

Rock ptarmigan (Lagopus muta) health studies in Northeast Iceland 2012: morphology and body reserves

Ólafur K. Nielsen, Nicolas de Pelsmaeker and Guðmundur A. Guðmundsson



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Útdráttur

A research project on the relationship between rock ptarmigan health and population change was started in 2006 in Northeast Iceland. This is a progress report on the 2012 cata collection, morphology and body reserves of the birds. The birds were collected in 7 days (30 September to 6 October). The sample analyzed was 100 birds (60 juveniles, 40 adults). Fifteen persons took part in the expedition to the northeast, and preparation, travel, field work, laboratory work and packing involved 116 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 5 persons and 110 man-days. The ptarmigan is sexually size dimorphic, males are larger than females. Structural size in our sample 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. This has implication for body condition as the locomotor muscles form the largest part of the protein reserves of the individual. Accordingly, a body condition index calculated using lean dry body mass and structural size showed age difference, adults had larger reserves than juveniles. The other main type of body reserves are fat deposits. Fat reserves differed from protein reserves by showing no relation with neither structural size nor 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 did not show a relation with body size except for the gizzard. The size of the system and mass of ingesta was age related; juveniles had a bigger 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 testis than juveniles and comb size was related to testis 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, Northeast Iceland	MH

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1 INTRODUCTION

The rock ptarmigan (*Lagopus muta*) is the only grouse species (Tetraonidae) breeding in Iceland. It is common and widespread within the country and highly regarded by the populace both because of its role as the characteristic bird of upland areas and also for being the prime quarry species. The population shows multi-annual cycles with peaks in numbers approximately every 11 years (Nielsen and Pétursson 1995). It is not known what drives these cycles. Recent studies from Scandinavia indicate that parasites could play a role in grouse cycles (Holmstad et al. 2005). For cyclic changes of red grouse (*Lagopus lagopus scoticus*) it has been shown that parasites have an important role in driving the population changes (Hudson et al. 1998). In 2006 a study was initiated in Iceland on the health condition of the rock ptarmigan. 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 relation with rock ptarmigan numbers (expected lag 2-4 years)? The study will cover 12 years (2006 through 2017). The purpose of this report is to describe the 2012 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 was centered on Lake Mývatn in Northeast Iceland. The field base and laboratory 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 15 persons took part in the expedition. The hunters were Daði Lange, Finnur L. Jóhannsson, Friðrik Jónasson, Guðmundur A. Guðmundsson, Halldór W. Stefánsson, Haukur Haraldsson, Þorkell L. Þórarinsson and Þorvaldur Þ. Björnsson. Aðalsteinn Ö. Snæþórsson assisted hunters. Kiesha Pelltier, Maden Le Barh, Nicolas de Pelsmaeker and Ute Stenkewitz assisted hunters or worked in the laboratory. Karl Skírnisson and Ólafur K. Nielsen worked in the laboratory. Four of the personnel were local people and two of them started the collection of birds on 30 September. All personnel from Reykjavík, 10 people, arrived on the 30th, one hunter coming from Egilsstaðir in the East arrived on 1 October. Preparation in Reykjavík involved 4 man-days. Birds were collected during 7 days, 30 September to 6 October, involving a total of 61 man-days in the field for hunters (42 days) and assistants (19 days) combined. The laboratory operated for 9 days, 1 to 9 October, involving a total of 37 man-days in the lab. Packing samples, clearing the laboratory and cleaning the facilities was done on the 10th, involving 4 man-days. Travel to and from the study area for team members coming from Reykjavík and Egilsstaðir involved some 10 man-days. Total the expedition accounted for 116 man-days in preparation, travel, field work, laboratory work and packing.

2.3 Collecting of birds

A total of 254 birds were collected, 253 were shot and one was found freshly dead after having flown into a fence (Table 1). Immediately after collecting each bird was individually labeled 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,

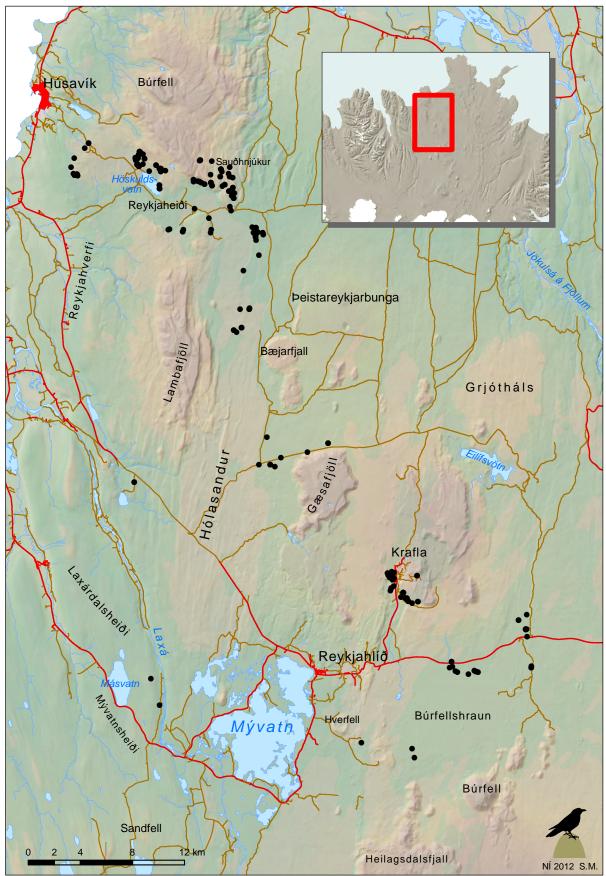


Fig. 1. The study area in Northeast Iceland in 2012. Black dots are collection sites of rock ptarmigan. A dot can present more than one bird.

flock size and number of birds caught from each flock. If the bird defecated the dropping was collected and put into a marked plastic bag. During processing any hippoboscid flies seen were collected if possible and placed into a marked plastic tube filled with 70% ethanol. It was noted in field book how many flies were caught and how many escaped in each case. 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 along with possible samples (scats or hippoboscids) and the bag then sealed with staples. When at the car the packed birds were stored in Styrofoam boxes with cooling elements and kept that way until being processed at the lab.

The hunters worked in three teams. The number of birds shot each day was highly variable and ranged between 13 to 70 birds (Table 1). This was determined largely by weather but also the number of hunters taking part each day (4 to 8). Weather was fair on 30 September, but the conditions were difficult during the first 4 days in October, rain, wet snow or snow and high winds prevailed. Conditions were especially hard on the 3rd and the 4th. On the 5th and the 6th conditions were good, clear skies, little wind and below zero temperatures and on these two last days of hunting 54% of the birds were caught.

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

Date	Sex	Ad	Juv	Total
30 September	Female	2	11	13
	Male	1	10	11
	Total	3	21	24
1 October	Female	0	9	9
	Male	8	13	21
	Total	8	22	30
2 October	Female	2	11	13
	Male	2	22	24
	Total	4	33	37
3 October	Female	0	2	2
	Male	1	10	11
	Total	1	12	13
4 October	Female	0	4	4
	Male	3	7	10
	Total	3	11	14
5 October	Female	4	20	24
	Male	7	39	46
	Total	11	59	70
6 October	Female	1	25	26
	Male	9	31	40
	Total	10	56	66
	Grand total	40	214	254

Table 1. Rock ptarmigan collected for health studies in Northeast Iceland 2012 according to collecting date, sex and age. **Ad** are adult birds, 15 months and older, **juv** are juvenile birds and approximately 3 months old.

