both age groups have spleen. In both 2012 and 2013 juveniles had larger spleens than adults. Juveniles obviously invested more than adults in immunological defenses.

Age effect was also apparent in the reproductive system as exemplified by smaller testis in juvenile males compared with adult males in both 2012 and 2013. Testicular androgens, testosterone being the principle androgen, are produced in the testis (King and McLelland 1984). These hormones effect the growth of the deferent ducts and the development of secondary sexual characteristics including plumage and appendages such as wattles and combs, and song and courtship behavior (King and McLelland 1984). Therefore it should not come as a surprise that comb size of rock ptarmigan was correlated with testis size.

Body reserves – metabolizable tissues – are of two form, fat and protein. Fat reserves did not show any relation with structural size or sex or age of the birds. The reserves were not large and on average 8.3 g in 2012 (Nielsen et al. 2013) and 7.8 g in 2013. This is in accordance with what has been found for other populations of rock ptarmigan (Thomas and Popko 1981; Mortensen et al. 1985) and also the willow ptarmigan *Lagopus lagopus* (West and Meng 1968; Thomas 1986). The exception is the rock ptarmigan on Svalbard but those birds lay down fat reserves in autumn (Mortensen et al. 1983). Our index of protein reserves showed a different pattern and there was an age relationship, adults had larger protein reserves than juveniles in both 2012 and 2013. The two energy stores were positively correlated in 2012 and 2013, those birds having large fat reserves also tended to have large protein stores and vice versa.

In summary our 2013 data showed the same general pattern as in 2012 (Nielsen et al. 2013) including a clear sexual size dimorphism size of the different organ systems. The main contrast both years was larger investment by juveniles in the lymphatic system and the digestive system. Juveniles were in worse condition than adults with respect to protein reserves but this was not the case for fat reserves. There was a positive correlation between protein reserves and fat reserves.

5 REFERENCES

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

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

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

Environment Agency of Iceland. *Umhverfisstofnun.* www.ust.is/umhverfisstofnun [07.12.2014]

Guðmundsson, F. 1960. Some reflections on ptarmigan cycles in Iceland. In *Proceedings of the 12th International Ornithological Congress*, p. 259-265. Helsinki.

Holmstad, P.R., O. Holstad, G. Karbol, J.O. Revhaug, E. Schei, V. Vandvik and A. Skorping 2004. Parasite tags in ecological studies of terrestrial hosts: a study on ptarmigan (*Lagopus* spp.) dispersal. *Ornis Fennica* 81: 128-136.

Holmstad, P.R., P.J. Hudson, V. Vandvik and A. Skorping 2005. Can parasites synchronise the population fluctuations of sympatric tetraonids? - Examining some minimum conditions. *Oikos* 109: 429–434.

Hudson, P.J., A.P. Dobson and D. Newborn 1998. Prevention of population cycles by parasite removal. *Science* 282: 2256–2258.

King, A.S. and J. McLelland 1984. *Birds, their Structure and Function.* London: Bailliére Tindall.

Krebs, C.J., S. Boutin and R. Boonstra, editors, 2001. *Ecosystem Dynamics of the Boreal Forest.* Oxford: Oxford University Press.

Leopold, A.S. 1953. Intestinal morphology of gallinaceous birds in relation to food habits. *Journal of Wildlife Management* 17: 197–203.

Magnússon, K.G., J. Brynjarsdóttir and O.K. Nielsen 2004. *Population cycles in rock ptarmigan* Lagopus muta: *modelling and parameter estimation.* Science Institute, University of Iceland, RH-19-2004. Reykjavík: Science Institute.

Martínez-Padilla, J., S. M. Redpath, M. Zeineddine and F. Mougeot 2014. Insights into population ecology from longterm studies of red grouse *Lagopus lagopus scoticus*. *Journal of Animal Ecology* 83: 85-98.

Mironov, S.V., K. Skirnisson, S.T. Thorarinsdottir and O.K. Nielsen 2010. Feather mites (Astigmata: Psoroptidia) parasitising the rock ptarmigan *Lagopus muta* (Montin) (Aves: Galliformes) in Iceland. *Systematic Parasitology* 75: 187-206.

Mortensen, A., E.S. Nordoy and A.S. Blix 1985. Seasonal changes in the body composition of the Norwegian rock ptarmigan *Lagopus mutus*. *Ornis Scandinavica* 16: 25–28.

Mortensen, A., S. Unander, M. Kolstad and A.S. Blix 1983. Seasonal changes in body composition and crop content of Spitzbergen ptarmigan *Lagopus mutus hyperboreus*. *Ornis Scandinavica* 14: 144–148.

