

Annual patterns of body, tissue, and organ mass variation in long-tailed ducks *Clangula hyemalis*

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Abstract

Temporal variation in resource availability, physiological demands, and other factors are associated with many phenotypic changes in organisms. For example, there are often predictable stages of atrophy and hypertrophy in animals' organs to accommodate changes in diet. Timing of stages may differ by sex given differences in life histories (e.g., egg-laying versus male–male competition). In this context, we quantified changes over the annual cycle in 153 long-tailed duck (*Clangula hyemalis*) carcasses. We also tested whether timing of changes differed by sex. Total body mass was lowest in February and highest in November, whereas livers, spleens, kidneys, and salt glands were lightest in the middle of breeding seasons. Reductions in kidney and salt gland masses coincided with switches to using freshwater from marine habitats. Generally, timing in patterns of body mass change did not differ by sex. This was unexpected, and could arise from the compressed breeding season. We were also interested in evaluating whether changes in masses of tissues or organs were more dramatic for a species that breeds at such high latitudes than for species that breed at lower latitudes, but were unable to glean this information from the literature. We present coefficients of variation to facilitate future comparisons.

Key words: atrophy, endogenous stores, phenotypic organ flexibility, hypertrophy, lipid stores, spleen,

Introduction

Many animals experience seasonal changes in resource availability concomitant with seasonal changes in energetic demands for key activities such as breeding, moult, and migration (Ankney 1979; Silverin et al. 1999; Bauchinger et al. 2005; McGuire et al. 2013). Seasonal changes affect allocation to tissues and organs; thus, it is not surprising that animals undergo substantial temporal changes in mass and size of tissues and organs (Piersma and Lindström 1997; Piersma and Drent 2003; McWilliams and Karasov 2005; Sandri 2008). Larger tissues and organs may be more effective at their tasks, but tissue and organ sizes are positively and allometrically related to maintenance costs, resulting in trade-offs between functionality and maintenance costs (Piersma 1998; Vezina and Williams 2003; Fox and Kahlert 2005; Provencher et al. 2016).

Many animal species are sexually dimorphic because their optimal morphologies are shaped by differences in demands. For example, only female birds produce eggs, and in many species of waterfowl, only females incubate and care for young (Alisauskas and Ankney 1992), freeing males to migrate earlier. Such differences in timing and magnitude of physiological demands would therefore be expected to be associated with sex differences in the timing of fluctuations in tissue and organ masses and sizes (e.g., Provencher et al. 2016).

Trade-offs in organ functionality versus maintenance may be particularly important for species that remain at higher latitudes year-round, where resources can rapidly become scarce as day length decreases (Alerstam 1990; for exceptions, see Piersma et al. 2005; Escudero et al. 2012; Ruthrauff et al. 2013). Terrestrial species that forage in aquatic habitats face an additional challenge in winter because ice may add an additional barrier to accessing food resources (Rappole and McDonald 1994; Moore and Huntington 2008). A few species manage to find sufficient winter resources in high latitude bodies of seawater that do not freeze in winter (i.e., polynyas; Stirling 1997), but the majority of arctic and subarctic bird species and individuals migrate. Migration entails significant physiological changes, including accumulation of stores (sensu Lindström and Piersma 1993; van der Meer and Piersma 1994) of fat and protein (enlarged muscle mass) to sustain prolonged flight (Piersma 1990; Jenni and Jenni-Eiermann 1998; McWilliams and Karasov 2005); these physiological changes may be associated with concomitant reductions in other tissues and organs, such as immune and digestive organs, that may be less essential at these times (Piersma and Gill 1998; Klaassen et al. 2001; Baak et al. 2020). Magnitudes of changes in these tissues and organs can be enormous; for example, some species may double in mass (Odum 1958; Harrington et al. 1991; Dunn 2002; Battley and Piersma 2005; Baak et al. 2020).