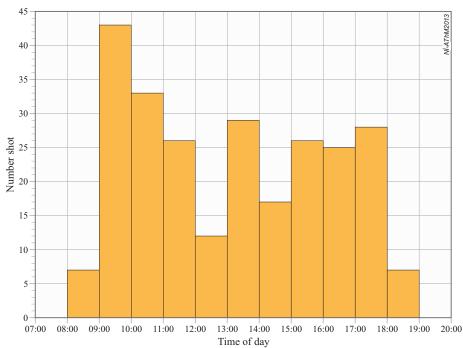


Fig. 2. Time of the day when rock ptarmigan were collected in Northeast Iceland 30 September to 6 October 2012.

were shot between 8:00 and 19:00, with a peak in the early morning (9:00-11:00), low during midday and a moderate rise towards the end of the day (Fig. 2).

2.4 Processing of birds at Lake Mývatn

The field laboratory was at the Lake Mývatn Research Station. Processing of the birds started on 1 October and lasted for 9 days. The birds were divided into two groups: the sample for the health study and other birds. The sample for the health study, 100 birds, was prioritized in the processing and the necropsies were done on those birds during 1 to 7 October. The other birds were processed on 5, 8 and 9 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) or AND HR-120 (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 first step was always to un-wrap the bird and visually search for hippoboscid flies both in the wrappings and on the bird itself. The bird was then vacuumed for approximately one minute with a hand-held Princess® (Type 2755) vacuum cleaner having a 110 cm² filter clipped 14 cm behind the 4×1.5 cm nozzle. The filter along with the bird's wrapping and the filter's content was put in a plastic bag and preserved frozen. The bird was then photographed for reference.

The body mass was measured and eight external morphometrics recorded: (a) <u>wing length</u>, measured on the folded wing with a zero-stop ruler from the carpal joint to the tip of the flattened and straightened wing; (b) <u>head + bill</u>, 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) <u>tarsus length</u>, measured with vernier calipers from the joint between tarsus and toes to the intertarsal joint, the toes were bent backward approximately 90° to the tarsus, the tibia was at the same angle; (d) <u>tarsus + mid-toe</u>, measured with a zero stop ruler, the intertarsal joint was pressed to the stop and the tarsus and the toes stretched out on the ruler and the distance read was between the joint and the base of the central claw, to facilitate reading the claw was cut off at the base; (e) <u>circumference</u>, measured with a measuring tape placed round the body immediately behind the wings; (f) <u>width across shoulders</u>, the index finger and thumb of one hand were used to touch the shoulder joint (the humerus head) from the outside and the distance between the fingers was measured with calipers; (g) <u>comb size</u>, the comb was flattened and the length and width measured with a ruler; and (h) <u>wing area</u>, 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 December 2012 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) <u>right pectoralis major</u>; (b) <u>right pectoralis minor</u>; (c) <u>right leg</u> (minus the tarsus and toes); (d) <u>heart</u>; (e) <u>liver</u>; (f) <u>gizzard</u>; (g) <u>spleen</u>; (h) <u>adrenal glands</u>; (i) <u>testes</u>; and (j) <u>bursa of Fabricius</u>. All these parts except the spleen, the adrenal glands, the testes 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) <u>sternum length</u>, measured with vernier calipers from tip of *Spina externa* along center line to *Margo caudalis*; (b) <u>sternum keel height</u>, 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) <u>sternum width</u>, measured with a tape from the base of the keel to the tip of the lateral notch, the tape follows the curvature of the sternum; and (d) <u>sternum-coracoid length</u>, 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 on those 6 variables to reflect structural size (see paragraph [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 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.

Also collected and preserved for further studies were kidney samples, muscle tissue for DNA analysis, 2 g of large intestine content, preen gland and tail, contour feathers and both wings.

2.4.2 Other birds

Juvenile birds dominated the catch (84%; Table 1). To get the required number of adult birds (40) a total of 154 extra juveniles were collected. These extra birds were all weighed and four external morphometrics were measured as described above: (a) wing length; (b) head + bill; (c)

<u>tarsus length</u>; and (d) <u>tarsus + mid-toe</u>. Also, the crop was removed and weighed. Processing each bird took little less than 10 minutes. Twenty birds were frozen and are reserved as stock for future reference if necessary. The rest, 124 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 Icelandic Institute of Natural History in Garðabær on 12 October 2012 and kept in a storage freezer at -18°C. During 15 October to 8 November the pectoralis major, pectoralis minor, heart, leg and liver of each bird were thawed for 24 hours, put into a aluminum tray of known mass 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 (Fig. 3). When the samples were no longer leaking fat into the petroleum ether and after 3 clear baths in a row they were placed in the drying oven at 55°C for 12 hours before being weighed to derive lean dry mass (for a detailed description of Soxhlet methods see Piersma et al. 1999).

Four people took part in the laboratory work: Guðmundur A. Guðmundsson operated the Soxhlet, Nicolas de Pelsmaeker, Kiesha Pelltier and Mira Lou Braun weighed, dried and packed the tissues and organs. Nicolas, Kiesha and Mira also entered all the data into Microsoft Excel spreadsheets and checked it for errors. Ólafur K. Nielsen analyzed the data files and wrote the report with Nicolas and Guðmundur. The laboratory work involved 60 man-days and data entering and checking, analyzing and report 50 man-days.



Fig. 3. The soxhlet apparatus used for fat extraction from rock ptarmigan tissues in autumn 2012. Photo Guðmundur A. Guðmundsson.

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 ptarmigan from the study area in Northeast Iceland (unpublished data). The function for total fat (TF) is:

 $TF = 0.8135 + 3.7476 \times FL + 1.4334 \times FPMA + 6.3327 \times FH + 2.2939 \times FPMI$

FL is fat content of legs in g, FPMA is fat content of the two pectoralis major in g, FH is fat content of heart in g, and FPMI 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 2012 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 stone analysis

The gizzard content – a matrix of vegetation and grit stones – 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 stones from the vegetation. Grit stones and seeds sank to the bottom but most of the vegetation floated on top. The floating material was then poured into a plastic tray ($35 \times 22 \times 5$ cm) with water added, and searched for grit stones using a 1.3-fold magnifying lamp (Lightcraft). Any grit stones found were 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 stones 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 2012). 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 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

Most frequently single birds were encountered by the hunters, the biggest group numbered 50 birds (Fig. 4). Mean group size for the total sample was 3.93 birds (95% confidence limits 3.26-5.14). There was no significant difference in mean groups size among age groups [2] nor in distribution of group sizes [3]. However there was a tendency for larger groups (>10 birds) to be encountered later in the day (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.

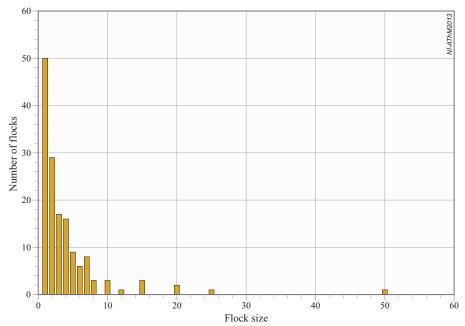


Fig. 4. The frequency distribution of group size of rock ptarmigan collected in Northeast Iceland 30 September to 6 October 2012. Birds were collected from 149 groups; single birds are included in this sample.

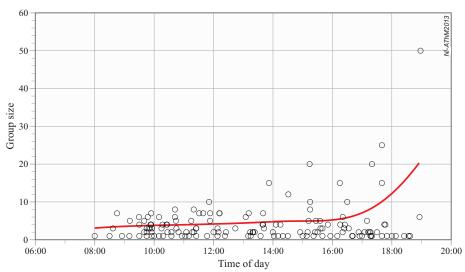


Fig. 5. Group size versus time of the day when encountered for rock ptarmigan collected in Northeast Iceland 30 September to 6 October 2012. Birds were collected from a total of 149 groups. Single birds are included in the data set. The fitted line is calculated using distance weighted least squares.