Moss, R. 1983. Gut size, body weight, and digestion of winter foods by grouse and ptarmigan. *Condor* 85: 185-193.

Moss, R. and A. Watson 2001. Population cycles in birds of the grouse family (Tetraonidae). *Advances in Ecological Research* 32: 53-111.

Myers, J.H., and J.S. Cory 2013. Population cycles in forest Lepidoptera revisited. *Annual Review of Ecology, Evolution, and Systematics* 44: 565-592.

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

Nielsen, Ó.K. 2014. *[Age ratios in rock ptarmigan harvest autumn 2013]*. Icelandic Institute of Natural History, NÍ-14002. Garðabær: Icelandic Institute of Natural History. In Icelandic.

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

Nielsen, Ó.K., N. de Pelsmaeker and G.A. Guðmundsson 2013. *Rock ptarmigan* (Lagopus muta) *health studies in Northeast Iceland 2012: morphology and body reserves.* Icelandic Instistute of Natural History, NÍ-13001. Garðabær: Icelandic Institute of Natural History.

Pennycuick, C.J. 1989. *Bird Flight Performance: a Practical Calculation Manual.* New York: Oxford University Press.

Piersma, T. and J. Drent 2003. Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution* 18: 228-233.

Piersma, T., G.A. Gudmundsson and K. Lilliendahl 1999. Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. *Physiological and Biochemical Zoology* 72: 405–415.

Skirnisson, K. and S.T. Thorarinsdottir 2007. Two new *Eimeria* species (Protozoa : Eimeriidae) from wild rock ptarmigans, *Lagopus muta islandorum*, in Iceland. *Parasitology Research* 101: 1077-1081.

Skirnisson, K., S.T. Thorarinsdottir and O.K. Nielsen 2012. The parasite fauna of rock ptarmigan *(Lagopus muta)* in Iceland: Prevalence, intensity, and distribution within the host population. *Comparative Parasitology* 79: 44-55.

Starck, J. M. 1999. Phenotypic flexibility of the avian gizzard: Rapid, reversible and repeated chances of organ size in response to changes in dietary fibre content. *Journal of Experimental Biology* 202: 317-3179.

StatSoft 2013. *STATISTICA (data analysis software system), version 12.* www.statsoft.com [viewed 7.12.2014]

Thomas, V.G. 1986. Body condition of willow ptarmigan parasitized by cestodes during winter. *Canadian Journal of Zoology* 64: 251–254.

Thomas, V.G. and R. Popko 1981. Fat and protein reserves of wintering and prebreeding rock ptarmigan from south Hudson Bay. *Canadian Journal of Zoology* 59: 1205–1211.

Turchin, P. 2003. *Complex Population Dynamics: a Theoretical/Empirical Synthesis.* Princeton: Princeton University Press.

Vibe, C. 1967. Arctic animals in relation to climatic fluctuations. *Meddelelser om Grønland* 170: 1-227.

Watson, A., R. Moss and P. Rothery 2000. Weather and synchrony in 10-year population cycles of rock ptarmigan and red grouse in Scotland. *Ecology* 81: 2126–2136.

Weeden, R.B. and J.B. Theberge 1972. The dynamics of a fluctuating population of rock ptarmigan in Alaska. *Proceedings of the International Ornithological Congress* 15: 90-106.

West, G.C. and M.S. Meng 1968. Seasonal changes in body weight and fat and the relation of fatty acid composition to diet in the willow ptarmigan. *Wilson Bulletin* 80: 426–441.

6 APPENDIX

Appendix 1

The results from statistical tests are numbered 1–39 and are referred to in the Result section of the report with the numbers in brackets.

1. Principal component analysis was done using 6 morphological variables, namely wing length, head + bill, tarsus length, tarsus + mid-toe, sternum length and sternum-coracoid length. The data set analyzed was limited to the 101 bird that were dissected. Mean substitution was used for missing values. The factor 1 coordinates of cases from the Principal component analysis was used as an index of structural size. Below are Eigenvalues of the correlation matrix in the first table and factor coordinates of variables in the second table. The first factor was positively correlated with the size variables and explained 72.8% of the total variance and is regarded as describing structural size.