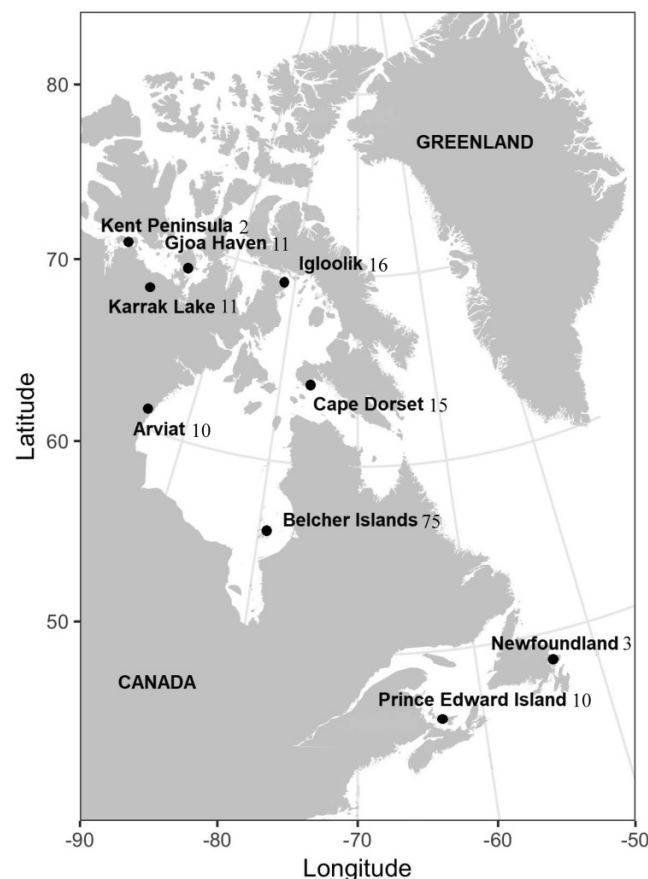
Long-tailed ducks (*Clangula hyemalis*) are an abundant species of diving duck with a circumpolar distribution (Alison 1975; Robertson and Savard 2002; Żydelis and Ruškytė 2005; Baldassarre 2014). In eastern North America, they migrate north in April from southerly wintering areas, refueling in staging areas (Johnson 1984; Leafloor et al. 1996; Jamieson et al. 2001; Mallory et al. 2006). Pairs arrive at their breeding grounds by July, where females are partially capital and partially income breeders (Peterson and Ellarson 1979; Goudie and Ankney 1986; Działa-Szczepańczyk 2008; Alisauskas and DeVink 2015). Clutches of 6 to 8 eggs are incubated by females alone for ~26 d (Lawson 2006; Schamber et al. 2009). Males remain nearby until their partner's eggs hatch, claiming foraging areas for themselves and their mates. After hatch, males begin short migrations to moulting areas (Howell et al. 2003; Petersen et al. 2003). Females remain to guard their nidifugous young until the latter fledge, after which time they all also migrate to moulting areas (Mallory et al. 2006; Schamber et al. 2009; Eadie and Savard 2015). Long-tailed ducks undergo a moult in July that leaves them flightless for 3–4 wk (Howell et al. 2003; Flint et al. 2004) and arrive at their wintering areas in late October (Mallory et al. 2006; White et al. 2009), spreading out in marine habitats and large lakes (Goudie and Ankney 1986). In winter, endogenous fat stores become depleted (Schummer et al. 2012), partly because excessive mass may make individuals more vulnerable to predators (Lima 1986), partly because thermoregulation may use them up (e.g., burning of lipids coupled with shivering of muscles to create heat; LaGrange and Dinsmore 1988; Nord et al. 2011), and partly from competition for mates (which may begin as early as autumn; Baldassarre 2014). In spring, birds head north once again (Alison 1975). Each stage of the annual cycle entails different demands and benefits, so that variation in tissue and organ allocation is expected.