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 wing length, tighter circumference and smaller wing area. The interaction effect sex \times age was significant in two cases: juvenile males had shorter wing than adult males, but juvenile and adult females did not differ in this respect; and juvenile hens had larger wing areas than adult hens, 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 1.2%. 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 30 September to 6 October 2012. 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	Ν	SE	Min	Max
Head + bill	mm	Female ad	52.16	9	0.228	51.29	53.35
		Female juv	51.96	74	0.125	49.61	54.32
		Male ad	54.91	28	0.201	52.24	56.81
		Male juv	54.27	121	0.115	50.90	56.86
		All groups	53.53	232	0.108	49.61	56.86
Wing length	mm	Female ad	188.4	9	0.88	185	192
		Female juv	188.2	81	0.46	176	200
		Male ad	201.4	31	0.76	190	211
		Male juv	197.2	131	0.35	187	206
		All groups	194.5	252	0.40	176	211
Wing area	cm^2	Female ad	194.3	9	4.97	167.0	211.3
		Female juv	212.7	30	2.39	182.0	235.9
		Male ad	225.0	31	2.17	194.8	251.1
		Male juv	220.7	30	2.68	184.6	252.2
		All Groups	217.3	100	1.59	167.0	252.2
Width across	mm	Female ad	58.9	9	0.56	55	61
shoulders		Female juv	59.1	30	0.47	54	64
		Male ad	62.9	31	0.45	58	68
		Male juv	62.4	30	0.41	57	68
		All Groups	61.3	100	0.30	54	68
Circumference	mm	Female ad	239.4	9	2.12	230	250
		Female juv	234.5	30	1.11	220	245
		Male ad	247.1	31	1.33	235	260
		Male juv	240.5	30	1.30	220	255
		All Groups	240.7	100	0.84	220	260

Parameter	Units	Sex & age	Mean	Ν	SE	Min	Max
Tarsus length	mm	Female ad	32.61	9	0.167	31.83	33.15
		Female juv	32.65	80	0.080	30.45	34.40
		Male ad	33.65	31	0.150	31.15	34.98
		Male juv	33.62	129	0.076	31.31	35.73
		All groups	33.27	249	0.059	30.45	35.73
Tarsus + mid-	mm	Female ad	62.9	9	0.48	60	65
toe		Female juv	63.2	78	0.15	59	66
		Male ad	64.1	31	0.30	60	67
		Male juv	64.5	125	0.15	60	69
		All groups	64.0	243	0.11	59	69
Sternum length	mm	Female ad	83.0	9	0.47	81.42	85.42
		Female juv	83.2	30	0.37	79.47	88.51
		Male ad	87.3	31	0.43	81.83	91.67
		Male juv	86.8	30	0.43	79.49	90.93
		All groups	85.5	100	0.29	79.47	91.67
Sternum cora-	mm	Female ad	107.3	9	0.59	104.81	110.11
coid length		Female juv	107.9	30	0.36	103.86	111.73
		Male ad	112.3	30	0.44	107.56	117.17
		Male juv	111.8	29	0.47	103.23	115.20
		All groups	110.3	98	0.31	103.23	117.17
Sternum width	mm	Female ad	43.13	8	0.398	41	44
		Female juv	43.50	30	0.229	41	46
		Male ad	44.84	31	0.259	41	49
		Male juv	44.90	29	0.201	43	47
		All groups	44.31	98	0.145	41	49
Sternum height	mm	Female ad	22.13	8	0.227	21	23
		Female juv	21.87	30	0.213	19	24
		Male ad	23.23	31	0.201	21	27
		Male juv	23.73	30	0.179	22	27
		All groups	22.88	99	0.132	19	27

Table 2. Continued.

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 30 September to 6 October 2012. **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	Ν	SE	Min	Max
Gross body	g	Female ad	482.2	9	8.5	452	526
mass		Female juv	465.1	81	3.8	380	565
		Male ad	535.0	31	5.1	476	610
		Male juv	510.4	132	3.2	408	590
		All groups	497.9	253	2.7	380	610
Net body mass	g	Female ad	480.1	9	7.7	452	512
		Female juv	458.8	80	3.4	368	514
		Male ad	532.3	31	4.9	474	595
		Male juv	503.3	132	3.0	389	548
		All groups	491.9	252	2.5	368	595

Table 3. Continued.

Parameter	Units	Sex & age	Mean	Ν	SE	Min	Max
Crop content	g	Female ad	2.10	9	1.11	0	8.79
fresh mass		Female juv	7.38	80	1.33	0	71.38
		Male ad	2.71	31	0.70	0	16.16
		Male juv	7.15	132	0.91	0	58.31
		All groups	6.50	252	0.65	0	71.38
Comb length	mm	Female ad	15.56	9	0.338	14	17
		Female juv	15.00	77	0.131	12	17
		Male ad	18.52	31	0.231	17	22
		Male juv	16.65	124	0.091	14	19
		All groups	16.32	241	0.101	12	22
Comb width	mm	Female ad	5.11	9	0.111	5	6
		Female juv	4.69	77	0.075	3	6
		Male ad	6.94	31	0.185	5	9
		Male juv	5.78	124	0.076	4	7
		All groups	5.56	241	0.069	3	9
Comb area	mm^2	Female ad	79.3	9	1.50	70	85
		Female juv	70.6	77	1.45	36	102
		Male ad	128.9	31	4.30	85	189
		Male juv	96.5	124	1.51	56	133
		All groups	91.8	241	1.59	36	189
Bursa mass	g	Female juv	0.250	28	0.0155	0.1016	0.4124
		Male juv	0.258	30	0.0138	0.1463	0.4500
		All groups	0.254	58	0.0103	0.1016	0.4500
Spleen mass	g	Female ad	0.054	9	0.0040	0.0382	0.0719
		Female juv	0.076	30	0.0051	0.0416	0.1722
		Male ad	0.059	31	0.0036	0.0331	0.1125
		Male juv	0.066	30	0.0040	0.0258	0.1260
		All groups	0.066	100	0.0024	0.0258	0.1722
Adrenal mass	g	Female ad	0.0427	9	0.00325	0.0254	0.0582
		Female juv	0.0475	30	0.00232	0.0243	0.0782
		Male ad	0.0470	31	0.00164	0.0242	0.0639
		Male juv	0.0435	30	0.00144	0.0300	0.0628
		All groups	0.0457	100	0.00101	0.0242	0.0782
Testis mass	g	Male ad	0.0511	28	0.00188	0.0335	0.0711
		Male juv	0.0285	26	0.00127	0.0175	0.0410
		All groups	0.0402	54	0.00192	0.0175	0.0711

3.4 Digestive system: gizzard, gut and liver

Mean lean dry (FFDM) gizzard mass was 4.05 g (Table 4). Gizzard mass was correlated with structural size [6]. Controlling for structural size in the General Linear Model showed that there was no sex or age related difference in gizzard mass [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). Sex did not show any relation to gut length but age and age \times sex interaction effect did [9]. Juveniles had longer guts than adults and juvenile females had longer guts than juvenile males but *vice versa* for adults.

Mean fresh mass of liver was 12.23 g but FFDM was 3.20 g (Table 4). Liver mass did not show any relation with structural size [10] nor was there an age or sex related difference [11].