Eigenvalues of correlation matrix, and related statistics

Factor	Eigenvalue	% total – variance	Cumulative Eigenvalue	Cumulative – %
1	4.366	72.8	4.366	72.8
2	0.649	10.8	5.015	83.6
3	0.371	6.2	5.386	89.8
4	0.289	4.8	5.675	94.6
5	0.249	4.1	5.924	98.7
6	0.076	1.3	6.000	100.0

Factor coordinates of the variables, based on correlations

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Wing length	0.831	-0.390	0.137	0.068	0.366	0.014
Head + bill	0.847	-0.241	-0.261	0.343	-0.196	-0.008
Tarsus length	0.805	0.372	-0.404	-0.141	0.175	-0.024
Tars + mid-toe length	0.757	0.532	0.304	0.227	0.004	0.020
Sternum length	0.931	-0.097	0.159	-0.201	-0.144	-0.194
Sternum-coracoid length	0.934	-0.090	0.058	-0.235	-0.159	0.192

General Linear Model was used to compare structural size (the factor 1 from the Principal component analysis) among age and sex groups and for age × sex interaction effect. Standard error of estimate was 1.2813. Sex came out as significant , males were larger than females.

	SS	Degr. of freedom	MS	F	p
Intercept	2.337	1	2.337	1.423	0.236
Sex	253.366	1	253.366	154.323	< 0.001
Age	1.306	1	1.306	0.795	0.375
Sex×Age	0.009	1	0.009	0.005	0.943
Error	159.253	97	1.642		

2. Comparison of mean group size between adults and juveniles. Sample size: adults = 36; juveniles = 95; sample mean: adults = 2.58; juveniles = 2.38; sample standard deviation: adults = 2.27; juveniles = 2.14. Number of bootstrap replications = 2000.

   Bootstrap 2-sample t-test, $t = 0.467$ $p = 0.643$.

3. Comparison of equality of group size distributions.

   Brunner-Munzel test, $p = 0.598$.

4. General linear model was used to compare wing length, head + bill, tarsus length, tarsus + mid-toe length, sternum length, sternum breadth, sternum height, sternum-coracoid length, back, circumference and wing area among age and sex groups and for age × sex interaction effect. Males were always bigger than females. For wing length, head + bill and circumference adults were bigger than juveniles. The interaction effect was significant for wing length and wing area (juvenile males had smaller wings than adult males, but there was no difference between female age groups) and sternum height (adult females were larger than juvenile females, but there was no difference between male age groups).

   Wing length (mm); standard error of estimate was 3.6094.

	SS	Degr. of freedom	MS	F	p
Intercept	4579731	1	4579731	351529	< 0.001
Sex	3578	1	3578	275	< 0.001
Age	130	1	130	10	0.002
Sex×Age	296	1	296	23	< 0.001
Error	2384	183	13		

   Head + bill (mm); standard error of estimate was 1.0914.

	SS	Degr. of freedom	MS	F	p
Intercept	330538.1	1	330538.1	277491.0	< 0.001
Sex	177.0	1	177.0	148.6	< 0.001
Age	8.8	1	8.8	7.4	0.007
Sex×Age	0.1	1	0.1	0.1	0.802
Error	190.6	160	1.2		

   Tarsus length (mm); standard error of estimate was 0.9199.

	SS	Degr. of freedom	MS	F	p
Intercept	132237.0	1	132237.0	156239.0	< 0.001
Sex	23.9	1	23.9	28.2	< 0.001
Age	0.1	1	0.1	0.1	0.775
Sex×Age	0.8	1	0.8	0.9	0.338
Error	151.5	179	0.8		

Tarsus + mid-toe length (mm); standard error of estimate was 1.6630.

	SS	Degr. of freedom	MS	F	p
Intercept	485173.9	1	485173.9	175422.9	< 0.001
Sex	38.7	1	38.7	14.0	< 0.001
Age	4.2	1	4.2	1.5	0.221
Sex×Age	0.4	1	0.4	0.1	0.712
Error	481.2	174	2.8		

Sternum length (mm); standard error of estimate was 1.7486.

	SS	Degr. of freedom	MS	F	p
Intercept	676499.8	1	676499.8	221236.0	< 0.001
Sex	406.3	1	406.3	132.9	< 0.001
Age	1.4	1	1.4	0.5	0.494
Sex×Age	1.5	1	1.5	0.5	0.483
Error	296.6	97	3.1		

Sternum width (mm); standard error of estimate was 1.3565.

	SS	Degr. of freedom	MS	F	p
Intercept	175647.7	1	175647.7	95442.7	< 0.001
Sex	23.5	1	23.5	12.8	0.001
Age	0.1	1	0.1	0.1	0.787
Sex×Age	2.2	1	2.2	1.2	0.275
Error	176.7	96	1.8		

Sternum height (mm); standard error of estimate was 1.0565.