Despite their abundance, broad geographic range, and profound variation in resource availability and seasonal demands that they experience, little is known about seasonal changes in long-tailed duck physiology (Mallory et al. 2006). To investigate patterns of atrophy and hypertrophy, we analyzed total body mass change as well as changes in 10 different tissues and organs during the birds' annual cycle. Because of the compact season in which breeding can occur for northerly populations and species (e.g., Mallory and Forbes 2007; Winkler et al. 2014), we predicted that mass changes would be fast and extreme for this high latitude species, and that the magnitude of changes would be similar for each sex. We also predicted that kidneys and salt glands would be smallest when the birds had stronger associations with freshwater habitats (during breeding; e.g., Cornelius 1982). Finally, although we expected similar rapid changes in mass and morphology for each sex, we predicted different timing of those changes given their distinct reproductive ecologies (Robertson and Savard 2002; Provencher et al. 2016; Bartzen et al. 2017; Vestbo et al. 2019).

Methods

Research was conducted under approved Government of Nunavut Wildlife Research Licences and Canadian Wildlife

Fig. 1. Locations in Canada from which long-tailed ducks (*Clangula hyemalis*) were obtained between 1998 and 2002. Sample sizes adjacent to locations. Details in text. Map created using basemap in ArcView for GIS (ESRI 1996), using NAD83 and a Lambert conical projection; sampling locations are approximate.



Service Scientific Collection permits; however, this was ~25 years ago and we no longer have specific numbers for all permits. Some collections were made under NUN-SCI-01-02. Collections were made pursuant to approved Canadian Wildlife Service Animal Care Committee permits, which follow CCAC guidelines.

All but 10 birds were shot (see below) by Indigenous hunters or resource officers (under appropriate federal and territorial collection permits), frozen (–20 °C), and shipped to us for full body dissections; tissues were disposed of after dissection. The 10 birds collected in Prince Edward Island (PEI), were retrieved as bycatch from fishing nets. Ducks were obtained from nine different locales (sample sizes follow names of locales; Arviat 10, Belcher Islands 75, Cape Dorset 15, Gjoa Haven 11, Igloolik 16, Karrak Lake 11, Kent Peninsula 2, Newfoundland and Labrador 3, and PEI 10; Fig. 1) ranging from 46.5° to 56.3° north latitude, and from –107.0° to –81.8° west longitude. Precise latitudes and longitudes of duck provenance were not recorded, so we were unable to rigorously test for spatial variation. In addition, for 11 ducks, only month of collection was recorded and not day of the month, which reduced temporal resolution in our data; in these cases and for

Table 1. Summary statistics for continuous variables measured on long-tailed ducks collected from Canada between February 1998 and November 2002.

Variable	Units	Females							Males				
		N	Minimum	Maximum	Median	Mean	SD	n	Minimum	Maximum	Median	Mean	SD
Wing chord	mm	71	184.0	230.0	209.0	207.4	10.3	80	189.0	240.0	222.5	221.0	11.2
9th primary	mm	70	110.0	151.0	136.0	133.9	9.0	80	122.0	161.0	143.5	143.6	7.8
Keel	mm	71	86.0	109.0	95.0	95.1	5.1	76	92.0	121.0	103.0	102.9	5.8
Head	mm	65	70.3	82.0	76.6	76.7	2.3	73	76.5	86.5	81.7	82.0	2.2
Tarsus wrist	mm	72	29.8	39.1	34.3	34.1	1.5	80	30.5	39.0	35.3	35.0	1.6
Culmen	mm	68	24.0	29.1	25.8	26.0	1.2	77	22.4	30.6	27.5	27.3	1.5
Mass	g	72	524.0	960.0	696.5	693.0	87.0	81	600.0	1090.0	772.0	791.2	100.2
Breast muscles	g	72	41.7	82.2	65.4	64.5	8.1	80	41.8	96.5	73.5	73.7	7.9
Liver	g	68	16.9	60.1	30.9	32.8	9.6	77	15.1	66.5	35.1	35.4	10.7
Leg muscles	g	72	11.4	23.9	16.7	16.7	3.0	81	8.9	26.0	18.5	18.2	2.8
Gizzard (empty)	g	69	7.3	26.4	12.2	12.9	4.0	79	8.2	32.8	14.0	14.8	5.1
Kidneys	g	37	7.0	13.5	9.6	9.8	1.7	41	7.7	14.2	11.3	11.1	1.9
Heart	g	72	5.7	11.1	7.9	8.0	1.1	79	6.3	14.6	8.7	8.9	1.5
Abdominal fat pad	g	71	0.0	34.8	2.9	4.8	6.1	80	0.0	42.7	3.0	6.2	8.1
Leg fat pad	g	71	0.0	21.7	3.3	4.3	3.6	76	0.0	24.7	3.3	5.0	4.6
Spleen	g	43	0.1	1.4	0.3	0.4	0.3	45	0.0	1.4	0.3	0.4	0.3
Total salt glands	g	35	0.2	0.9	0.5	0.6	0.2	42	0.3	1.1	0.7	0.7	0.2