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, 30 September to 6 October 2012. 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) Ν wM SE SE Sex & age FFDM SE Fat SE Water Range Range Range Range Means Means Means % Means Female ad 9 50.75 0.88 47.13-55.91 13.74 0.226 12.51-15.01 0.43 0.047 0.30-0.73 72.07 0.127 71.48-72.69 Female juv 30 50.06 0.67 41.11-56.09 13.24 0.196 10.70-15.39 0.41 0.038 0.19-1.13 72.75 0.157 71.42-76.19 Male ad 31 57.41 0.69 49.98-67.83 15.47 0.171 13.37-17.38 0.52 0.040 0.28-1.42 72.13 0.084 71.26-73.14 Male juv 0.20-0.92 71.04-73.15 30 54.86 1.03 37.58-62.46 14.77 0.291 10.09-17.00 0.42 0.030 72.32 0.100 71.04-76.19 100 53.84 0.53 37.58-67.83 14 44 0.150 10.09-17.38 0.45 0.020 0.19-1.42 72 37 0.067 All groups

Pectoralis minor (one)

Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	water % - Means	SE	Range
Female ad	9	12.58	0.268	11.51-13.74	3.35	0.084	2.91-3.70	0.182	0.0142	0.13-0.26	71.95	0.151	71.20-72.72
Female juv	30	11.67	0.166	9.27-13.50	3.04	0.045	2.42-3.54	0.173	0.0077	0.10-0.27	72.49	0.115	71.31-74.60
Male ad	31	13.53	0.174	11.23-15.14	3.57	0.046	3.01-3.87	0.187	0.0088	0.13-0.36	72.23	0.081	71.14-73.10
Male juv	30	12.56	0.208	9.07-14.40	3.32	0.058	2.39-3.93	0.166	0.0091	0.05-0.25	72.27	0.094	71.21-73.21
All groups	100	12.60	0.122	9.07-15.14	3.31	0.034	2.39-3.93	0.176	0.0047	0.05-0.36	72.29	0.054	71.14-74.60

Leg (one)	Leg (one)												
Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	water % - Means	SE	Range
Female ad	9	22.85	0.37	21.32-24.43	7.13	0.163	6.63-8.19	0.34	0.030	0.21-0.48	67.30	0.686	62.31-69.44
Female juv	30	21.34	0.34	18.66-26.61	6.52	0.114	5.59-7.97	0.35	0.045	0.01-1.28	67.89	0.318	63.24-71.21
Male ad	31	25.59	0.35	21.34-30.82	7.83	0.111	6.70-9.29	0.37	0.035	0.10-1.04	67.98	0.204	65.96-71.28
Male juv	30	23.19	0.36	16.28-26.03	7.06	0.110	4.99-7.96	0.34	0.043	0.09-1.14	68.11	0.275	63.92-71.07
All groups	100	23.35	0.25	16.28-30.82	7.14	0.079	4.99-9.29	0.35	0.022	0.01-1.28	67.93	0.153	62.31-71.28

Table 4. Continued.

Liver													
Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	water % - Means	SE	Range
Female ad	9	11.79	0.54	10.06-15.25	3.07	0.097	2.65-3.40	0.108	0.0303	0.05-0.33	72.85	0.91	68.89-78.75
Female juv	30	12.14	0.40	8.85-17.89	3.15	0.114	2.29-4.68	0.107	0.0142	-0.11-0.24	73.17	0.43	67.82-77.75
Male ad	31	12.46	0.52	9.03-19.35	3.24	0.109	2.51-4.53	0.092	0.0131	-0.10-0.29	72.96	0.40	68.35-77.09
Male juv	30	12.22	0.42	8.92-19.54	3.24	0.106	2.22-4.56	0.122	0.0157	-0.08-0.30	72.41	0.31	69.03-76.00
All groups	100	12.23	0.24	8.85-19.54	3.20	0.058	2.22-4.68	0.107	0.0080	-0.11-0.33	72.85	0.22	67.82-78.75

Gizzard	Gizzard												
Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	water % - Means	SE	Range
Female ad	9	14.87	0.562	12.09-16.98	3.84	0.155	3.15-4.58	0.209	0.0369	0.09-0.45	72.80	0.554	70.27-76.06
Female juv	30	14.68	0.233	12.51-18.25	3.83	0.062	3.35-5.02	0.213	0.0290	-0.04-0.82	72.40	0.378	65.21-75.25
Male ad	31	15.72	0.267	12.16-19.65	4.14	0.071	3.13-5.37	0.224	0.0186	0.04-0.58	72.26	0.215	69.72-74.60
Male juv	30	16.39	0.248	14.13-19.58	4.25	0.060	3.62-4.85	0.196	0.0113	0.09-0.32	72.82	0.288	67.16-74.86
All groups	100	15.53	0.155	12.09-19.65	4.05	0.040	3.13-5.37	0.211	0.0113	-0.04-0.82	72.52	0.164	65.21-76.06

Heart													
Sex & age	N	WM Means	SE	Range	FFDM Means	SE	Range	Fat Means	SE	Range	water % - Means	SE	Range
Female ad	9	10.50	0.266	9.60-1.83	2.43	0.063	2.20-2.73	0.38	0.060	0.20-0.72	73.17	0.410	71.15-74.72
Female juv	30	9.66	0.123	8.55-1.15	2.14	0.031	1.85-2.50	0.41	0.031	0.10-0.81	73.57	0.256	71.00-77.41
Male ad	31	11.29	0.161	9.34-2.81	2.55	0.048	2.01-3.15	0.46	0.033	0.13-1.11	73.31	0.188	70.64-75.00
Male juv	30	10.56	0.176	7.73-1.77	2.37	0.049	1.55-2.83	0.46	0.030	0.22-0.80	73.26	0.238	70.00-76.07
All groups	100	10.51	0.105	7.73-2.81	2.36	0.028	1.55-3.15	0.44	0.017	0.10-1.11	73.36	0.124	70.00-77.41

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 30 September to 6 October 2012. Total gut length is the combined length of small intestines plus rectum plus $2 \times$ 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	Ν	SE	Min	Max
Small intestines length	cm	Female ad	91.9	9	1.23	86	98
		Female juv	95.3	28	0.75	87	105
		Male ad	93.0	29	0.83	82	100
		Male juv	93.6	29	0.61	89	103
		All groups	93.7	95	0.41	82	105
Rectum length	cm	Female ad	12.0	9	0.17	11	13
		Female juv	11.8	30	0.15	10	13
		Male ad	11.6	30	0.12	11	13
		Male juv	11.6	30	0.10	11	13
		All groups	11.7	99	0.07	10	13
Cecum length	cm	Female ad	41.7	9	0.73	38	44
(only one measured)		Female juv	45.4	30	0.47	40	50
		Male ad	43.2	30	0.52	37	49
		Male juv	44.8	30	0.41	41	50
		All groups	44.2	99	0.28	37	50
Total gut length	cm	Female ad	187.2	9	2.39	178	198
		Female juv	198.1	29	1.36	186	211
		Male ad	191.3	30	1.61	171	203
		Male juv	195.0	30	1.11	185	207
		All groups	194.1	98	0.82	171	211

3.5 Vegetative content of crop and gizzard and grit stones

The mean fresh mass of the crop content was 6.50 g (Table 3). Some crops were empty but the heaviest crop contained 71.38 g of vegetation. Crop content mass was age related, juveniles

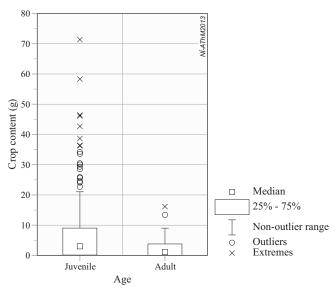


Fig. 6. A box plot for fresh mass (g) of crop content of rock ptarmigan collected in Northeast Iceland 30 September to 6 October 2012.

had heavier crops than adults (Fig. 6) and the difference was highly significant [12]. There was also a diurnal pattern with respect to crop content. Birds shot late in the day tended to have heavier crops that those shot early. This was apparent for juveniles but not adults (Fig. 7).

Gizzard content was separated into two parts, vegetation and grit stones (Table 6). A priori one would expect that gizzard size (here mass) should show a significant relationship with vegetative content and grit stone numbers or mass. This was the case for the vegetative content but not for either grit stone number or mass [13]. So heavier (= bigger) gizzards contained more vegetation than lighter (= smaller) but this was not so for the grit. The vegetative content showed an age relationship, juveniles had more vegetation in gizzards than adults [14]. This relationship was still significant when gizzard mass was added to the analysis as an explanatory variable [15].

Only 2 (2%) of the birds did not have any grit stones. Mean number of grit stones per bird was 30.73 (Table 6). Grit stone number and grit stone mass were highly correlated [16]. There was no relation between age and sex groups with respect to grit stone number [17] and mass [18]. The only relationship found was between water content of gizzard vegetation and grit stone number and grit stone mass [19]. The higher the water contents of the gizzard vegetation the more grit stones there were in the gizzard.