	SS	Degr. of freedom	MS	F	p
Intercept	53992.7	1	53992.7	48368.3	< 0.001
Sex	29.3	1	29.3	26.2	< 0.001
Age	2.9	1	2.9	2.6	0.108
Sex×Age	5.3	1	5.3	4.8	0.031
Error	108.3	97	1.1		

Sternum-coracoid length (mm); standard error of estimate was 2.0580.

	SS	Degr. of freedom	MS	F	p
Intercept	1089784.9	1	1089784.9	257301.9	< 0.001
Sex	494.0	1	494.0	116.6	< 0.001
Age	0.3	1	0.3	0.1	0.803
Sex×Age	1.6	1	1.6	0.4	0.541
Error	402.4	95	4.2		

Width across shoulders (mm); standard error of estimate was 2.7274.

	SS	Degr. of freedom	MS	F	p
Intercept	330594.5	1	330594.5	44440.1	< 0.001
Sex	249.1	1	249.1	33.5	< 0.001
Age	16.6	1	16.6	2.2	0.138
Sex×Age	7.5	1	7.5	1.0	0.318
Error	706.7	95	7.4		

Circumference (mm); standard error of estimate was 0.6706.

	SS	Degr. of freedom	MS	F	p
Intercept	52596.8	1	52596.8	116957.5	< 0.001
Sex	24.0	1	24.0	53.3	< 0.001
Age	2.7	1	2.7	6.1	0.015
Sex×Age	0.1	1	0.1	0.1	0.735
Error	42.3	94	0.4		

Wing area (cm^2); standard error of estimate was 10.3786.

	SS	Degr. of freedom	MS	F	p
Intercept	4959731	1	4959731	46044.1	< 0.001
Sex	5821	1	5821	54.0	< 0.001
Age	26	1	26	0.2	0.622
Sex×Age	888	1	888	8.2	0.005
Error	10449	97	108		

5. General Linear Model was used to compare gross and net body mass among age and sex groups and for age × sex interaction effect. Males were heavier than females and adults heavier than juveniles for both mass values. Net body mass is gross body mass minus crop content.

Gross body m (g); standard error of estimate was 32.9084.

	SS	Degr. of freedom	MS	F	p
Intercept	31689306	1	31689306	29261.6	< 0.001
Sex	56416	1	56416	52.1	< 0.001
Age	15651	1	15651	14.5	< 0.001
Sex×Age	1.4	1	1.4	0.001	0.972
Error	200348	185	1083		

Net body mass (g); standard error of estimate was 31.5953.

	SS	Degr. of freedom	MS	F	p
Intercept	30999359	1	30999359	31053.3	< 0.001
Sex	53813	1	53813	53.9	< 0.001
Age	12987	1	12987	13.0	< 0.001
Sex×Age	1.8	1	1.8	0.002	0.966
Error	184679	185	998		

6. Correlations between structural size and gizzard fat free dry mass. There were no missing values in the data matrix.

   Pearson product-moment correlation coefficient: r = 0.192, n = 101, p = 0.053.

7. General Linear Model was used to compare gizzard fat free dry mass among age and sex groups, for age × sex interaction effect, and controlling for structural size. Standard error of estimate was 0.3930. Juveniles had bigger gizzards than adults.

	SS	Degr. of freedom	MS	F	p
Intercept	1433.58	1	1433.58	9280.86	< 0.001
Structural size	0.80	1	0.80	5.21	0.025
Sex	0.15	1	0.15	0.99	0.323
Age	0.90	1	0.90	5.84	0.018
Sex×Age	0.04	1	0.04	0.23	0.632
Error	14.83	96	0.15		

8. Correlations between small intestines, rectum and caecum. The Pearson product-moment correlation coefficients are given in the table along with sample sizes (n) and p-values. For missing values a pairwise deletion of data points was used.

	Small intestines	Rectum	Caecum
Small intestines	1.000	…	…
	n =99	…	…
	p = ---	…	…
Rectum	0.138	1.000	…
	n = 99	n = 100	…
	p = 0.173	p = ---	…
Caecum	0.493	0.142	1.000
	n = 99	n = 100	n = 100
	p < 0.001	p = 0.157	p = ---

9. Correlations between structural size and gut length (= small intestines + rectum + (2 × cecum)). There were 2 missing values in the data matrix.

   Pearson product-moment correlation coefficient: r = -0.078, n = 99, p = 0.441.

10. General Linear Model was used to compare gut lengths among age and sex groups and for age × sex interaction effect. Standard error of estimate was 8.6424. Juveniles had longer guts than adults.