Note: SD is standard deviation. Some variables were not measured for some ducks, so sample sizes vary.

consistency, we converted date to 15th of the month. Ducks were collected in eight different months (Supplementary Table 1), the earliest on 1 February 1998 and the latest on 28 November 2002.

Birds were sexed by plumage and aged by the size of the bursa of Fabricius and plumage characteristics (Glick 1983; Robertson and Savard 2002). Morphometric measurements (listed in Table 1) were taken of all birds by the same observer (SEJ) using digital calipers (accurate to 0.1 mm), or with a stopped ruler to the nearest mm. Body, tissue, and organ mass measurements (listed in Table 1) were taken with a digital scale to the nearest 0.5 g. Further details of data collection protocols for waterfowl dissections are in Jamieson et al. (2006a). We used specimens that were in good condition, that is, freshly harvested with full body intact. However, occasional damage from shooting meant that for some samples, measurements could not be taken for certain characters (hence variation in sample sizes in Table 1). Furthermore, some organs were measured as part of a specific project but not analysed for the entire set of carcasses (e.g., spleen, salt glands, kidneys). Analyses were run within each organ dataset so there were no corrections necessary for sample size differences.

Because ducks were collected opportunistically, we suggest that our statistical analyses be interpreted cautiously. Statistical analyses were conducted in SAS (version 9.4, Cary, North Carolina, USA). Because long-tailed ducks are sexually size dimorphic (e.g., males weigh ~15% more than females; Robertson and Savard 2002), data were sometimes analysed separately by sex. Data for this species are limited, so we report external morphological information (Table 1), but our temporal analyses were exclusively on mass variables because linear measurements were not expected to show sub-

stantial seasonal variation. We present plots of variation in mass with Lowess regressions to capture temporal patterns in change, and we quantified the extent of these changes using coefficients of variation (CVs). We tested if CVs were related to proportion of mass using Pearson correlations. We also used Pearson correlations to evaluate covariation in mass among organs. Finally, we used general linear models (GLMs) to test for seasonal differences in timing of mass changes between females and males, where mass variables were responses, and day of the year, sex, and the interaction were explanatory variables. When response variables were not normally distributed, log transformations were used to improve their fit. Body size may influence the associations for which we were testing, so we repeated GLMs with the first principal component, derived from a principal components analysis (PCA) of the six morphological measurements (Table 1), as an additional explanatory variable. Because of incomplete data for some measures, this reduced sample sizes from the initial GLMs. The PCA normalized data for the six morphological traits, used the correlation matrix to derive PCs, and used no rotations (which would not affect results because we only retained the first PC; see Results section).

Results

Of 153 ducks we obtained, 13 were immature females, 37 were adult females, 22 were females of unknown age, 11 were immature males, 44 were adult males, and 26 were males of unknown age. Data for immature and unknown age birds were for the most part interspersed among those for adults (Fig. 2). Thus, we retained all birds in overall calculations of morphometrics (Table 1). Moreover, removing immature and

Fig. 2. Temporal variation in body, tissue, and organ mass measurements for female (left) and male (right) long-tailed ducks (*Clangula hyemalis*), with open circles denoting adults (AD in legend), open circles with xs denoting unknown age (UNK), and triangles denoting immature individuals (IM). Solid lines are Lowess regressions with a smoothing parameter of 0.5 over 2 steps.