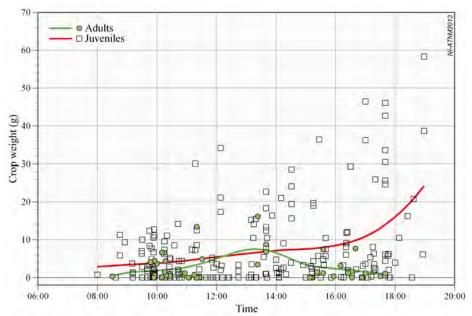


Fig. 7. Fresh mass (g) of crop content versus time of the day when collected for rock ptarmigan in Northeast Iceland 30 September to 6 October 2012. The fitted lines are calculated using distance weighted least squares.

Table 6. Gizzard content – vegetation and grit stones – of rock ptarmigan collected for health studies in Northeast Iceland 30 September to 6 October 2012. 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	Ν	SE	Min	Max
Gizzard vegetation dry mass	g	Female ad	2.37	9	0.120	1.86	2.93
		Female juv	2.44	30	0.087	1.41	3.41
		Male ad	2.29	31	0.087	1.39	3.18
		Male juv	2.72	30	0.087	1.82	3.82
		All groups	2.47	100	0.049	1.39	3.82
Grit stones	g	Female ad	0.284	8	0.072	0.011	0.533
		Female juv	0.380	29	0.060	0.035	1.232
		Male ad	0.381	31	0.059	0.011	1.582
		Male juv	0.530	30	0.074	0.003	1.516
		All groups	0.418	98	0.035	0.003	1.582
Grit stones	number	Female ad	19.38	8	4.54	1	38
		Female juv	29.48	29	4.92	2	87
		Male ad	26.61	31	4.15	1	97
		Male juv	39.23	30	6.21	1	151
		All groups	30.73	98	2.79	1	151

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 0.254 g (Table 3). The bursa mass was not correlated with the structural size index [20] nor was there a sex related difference in bursa mass [21]. Mean fresh mass of spleen was 0.066 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].

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. The interaction effect age \times sex was significant and was expressed by difference in juvenile females and males; juvenile males had smaller combs than adults but juvenile females did not differ from adult females.

Testis mass was correlated with structural size [27]. Mean fresh mass of testis was 0.0402 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 0.0457 g (Table 3). Mass of adrenal glands was not 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 [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); liver; gizzard; and heart (Table 5).

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. 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 67.93%, and highest for heart, 73.36%. It's relation to age and sex of bird and age × sex interaction effects differed. For the two pectoral muscles, the pectoralis major and minor, adults had lower water content then juveniles. The interaction effect was significant for the pectoralis minor, juvenile males did not differ from adult males but juvenile females had higher water content in tissue compared with adult females. For leg, heart, liver and gizzard none of the explanatory variables were significant [33].

Mean fat mass was under a gram for the different organs and tissues measured (Table 4). Most fat was on the heart (mean for all groups 0.44 g) and the pectoralis major (0.45 g). Fat content did not show any relation to structural size except for fat on pectoralis major [34]. Sex and age and sex \times age interaction effect did not explain the variation in fat content of any of the tissues or organs [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 8.30 g (range 3.05-18.64, SE = 0.271). 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].

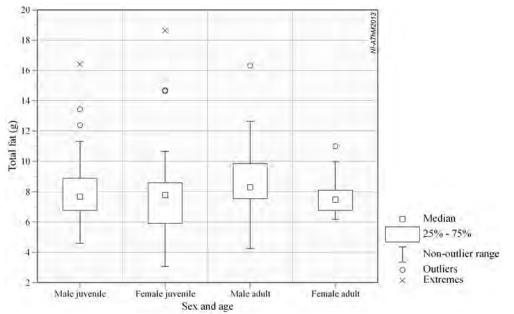


Fig. 8. A box plot for total calculated fat reserves (g) of rock ptarmigan collected in Northeast Iceland 30 September to 6 October 2012. Fat reserves were calculated using a function relating fat content of leggs, pectoralis major, pectoralis minor and heart to total fat. Fourty adult birds were 15 months and older and 60 juvenile birds were approximately 3 months old.

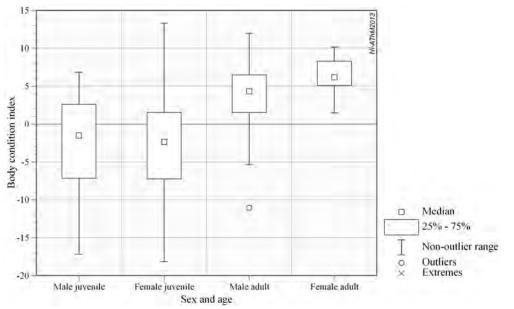


Fig. 9. A box plot for body condition index of rock ptarmigan collected in Northeast Iceland 30 September to 6 October 2012. The values are the residuals from regressing lean dry body mass (LDBM) on body size. Body size was taken as the factor 1 from from a Principal component analysis of 6 structural size variables. LDBM was calculated using a function relating LDBM to lean lean dry mass of Pectoralis major, legs and heart. Fourty adult birds were 15 months and older and 60 juvenile birds were approximately 3 months old.

4 DISCUSSIONS

The last rock ptarmigan peak in northeast Iceland was in 2010 and the population has declined since (unpublished data). The autumn population 2012 was c. 46% of the 2010 population. It took the hunters 7 week days and 42 hunter man-days to collect the desired sample (40 adults and 60 juveniles). Seven days is the maximum that the hunters from Reykjavík have up to now been able to stay at the site. In all likelihood the population will continue down and the expected low will be during the years 2015-2017. To counter diminishing number of birds more effort may need to be put into the collecting process. This is probably best done by adding more hunters to the team. The age ratio in the late summer 2012 population from the study area was 80% (n = 361) and the age ratio in the catch was 84% (n = 253 shot), these ratios do not differ statistically (Fisher's exact test, two-tailed, p = 0.171). According to this the hunters are not able to use color or behavior to discern between the age classes.

We used 6 variables to describe structural size. 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 length 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 the adult birds were fully grown but some of the juveniles still had primary number 8 growing at the beginning of October. This could affect the wing length measurement as primary number 8 is the longest primary. Structural size was primarily related to sex, males were bigger than females. Only the wing length showed relation with age, juveniles had shorter wings than adults. This probably reflects a real age related difference in both wing length and wing area but also some of the juvenile birds did not have a fully grown wing. Wing length should probably in future analysis be left out in the calculation 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 at the beginning of October but total body mass and mass of the locomotor musculature was lighter than adults.

Organs of the digestive system – the gizzard, the gut and the liver – behaved differently compared with the locomotor muscles. Neither gizzard mass nor liver mass showed any relation to sex or age of the birds. Gut length on the other hand showed a clear relation with age but not sex, juveniles had longer guts than adults. There was also an interesting age related difference in the amount of ingesta. We had two such measures one relating to food in the crop and the other to food in the gizzard. Both showed the same pattern with more food in juvenile birds than adults. These characteristics of the digestive system 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 but the juveniles had larger spleens. 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. 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 on average 8.3 g. 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 exceptions are rock ptarmigans from Svalbard but those birds lay down fat reserves in autumn (Mortensen et al. 1983). Our index of protein reserves showed a different pattern compared with the fat reserves and there was an age relationship, adults had larger protein reserves than juveniles. The two energy stores were positively correlated, those birds having large fat reserves also tended to have large protein stores and vice versa.

In summary our 2012 data showed clearly the sexual size dimorphism that characterizes the rock ptarmigan and also the data shows that the juveniles had reached full body size by the first week of October or approximately 3 month of age. Juveniles and adults showed contrasting patters with respect to size of the different organ systems. The main contrast was larger investment by juveniles in the lymphatic system and the digestive system. Juveniles also had

more food in the digestive system.