	SS	Degr. of freedom	MS	F	p
Intercept	3172020	1	3172020	42468.13	< 0.001
Sex	39	1	39	0.52	0.472
Age	2878	1	2878	38.53	< 0.001
Sex×Age	74	1	74	0.99	0.323
Error	7096	95	75		

11. Correlations between structural size and liver fat free dry mass. There were no missing values in the data matrix.

Pearson product-moment correlation coefficient: r = 0.111, n = 101, p = 0.269.

12. Comparison of fat-free mass of livers among sex and age groups. The frequency distribution of liver mass was right skewed and the variance was non-homogeneous. A Kruskal-Wallis ANOVA by Ranks was used to compare the sex and age groups.

Kruskal-Wallis test: H (df = 3, n = 101) = 4.398, p = 0.222.

13. Comparison of wet mass of crop content among age and sex groups. Graphic exploration of crop data indicated little difference between these groups. The frequency distribution of crop content was right skewed and the variance was non-homogeneous among groups. A Kruskal-Wallis ANOVA by Ranks was used to compare the sex and age groups.

Kruskal-Wallis test: H (df = 3, n = 189) = 3.921, p = 0.270.

14. Correlations between fat-free dry mass of gizzard and wet and dry mass of vegetation in gizzard, dry mass of grit stones and grit number. The Pearson product-moment correlation coefficients are given in the table. There were no missing values in the data matrix (n = 101).

	Vegetation content wet mass	**Vegetation content dry mass**	**Grit stone mass**	**Grit stone number**
Gizzard FFDM	0.284	0.369	0.039	0.093
	p = 0.004	p < 0.001	p = 0.702	p = 0.356

15. General linear model was used to compare dry mass of gizzard vegetation among age and sex groups and for age × sex interaction effect. Standard error of estimate was 0.4319. There was no difference with respect to age, sex or interaction.

	SS	**Degr. of freedom**	**MS**	**F**	**p**
Intercept	475.04	1	475.04	2546.32	< 0.001
Sex	0.21	1	0.21	1.12	0.292
Age	0.12	1	0.12	0.64	0.426
Sex×Age	0.42	1	0.42	2.24	0.137
Error	18.10	97	0.19		

16. General linear model was used to compare dry mass of vegetative content of gizzard among age and sex groups and for age × sex interaction effect, while controlling for gizzard size. Fat-free dry mass of gizzard was taken as an index of gizzard size. Standard error of estimate was 0.4051. There was no difference with respect to age, sex or interaction.

	SS	**Degr. of freedom**	**MS**	**F**	**p**
Intercept	0.54	1	0.5381	3.2776	0.073
Gizzard empty FFDM	2.34	1	2.3363	14.2317	< 0.001
Sex	0.07	1	0.0681	0.4151	0.521
Age	0.0001	1	0.0001	0.0003	0.985
Sex×Age	0.33	1	0.3256	1.9835	0.162
Error	15.76	96	0.1642		

17. Correlations between grit mass and grit stone number.

    Pearson product-moment correlation coefficient: r = 0.910, n = 90, p < 0.001.

18. Comparison of grit number and grit mass between age and sex groups. Graphic exploration of data indicated that the main contrast was between the two sex groups. Males had significantly more grit than females but this was just above the rejection limits for grit mass. This was tested using non-parametric Mann-Whitney U Test.

    Grit number:

    Rank sum females = 2004.5, rank sum males = 3146.6, U = -1.981, Z = 0.0475, p = 0.047.

    Grit mass:

    Rank sum females = 2024.0, rank sum males = 3127.0, U = 989.0, Z = -1.8482, p = 0.065.

19. Correlations between water content of gizzard vegetation (calculated as 1 minus the ratio dry mass versus wet mass) and grit number and mass. The Pearson product-moment correlation coefficients are given in the table along with sample size and p-values. There were no missing values in the data matrix. All dissected birds were included in the analysis (n = 101).

	Grit mass	Grit number
% water in gizzard content	0.234	0.155
	n = 101	n = 101
	p = 0.019	p = 0.123

20. Correlations between bursa mass and structural size.

    Pearson product-moment correlation coefficient: r = 0.218, n = 60, p = 0.094.

21. General linear model was used to compare bursa mass among sex groups, while controlling for structural size. Fat-free dry mass of gizzard was taken as an index of gizzard size. Standard error of estimate was 0.0799. Males had heavier bursas than females.