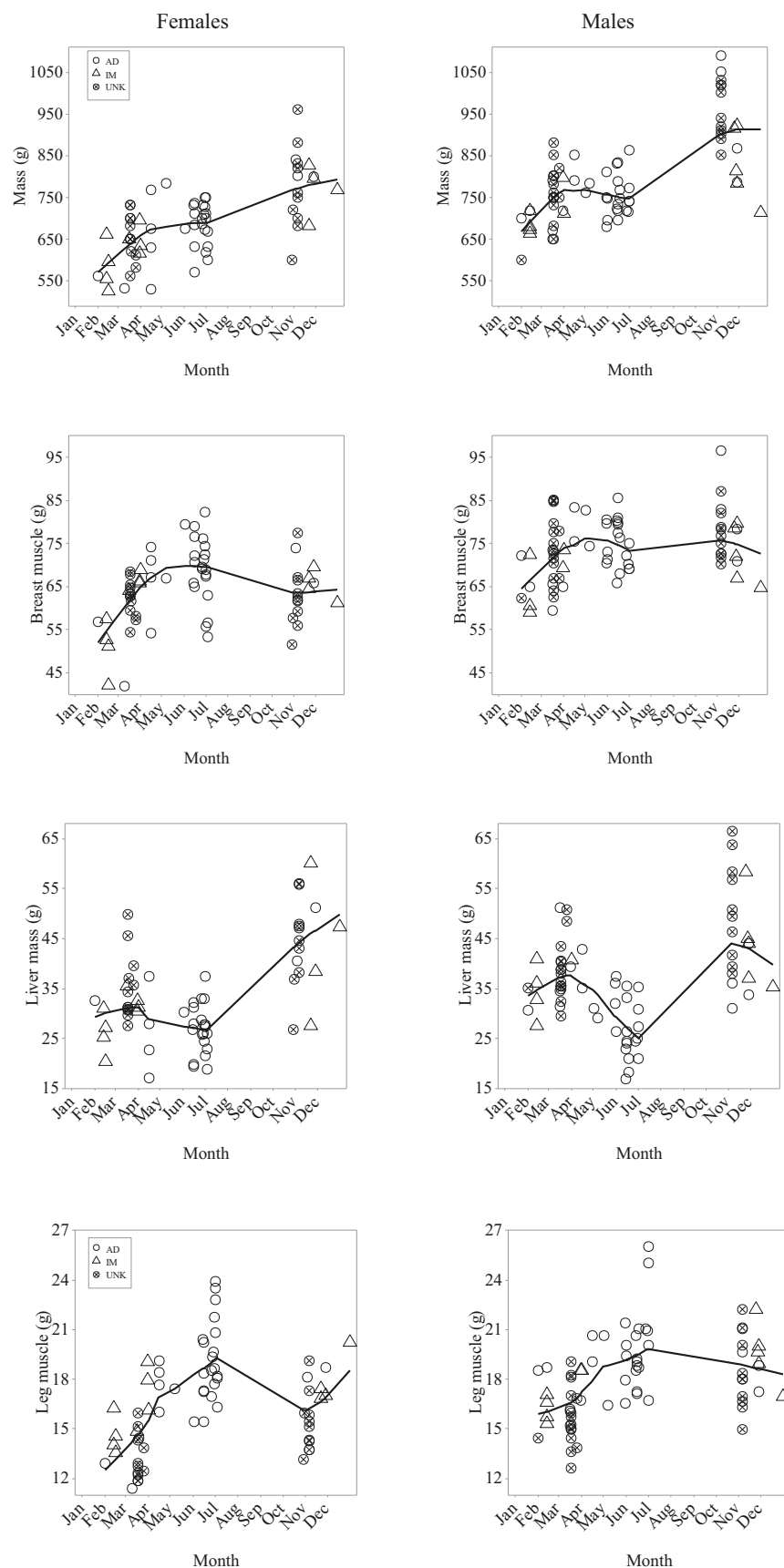


Fig. 2. (continued).