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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 100 birds 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 71.9% of the total variance and is regarded as describing structural size.

Factor	Eigenvalue	% total – variance	Cumulative – Eigen- value	Cumulative – %
1	4.313	71.9	4.313	71.9
2	0.681	11.3	4.994	83.2
3	0.392	6.5	5.386	89.8
4	0.308	5.1	5.694	94.9
5	0.232	3.9	5.926	98.8
6	0.074	1.2	6.000	100.0

Eigenvalues of correlation matrix, and related statistics

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
Wing length	0.816	0.361	0.312	-0.228	-0.233	-0.012
Head + bill	0.874	0.243	0.114	-0.027	0.403	0.000
Tarsus length	0.819	-0.311	0.291	0.379	-0.061	0.015
Tars + mid-toe length	0.726	-0.610	-0.025	-0.313	0.029	-0.021
Sternum length	0.912	0.118	-0.319	0.110	-0.071	-0.186
Sternum-coracoid length	0.923	0.090	-0.307	0.028	-0.074	-0.197

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 \times sex interaction effect. Standard error of estimate was 1.4418. Sex came out as significant.

	SS	Degr. of freedom	MS	F	р
Intercept	12.131	1	12.131	5.836	0.018
Sex	192.850	1	192.850	92.773	0.000
Age	0.007	1	0.007	0.003	0.955
Sex×Age	3.501	1	3.501	1.684	0.197
Error	199.558	96	2.079		

Comparison of mean group size between adults and juveniles. Sample sizes: adults 34; juveniles 127; sample means: adults 3.29; juveniles 4.14; sample standard deviation: adults 3.60; juveniles 4.14. Number of bootstrap replications = 2000.

Bootstrap 2-sample t-test, t = -1.071, p = 0.27.

3. Comparison of equality of group size distributions.

Brunner-Munzel test, p = 0.33.

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, circumference and wing area adults were bigger than juveniles. The interaction effect was significant for wing length (juvenile males had shorter wings than adult males) and wing area (juvenile females had larger wing area than adults, but there was no difference between adult and juvenile males).

	SS	Degr. of freedom	MS	F	р
Intercept	3679043	1	3679043	225721	< 0.001
Sex	2933	1	2933	179.9	< 0.001
Age	117	1	117	7.2	0.008
Sex×Age	95	1	95	5.8	0.017
Error	4042	248	16		

Wing length (mm); standard error of estimate was 4.037.

	SS	Degr. of freedom	MS	F	р
Intercept	269841	1	269841	198784.3	< 0.001
Sex	152.0	1	152.0	112.0	< 0.001
Age	4.2	1	4.2	3.1	0.079
Sex×Age	1.1	1	1.1	0.8	0.362
Error	309.5	228	1.4		

Head + bill (mm); standard error of estimate was 1.165.

Tarsus length (mm); standard error of estimate was 0.803.

	SS	Degr. of freedom	MS	F	р
Intercept	107332	1	107332	166284	< 0.001
Sex	24.7	1	24.7	38.3	< 0.001
Age	0.0	1	0.0	0.0	0.969
Sex×Age	0.0	1	0.0	0.0	0.851
Error	158.1	245	0.6		

	SS	Degr. of freedom	MS	F	р
Intercept	394984	1	394984	162495	< 0.001
Sex	38.8	1	38.8	16.0	< 0.001
Age	2.4	1	2.4	1.0	0.323
Sex×Age	0.0	1	0.0	0.0	0.944
Error	580.9	239	2.4		

Tarsus + mid-toe length (mm); standard error of estimate was 1.559.

Sternum length (mm); standard error of estimate was 2.202.

	SS	Degr. of freedom	MS	F	р
Intercept	551324	1	551324	113680	< 0.001
Sex	294.8	1	294.8	60.8	< 0.001
Age	0.2	1	0.2	0.0	0.849
Sex×Age	2.4	1	2.4	0.5	0.485
Error	465.6	96	4.8		

Sternum width (mm); standard error of estimate was 1.2601.

	SS	Degr. of freedom	MS	F	р
Intercept	138189	1	138189	87029	< 0.001
Sex	43.0	1	43.0	27.07	< 0.001
Age	0.8	1	0.8	0.52	0.471
Sex×Age	0.4	1	0.4	0.28	0.597
Error	149.3	94	1.6		

Sternum height (mm); standard error of estimate was 1.0643.

	SS	Degr. of freedom	MS	F	р
Intercept	36941	1	36941	32606	< 0.001
Sex	39.33	1	39.33	34.71	< 0.001
Age	0.28	1	0.28	0.24	0.622
Sex×Age	2.62	1	2.62	2.31	0.132
Error	107.63	95	1.13		

Sternum-coracoid length (mm); standard error of estimate was 2.2805.

	SS	Degr. of freedom	MS	F	р
Intercept	909126	1	909126	174805	< 0.001
Sex	375.0	1	375.0	72.1	< 0.001
Age	0.0	1	0.0	0.0	0.969
Sex×Age	5.5	1	5.5	1.1	0.307
Error	488.9	94	5.2		

	SS	Degr. of freedom	MS	F	р
Intercept	281814	1	281814	49234	< 0.001
Sex	254.7	1	254.7	44.50	< 0.001
Age	0.4	1	0.4	0.07	0.795
Sex×Age	2.4	1	2.4	0.42	0.516
Error	549.5	96	5.7		

Back width (mm); standard error of estimate was 2.3925.

Circumference (mm); standard error of estimate was 6.843.

	SS	Degr. of freedom	MS	F	р
Intercept	4401923	1	4401923	93992	< 0.001
Sex	887	1	887	18.95	< 0.001
Age	634	1	634	13.54	< 0.001
Sex×Age	13	1	13	0.28	0.600
Error	4496	96	47		

Wing area (cm²); standard error of estimate was 13.460.

	SS	Degr. of freedom	MS	F	р
Intercept	3461463	1	3461463	19105	< 0.001
Sex	7116	1	7116	39.27	< 0.001
Age	949	1	949	5.24	0.024
Sex×Age	2469	1	2469	13.63	< 0.001
Error	17393	96	181		

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 34.949.

	SS	Degr. of freedom	MS	F	р
Intercept	24318743	1	24318743	19909	< 0.001
Sex	58847	1	58847	48.1	< 0.001
Age	10617	1	10617	8.7	0.003
Sex×Age	341	1	341	0.3	0.598
Error	304142	249	1221		

Net body mass (g); standard error of estimate was 31.631

	SS	Degr. of freedom	MS	F	р
Intercept	23851951	1	23851951	23839	< 0.001
Sex	57071	1	57071	57.0	< 0.001
Age	15471	1	15471	15.5	< 0.001
Sex×Age	362	1	362	0.4	0.548
Error	248134	248	1001		

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 = 0.424, n = 100, p < 0.001.

7. General Linear Model was used to compare gizzard fat free dry mass among age and sex groups, for age \times sex interaction effect, and controlling for structural size. Standard error of estimate was 0.3620. None of the coefficients came out as significant, but body size was just above the rejection limit (p = 0.05).

	SS	Degr. of freedom	MS	F	р
Intercept	1169.01	1	1169.01	8921.06	< 0.001
Structural size	0.486	1	0.486	3.706	0.057
Sex	0.390	1	0.390	2.980	0.088
Age	0.054	1	0.054	0.410	0.524
Sex×Age	0.122	1	0.122	0.931	0.337
Error	12.449	95	0.131		

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	0.081	0.394
	n =95	n = 95	n=95
	p =	p = 0.434	p = 0.000
Rectum	0.081	1.000	0.014
	n = 95	n = 99	n = 99
	P = 0.434	p =	P = 0.892
Caecum	0.394	0.014	1.000
	n = 95	n = 99	n = 99
	P = 0.000	p = 0.892	p =

9. 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 7.466. Juveniles had longer guts than adults. The interaction effect was longer guts for juvenile females compared with juvenile males, but vice versa for adults.