	SS	Degr. of freedom	MS	F	p
Intercept	4.102	1	4.102	642.0	< 0.001
Structural size	0.038	1	0.038	6.0	0.018
Sex	0.118	1	0.118	18.5	< 0.001
Error	0.364	57	0.006		

22. Correlations between spleen mass and structural size. The main contrast in spleen mass is between age groups – juveniles have bigger spleen than adults – therefore three correlations were done, one for the whole data set and the other two according to age.

    Pearson product-moment correlation coefficient (both age groups): r = 0.067, n = 101, p = 0.507.

    Pearson product-moment correlation coefficient (adults): r = 0.073, n = 41, p = 0.649.

    Pearson product-moment correlation coefficient (juveniles): r = 0.132, n = 60, p = 0.315.

23. General Linear Model was used to compare spleen mass among age and sex groups and for age × sex interaction effect. The standard error of estimate was 0.0281. Age was significant and juveniles had heavier spleens than adults.

	SS	Degr. of freedom	MS	F	p
Intercept	0.43209	1	0.43209	548.999	< 0.001
Sex	0.00012	1	0.00012	0.156	0.694
Age	0.00412	1	0.00412	5.233	0.024
Sex×Age	0.00004	1	0.00004	0.052	0.820
Error	0.07634	97	0.00079		

24. Correlations between spleen mass and bursa mass.

Pearson product-moment correlation coefficient: $r = -0.110$, $n = 60$, $p = 0.404$.

25. Correlations between comb area (mm^2) and structural size.

Pearson product-moment correlation coefficient: $r = 0.741$, $n = 97$, $p < 0.001$.

26. General linear model was used to compare comb area among age and sex groups and for age × sex interaction effect while controlling for structural size. Standard error of estimate was 0.1447. Males had bigger combs than females, and adults bigger than juveniles.

	SS	Degr. of freedom	MS	F	p
Intercept	1871.05	1	1871.05	89282.0	< 0.001
Structural size	0.31	1	0.31	14.9	< 0.001
Sex	0.61	1	0.61	29.3	< 0.001
Age	0.73	1	0.73	34.7	< 0.001
Sex×Age	0.03	1	0.03	1.2	0.267
Error	1.93	92	0.02		

27. Correlations between testis mass g and structural size.

Pearson product-moment correlation coefficient: $r = 0.215$, $n = 55$, $p = 0.114$.

28. A t-test was used to compare testis mass among age groups. Adult males had heavier testis than juvenile males.

$t = -8.291$, $df = 53$, $p < 0.001$.

29. Correlations between adrenal mass g and structural size.

Pearson product-moment correlation coefficient: $r = 0. 266$, $n = 100$, $p = 0.008$.

30. General linear model was used to compare adrenal gland mass among age and sex groups and for age × sex interaction effect while controlling for structural size. Standard error of estimate was 0.0103. There was no significant difference among groups or interaction.

	SS	Degr. of freedom	MS	F	p
Intercept	0.18841	1	0.188411	1775.82	< 0.001
Structural size	0.00007	1	0.000066	0.62	0.434
Sex	0.00011	1	0.000106	1.00	0.320
Age	0.00004	1	0.000041	0.38	0.538
Sex×Age	0.00001	1	0.000006	0.05	0.818
Error	0.01008	95	0.000106		

31. Correlations between adrenal gland mass, testis mass and comb area. The Pearson product-moment correlation coefficients (r) are given in the table. For missing values a pairwise deletion of data points was used.

	Adrenal mass	Testis mass	Comb area
Adrenal mass	r = 1.000	…	…
	n = 100	…	…
	p = ---	…	…
Testis mass	r = 0.356	r = 1.0000	…
	n = 55	n = 54	…
	p = 0.008	p = ---	p < 0.001
Comb area	r = 0.187	r = 0.527	r = 1.0000
	n = 96	n = 54	n = 171
	p = 0.067	p < 0.001	p = ---

32. General linear models were used to compare fat free dry mass of pectoralis major, pectoralis minor, leg and heart among age and sex groups and for age × sex interaction effect while controlling for structural size. Adult birds were heavier than juveniles for all variables except heart; neither sex nor age × sex interactions were significant.

Pectoralis major fat free dry mass (FFDM); standard error of estimate 0.8956.

	SS	Degr. of freedom	MS	F	p
Intercept	22862.6	1	22862.6	28499.8	< 0.001
Structural size	49.5	1	49.5	61.7	< 0.001
Sex	0.2	1	0.2	0.2	0.655
Age	3.2	1	3.2	4.0	0.049
Sex×Age	0.4	1	0.4	0.5	0.476
Error	77.0	96	0.8		

Pectoralis minor fat free dry mass; standard error of estimate 0.2225.