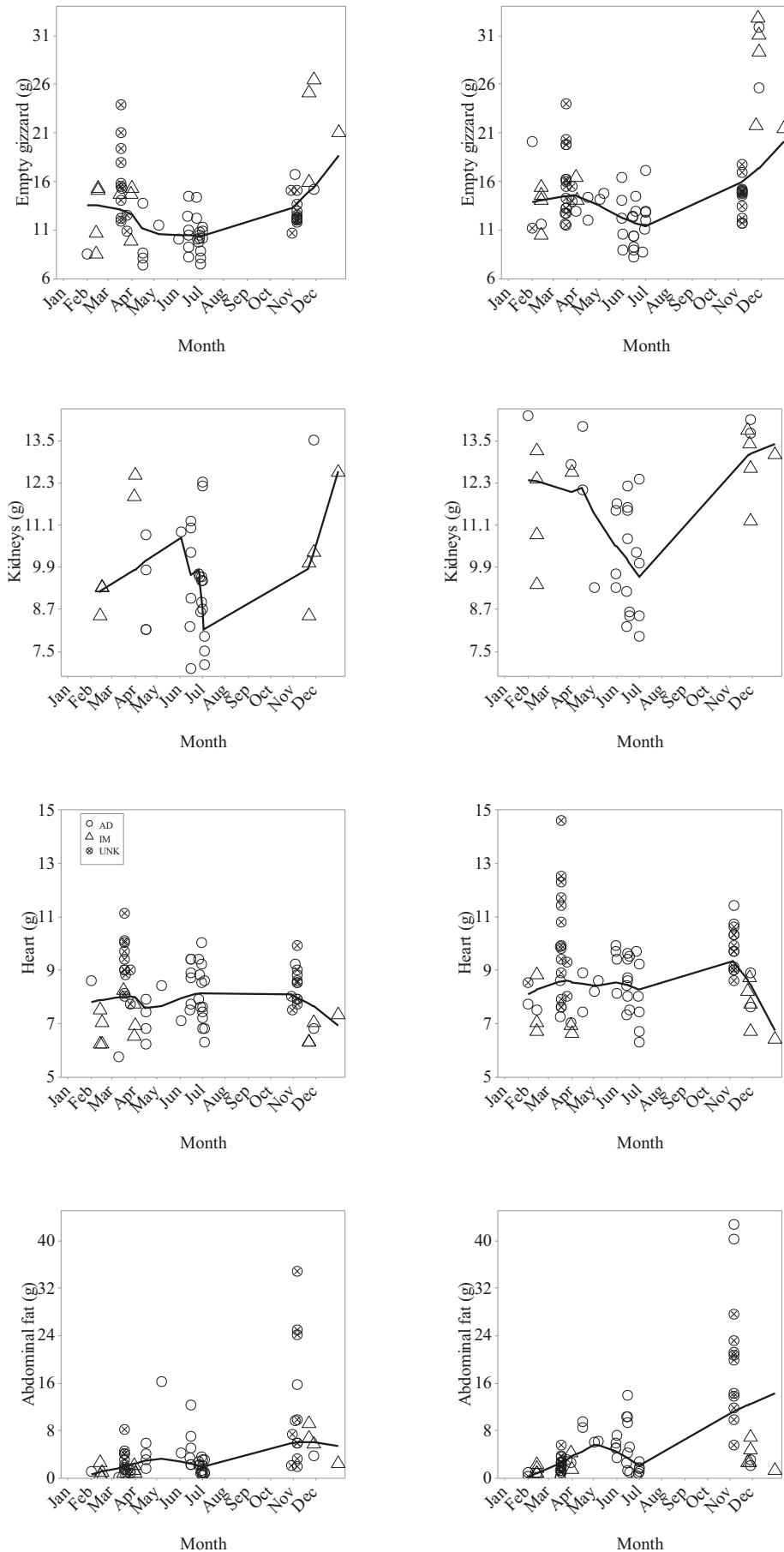