	SS	Degr. of freedom	MS	F	р
Intercept	2805194	1	2805194	50327	< 0.001
Sex	5	1	5	0.08	0.774
Age	999	1	999	17.93	< 0.001
Sex×Age	244	1	244	4.38	0.039
Error	5239	94	56		

10. 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 = 0.149, n = 100, p = 0.138.

11. General Linear Model was used to compare liver fat free dry mass among age and sex groups and for age \times sex interaction effect. Standard error of estimate was 0.58476. None of the coefficients came out as significant.

	SS	Degr. of freedom	MS	F	р
Intercept	767.1309	1	767.1309	2243.435	< 0.001
Sex	0.3413	1	0.3413	0.998	0.320
Age	0.0298	1	0.0298	0.087	0.768
Sex×Age	0.0339	1	0.0339	0.099	0.754
Error	32.8267	96	0.3419		

12. Comparison of wet mass of crop content among age groups. Graphic exploration of crop data indicated that the contrast was between adults and juveniles. The frequency distribution of crop content was right skewed and the variance was non-homogeneous among the two age groups. A Mann-Whitney U test was used to compare the age groups.

Mann-Whitney U test: U = 3168.500, $n_1 = 212$, $n_2 = 40$, p = 0.011.

13. Correlations between fat-free dry gizzard mass and dry mass of vegetation in gizzard, dry mass of grit stones and grit stone number. The Pearson product-moment correlation coefficients are given in the table. There were no missing values in the data matrix.

	Content dry mass	Grit stone mass	Grit stone number
Gizzard FFDM	0.4613	0.077	-0.004
	n = 100	n = 98	n = 98
	p < 0.001	p = 0.451	p = 0.969

14. 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 0.4705. There was a significant difference with respect to age groups; juveniles had more vegetation in gizzard than adults.

	SS	Degr. of freedom	MS	F	р
Intercept	460.076	1	460.0769	2078.38	< 0.001
Sex	0.1943	1	0.1943	0.878	0.351
Age	1.2013	1	1.2013	5.427	0.022
Sex×Age	0.5903	1	0.5903	2.667	0.106
Error	21.2509	96	0.2214		

15. 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 0.4148. Gizzard vegetation was explained by gizzard size (= mass) and age (juveniles had more vegetation in gizzards than adults).

	SS	Degr. of freedom	MS	F	р
Intercept	0.000	1	0.000	0.001	0.974
Gizzard empty FFDM	4.907	1	4.907	28.521	< 0.001
Sex	0.228	1	0.228	1.327	0.252
Age	0.900	1	0.900	5.233	0.024
Sex×Age	0.368	1	0.368	2.139	0.147
Error	16.344	95	0.172		

16. Correlations between grit stone mass and grit stone number.

Pearson product-moment correlation coefficient: r = 0.921, n = 98, p < 0.001.

17. Comparison of grit stone number between age and sex groups.

Kruskal-Wallis ANOVA H (3, N = 100) = 4.225 p = 0.24).

18. General Linear Model was used to compare grit stone mass among age and sex groups and for age \times sex interaction effect. The standard error of estimate was 0.3467. Only included were birds that had grit stones (n = 98). There was no difference between either age or sex groups.

	SS	Degr. of freedom	MS	F	р
Intercept	11.023	1	11.023	91.72	< 0.001
Sex	0.268	1	0.268	2.23	0.139
Age	0.266	1	0.266	2.22	0.140
Sex×Age	0.012	1	0.012	0.10	0.749
Error	11.296	94	0.120		

19. Correlations between water content of gizzard vegetation (calculated as 1 minus the ratio dry mass versus wet mass) and grit stone numbers and mass. The Pearson product-moment correlation coefficients are given in the table along with p-values. There were no missing values in the data matrix. All dissected birds were included in the analysis (n = 100).

	Grit stones DM	Grit stones no
% water in gizzard content	0.365	0.370
	p < 0.001	p < 0.001

20. Correlations between bursa mass and structural size.

Pearson product-moment correlation coefficient: r = 0.124, n = 58, p = 0.354.

21. Comparison of bursa mass between juvenile males and females.

t-test: $t_{56} = -0.393$, p = 0.696.

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 = 0.071, n = 100, p = 0.485.

Pearson product-moment correlation coefficient (adults): r = 0.264, n = 40, p = 0.099.

Pearson product-moment correlation coefficient (juveniles): r = 0.079, n = 60, p = 0.551.

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. 32078. Spleen mass was ln-transformed prior to analysis. Age was significant and juveniles had heavier spleens than adults.

	SS	Degr. of freedom	MS	F	р
Intercept	599.62	1	599.62	5826.8	< 0.001
Sex	0.029	1	0.0290	0.282	0.597
Age	0.801	1	0.8007	7.781	0.006
Sex×Age	0.222	1	0.2215	2.153	0.146
Error	9.879	96	0.1029		

24. Correlations between spleen mass In-transformed and bursa mass.

Pearson product-moment correlation coefficient: r = 0.018, n = 58, p = 0.893.

25. Correlations between comb area (mm²) and structural size.

Pearson product-moment correlation coefficient: r = 0.649, n = 100, 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 16.1585. Males had bigger combs than females, and adults bigger than juveniles. The interaction effect was bigger combs for adult males compared with juvenile males, the adult and juvenile females did not differ in this respect.

	SS	Degr. of freedom	MS	F	р
Intercept	665553.1	1	665553.1	2549.056	< 0.001
Structural size	3186.1	1	3186.1	12.203	0.001
Sex	5380.3	1	5380.3	20.606	< 0.001
Age	6845.0	1	6845.0	26.216	< 0.001
Sex×Age	2506.2	1	2506.2	9.599	0.003
Error	24804.3	95	261.1		

27. Correlations between testis mass g and structural size.

Pearson product-moment correlation coefficient: r = 0.339, n = 54, p = 0.012.

28. General Linear Model was used to compare testis mass among age and sex groups and for age \times sex interaction effect while controlling for structural size. Standard error of estimate was 0.00792. Adult males had heavier testis than juvenile males when controlling for structural size.

	SS	Degr. of freedom	MS	F	р
Intercept	0.05236	1	0.05236	835.500	< 0.001
Structural size	0.00051	1	0.00051	8.110	0.006
Age	0.00617	1	0.00617	98.417	< 0.001
Error	0.00320	51	0.000063		

29. Correlations between adrenal mass g and structural size.

Pearson product-moment correlation coefficient: r = 0.0387, n = 100, p = 0.702.

30. General Linear Model was used to compare adrenal gland mass among age and sex groups and for age \times sex interaction effect. Standard error of estimate was 0.0101. There was no significant difference among groups or interaction.

	SS	Degr. of freedom	MS	\mathbf{F}	р
Intercept	0.155457	1	0.1555	1530.004	< 0.001
Sex	0.000001	1	0.0001	0.004	0.950
Age	0.000007	1	0.0001	0.072	0.790
Sex×Age	0.000330	1	0.0003	3.250	0.075
Error	0.009754	96	0.0001		

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

	Adrenal mass	Testis mass	Comb area
Adrenal mass	1.000	0.418	0.102
	n = 100	n = 54	n = 100
	p =	p = 0.002	p = 0.314
Testis mass	0.4180	1.0000	0.5884
	n = 54	n = 54	n = 54
	p = 0.002	p =	p < 0.001
Comb area	0.1017	0.5884	1.0000
	n = 100	n = 54	n = 241
	p = 0.314	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, neither sex or age × sex interactions were significant.

	SS	Degr. of freedom	MS	F	р
Intercept	15074.14	1	15074.14	14875.98	< 0.001
Structural size	41.25	1	41.25	40.71	< 0.001
Sex	0.33	1	0.33	0.32	0.572
Age	7.07	1	7.07	6.97	0.010
Sex×Age	0.17	1	0.17	0.17	0.684
Error	96.27	95	1.01		

Pectoralis major fat free dry mass (FFDM); standard error of estimate 1.0066.