	SS	Degr. of freedom	MS	F	p
Intercept	1116.89	1	1116.89	22551.0	< 0.001
Structural size	2.19	1	2.19	44.3	< 0.001
Sex	0.05	1	0.05	1.0	0.332
Age	2.41	1	2.41	48.6	< 0.001
Sex×Age	0.03	1	0.03	0.6	0.452
Error	4.75	96	0.05		

Leg fat free dry mass; standard error of estimate 0.5569.

	SS	Degr. of freedom	MS	F	p
Intercept	5276.2	1	5276.2	17007.9	< 0.001
Structural size	14.4	1	14.4	46.3	< 0.001
Sex	0.3	1	0.3	0.8	0.365
Age	5.3	1	5.3	17.0	< 0.001
Sex×Age	0.2	1	0.2	0.7	0.396
Error	29.8	96	0.3		

Heart fat free dry mass; standard error of estimate 0.2247.

	SS	Degr. of freedom	MS	F	p
Intercept	615.18	1	615.18	12181.2	< 0.001
Structural size	1.21	1	1.21	24.0	< 0.001
Sex	0.02	1	0.02	0.4	0.536
Age	0.18	1	0.18	3.5	0.065
Sex×Age	0.09	1	0.09	1.9	0.175
Error	4.85	96	0.05		

33. General linear models were used to compare water content of pectoralis major, pectoralis minor, leg, gizzard, heart and liver among age and sex groups and for age × sex interaction effect. The only tissues or organs showing any significant differences in water content were the supracoracoid, juveniles had higher water content than adults, and the gizzard, adults had higher water content than juveniles. The variance for both leg and gizzard was non-homogeneous and this could not be remedied with a log-transformation. These two variables were tested using the non-parametric Kruskal-Wallis test. The results were the same as for the GLM, no significant differences in water content of tissues with respect to age and sex.

Pectoralis major % water; standard error of estimate 0.7102.

	SS	Degr. of freedom	MS	F	p
Intercept	464188.99	1	464188.99	920244.01	< 0.001
Sex	0.79	1	0.79	1.56	0.214
Age	0.01	1	0.01	0.01	0.915
Sex×Age	0.10	1	0.10	0.21	0.652
Error	48.93	97	0.50		

Pectoralis minor % water; standard error of estimate 0.5852.

	SS	Degr. of freedom	MS	F	p
Intercept	481449.85	1	481449.85	1405596.61	< 0.001
Sex	0.04	1	0.04	0.10	0.747
Age	5.15	1	5.15	15.03	0.000
Sex×Age	0.06	1	0.06	0.18	0.674
Error	33.22	97	0.34		

Leg % water; standard error of estimate 1.4603.

	SS	Degr. of freedom	MS	F	p
Intercept	424437.6	1	424437.6	199015.2	< 0.001
Sex	7.9	1	7.9	3.7	0.057
Age	0.4	1	0.4	0.2	0.648
Sex×Age	0.6	1	0.6	0.3	0.595
Error	206.9	97	2.1		

Heart % water; standard error of estimate 1.4604.

	SS	Degr. of freedom	MS	F	p
Intercept	500886.7	1	500886.7	375922.9	< 0.001
Sex	0.1	1	0.1	0.1	0.753
Age	5.0	1	5.0	3.8	0.055
Sex×Age	0.9	1	0.9	0.7	0.420
Error	129.2	97	1.3		

Liver % water; standard error of estimate 1.3585.

	SS	Degr. of freedom	MS	F	p
Intercept	491817.7	1	491817.7	266493.0	< 0.001
Sex	0.5	1	0.5	0.3	0.589
Age	0.2	1	0.2	0.1	0.749
Sex×Age	2.6	1	2.6	1.4	0.239
Error	179.0	97	1.8		

Gizzard % water; standard error of estimate 1.5597.

	SS	Degr. of freedom	MS	F	p
Intercept	467736.10	1	467736.10	192281.22	< 0.001
Sex	7.28	1	7.28	2.99	0.087
Age	9.91	1	9.91	4.07	0.046
Sex×Age	0.01	1	0.01	0.01	0.939
Error	235.96	97	2.43		

34. Correlations between structural size and fat content of pectoralis major, pectoralis minor, leg, heart, liver, gizzard, and calculated total fat content. The Pearson product-moment correlation coefficients are given in the table and the p-values. Sample size was 101 in all cases.