Pectoralis minor fat free dry mass; standard error of estimate 0.02187.

	SS	Degr. of freedom	MS	F	р
Intercept	812.46	1	812.4557	16987.72	< 0.001
Structural size	2.661	1	2.6609	55.64	< 0.001
Sex	0.131	1	0.1311	2.74	0.101
Age	1.494	1	1.4943	31.25	< 0.001
Sex×Age	0.116	1	0.1161	2.43	0.123
Error	4.544	95	0.0478		

Leg fat free dry mass; standard error of estimate 0.4859.

	SS	Degr. of freedom	MS	F	р
Intercept	3757.78	1	3757.78	15911.84	< 0.001
Structural size	12.79	1	12.787	54.15	< 0.001
Sex	0.341	1	0.341	1.44	0.233
Age	9.179	1	9.179	38.87	< 0.001
Sex×Age	0.018	1	0.018	0.08	0.781
Error	22.44	95	0.236		

Heart fat free dry mass; standard error of estimate 0.2195.

	SS	Degr. of freedom	MS	F	р
Intercept	413.37	1	413.37	8577.4	< 0.001
Structural size	0.785	1	0.785	16.28	< 0.001
Sex	0.0054	1	0.0054	0.113	0.738
Age	1.0506	1	1.051	21.80	< 0.001
Sex×Age	0.1150	1	0.115	2.386	0.126
Error	4.578	95	0.048		

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 two pectoralis muscles, juveniles had higher water content then adults. The interaction term was significant for the pectoralis minor; juvenile females had higher water content than adult females, but adult and juvenile males were similar to juvenile females.

	SS	Degr. of freedom	MS	F	р
Intercept	398381	1	398381	1008118	< 0.001
Sex	0.62	1	0.62	1.57	0.213
Age	3.64	1	3.64	9.21	0.003
Sex×Age	1.10	1	1.10	2.77	0.099
Error	37.94	96	0.40		

Pectoralis major % water; standard error of estimate 0.6286.

Pectoralis minor % water; standard error of estimate 0.5289.

	SS	Degr. of freedom	MS	F	р
Intercept	397482	1	397482	1420839	< 0.001
Sex	0.02	1	0.02	0.05	0.817
Age	1.53	1	1.53	5.48	0.021
Sex×Age	1.20	1	1.20	4.28	0.041
Error	26.86	96	0.28		

Leg % water; standard error of estimate 1.5349.

	SS	Degr. of freedom	MS	F	р
Intercept	350349	1	350349	148691	< 0.001
Sex	3.86	1	3.86	1.64	0.204
Age	2.42	1	2.42	1.03	0.313
Sex×Age	1.01	1	1.01	0.43	0.515
Error	226.20	96	2.36		

Heart % water; standard error of estimate 1.2543.

	SS	Degr. of freedom	MS	\mathbf{F}	р
Intercept	409601	1	409601	260334	< 0.001
Sex	0.2	1	0.2	0.1	0.757
Age	0.6	1	0.6	0.4	0.555
Sex×Age	1.0	1	1.0	0.6	0.435
Error	151.0	96	1.6		

	SS	Degr. of freedom	MS	F	р
Intercept	404254	1	404254	86411	< 0.001
Sex	2.04	1	2.0	0.44	0.511
Age	0.24	1	0.2	0.05	0.822
Sex×Age	3.60	1	3.6	0.77	0.382
Error	449.11	96	4.7		

Liver % water; standard error of estimate 2.1629.

Gizzard % water; standard error of estimate 1.6509.

	SS	Degr. of freedom	MS	F	р
Intercept	401208	1	401208	147192	< 0.001
Sex	0.07	1	0.07	0.02	0.877
Age	0.13	1	0.13	0.05	0.830
Sex×Age	4.34	1	4.34	1.59	0.210
Error	261.67	96	2.73		

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-value. Sample size was 100 in all cases.

	Structural size
Pectoralis minor fat	0.036
	p = 0.724
Pectoralis major fat	0.253
	p = 0.011
Leg fat	0.066
	p = 0.514
Heart fat	0.183
	p = 0.068
Liver fat	0.130
	p = 0.197
Gizzard fat	0.006
	p = 0.954
Fat total	0.167
	p = 0.094

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. None of the explanatory variables showed a significant relationship with fat content of tissues and organs.

Log-transformed pectoralis major fat (g); standard error of estimate 2.7200.

	SS	Degr. of freedom	MS	F	р
Intercept	4957.69	1	4957.69	670.06	< 0.001
Structural size	11.17	1	11.17	1.51	0.222
Sex	0.19	1	0.19	0.03	0.874
Age	1.31	1	1.31	0.18	0.675
Sex×Age	1.72	1	1.72	0.23	0.631
Error	702.89	95	7.40		

Log-transformed pectoralis minor fat (g); standard error of estimate 0.2782.

	SS	Degr. of freedom	MS	\mathbf{F}	р
Intercept	237.47	1	237.47	3067.42	< 0.001
Sex	0.01	1	0.01	0.09	0.771
Age	0.20	1	0.20	2.56	0.113
Sex×Age	0.03	1	0.03	0.43	0.516
Error	7.43	96	0.08		

Log-transformed leg fat (g); standard error of estimate 0.6382.

	SS	Degr. of freedom	MS	F	р
Intercept	110.42	1	110.42	271.08	< 0.001
Sex	0.02	1	0.02	0.04	0.838
Age	0.51	1	0.51	1.26	0.265
Sex×Age	0.01	1	0.01	0.03	0.868
Error	39.10	96	0.41		

Log-transformed heart fat (g); standard error of estimate 0.4167.

	SS	Degr. of freedom	MS	F	р
Intercept	66.28	1	66.28	381.63	< 0.001
Sex	0.49	1	0.49	2.81	0.097
Age	0.04	1	0.04	0.21	0.647
Sex×Age	0.02	1	0.02	0.12	0.735
Error	16.67	96	0.17		

Log-transformed liver fat (g); standard error of estimate 0.07293.

	SS	Degr. of freedom	MS	F	р
Intercept	0.7484	1	0.748	140.70	< 0.001
Sex	0.0000	1	0.000	0.00	0.990
Age	0.0033	1	0.003	0.62	0.434
Sex×Age	0.0037	1	0.004	0.69	0.407
Error	0.5107	96	0.005		

	SS	Degr. of freedom	MS	F	р
Intercept	2.6644	1	2.6644	348.79	< 0.001
Sex	0.0001	1	0.0001	0.01	0.915
Age	0.0023	1	0.0023	0.30	0.587
Sex×Age	0.0021	1	0.0021	0.27	0.604
Error	0.7333	96	0.0076		

Log-transformed gizzard fat (g); standard error of estimate 0.0874.

36. Regression of total lean dry body mass on structural size. Adjusted $R^2 = 0.561$, $F_{1,98} = 127.67$, p < 0.001.

	b×	SE of b×	b	SE of b	t(98)	р
Intercept			121.421	0.715	169.792	< 0.001
Structural size	0.752	0.067	3.910	0.346	11.299	< 0.001

37. General Linear Model was used to compare calculated total fat reserves among age and sex groups and for age \times 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 2.7273.

	SS	Degr. of freedom	MS	F	р
Intercept	5140.22	1	5140.22	691.06	< 0.001
Sex	7.17	1	7.17	0.96	0.329
Age	1.27	1	1.27	0.17	0.681
Sex×Age	3.12	1	3.12	0.42	0.519
Error	714.06	96	7.44		

38. Comparison of body condition index between age and sex groups.

Kruskal-Wallis ANOVA H (3, N = 100) = 27.546 p < 0.001.

39. Correlations between total fat reserves and protein reserves.

Pearson product-moment correlation coefficient: r = 0.542, n = 100, p < 0.001.