	Structural size
Pectoralis minor fat	-0.053 p = 0.602
Pectoralis major fat	0.226 p = 0.023
Leg fat	-0.155 p = 0.123
Heart fat	-0.002 p = 0.983
Liver fat	-0.125 p = 0.211
Gizzard fat	-0.176 p = 0.078
Fat total	-0.067 p = 0.504

35. General linear models were used to compare fat content of pectoralis major, pectoralis minor, leg, gizzard, heart and liver among age and sex groups and for age × sex interaction effect. Structural size as was used in the analysis of pectoral major fat content. Fat content of both heart and gizzard showed a significant relationship with age, juveniles had more fat than adults.

Log-transformed pectoralis major fat (g); standard error of estimate 0.0458.

	SS	Degr. of freedom	MS	F	p
Intercept	2.68419	1	2.68419	1278.67	< 0.001
Structural size	0.00605	1	0.00605	2.88	0.093
Sex	0.00078	1	0.00078	0.37	0.543
Age	0.00428	1	0.00428	2.04	0.157
Sex×Age	0.00038	1	0.00038	0.18	0.671
Error	0.20152	96	0.00210		

Pectoralis minor fat (g); standard error of estimate 0.0463.

	SS	Degr. of freedom	MS	F	p
Intercept	2.69280	1	2.69280	1258.35	< 0.001
Sex	0.00286	1	0.00286	1.34	0.251
Age	0.00529	1	0.00529	2.47	0.119
Sex×Age	0.00036	1	0.00036	0.17	0.683
Error	0.20758	97	0.00214		

Log-transformed leg fat (g); standard error of estimate 0.3822.

	SS	Degr. of freedom	MS	F	p
Intercept	129.748	1	129.748	888.38	< 0.001
Sex	0.515	1	0.515	3.53	0.063
Age	0.041	1	0.041	0.28	0.597
Sex×Age	0.134	1	0.134	0.92	0.341
Error	14.167	97	0.146		

Heart fat (g); standard error of estimate 0.1053.

	SS	Degr. of freedom	MS	F	p
Intercept	9.8929	1	9.893	892.28	< 0.001
Sex	0.0016	1	0.002	0.14	0.709
Age	0.0979	1	0.098	8.83	0.004
Sex×Age	0.0147	1	0.015	1.33	0.252
Error	1.0755	97	0.011		

Liver fat (g); standard error of estimate 0.0572.

	SS	Degr. of freedom	MS	F	p
Intercept	1.6987	1	1.6987	519.21	< 0.001
Sex	0.0102	1	0.0102	3.11	0.081
Age	0.0045	1	0.0045	1.37	0.244
Sex×Age	0.0035	1	0.0035	1.06	0.305
Error	0.3173	97	0.0033		

Log-transformed gizzard fat (g); standard error of estimate 0.4765.

	SS	Degr. of freedom	MS	F	p
Intercept	362.105	1	362.105	1595.131	< 0.001
Sex	0.672	1	0.672	2.961	0.088
Age	0.969	1	0.969	4.268	0.042
Sex×Age	0.018	1	0.018	0.081	0.776
Error	22.020	97	0.227		

36. Regression of total lean dry body mass on structural size. Adjusted $R^2 = 0.610$, $F_{1,99} = 157.30$, $p < 0.001$.

	b×	SE of b×	b	SE of b	t(99)	p
Intercept			125.627	0.675	186.01	< 0.001
Structural size	0.783	0.0625	4.119	0.328	12.54	< 0.001

37. General linear model was used to compare calculated total fat reserves among age and sex groups and for age × sex interaction effect. None of the explanatory variables showed a significant relationship with total fat content.

Calculated total fat reserves (g); standard error of estimate 1.9716.

	SS	Degr. of freedom	MS	F	p
Intercept	5722.77	1	5722.77	1472.258	< 0.001
Sex	9.36	1	9.36	2.408	0.124
Age	3.73	1	3.73	0.959	0.330
Sex×Age	4.06	1	4.06	1.045	0.309
Error	377.05	97	3.89		

38. General linear model was used to compare a body condition index based on lean dry body mass among age and sex groups and for age × sex interaction effect. Age showed a significant relationship with body condition, adults scored higher than juveniles.

Body condition index (g); standard error of estimate 6.4438.

	SS	Degr. of freedom	MS	F	p
Intercept	32.1	1	32.1	0.773	0.381
Sex	39.4	1	39.4	0.948	0.333
Age	522.3	1	522.3	12.578	0.001
Sex×Age	39.5	1	39.5	0.952	0.332
Error	4027.7	97	41.5		

39. Correlations between total fat reserves and protein reserves.

Pearson product-moment correlation coefficient: $r = 0.590$, $n = 101$, $p < 0.001$.