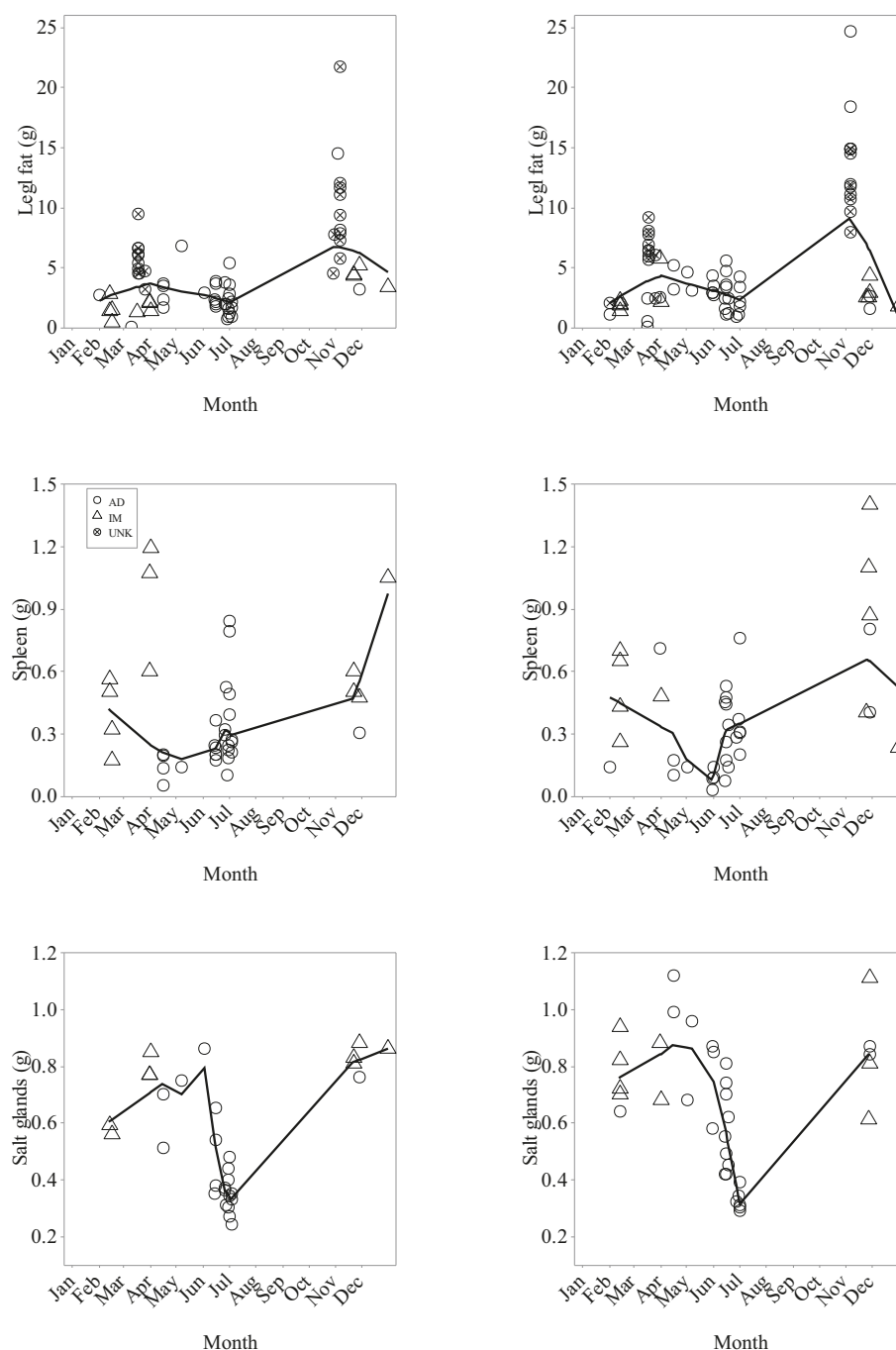


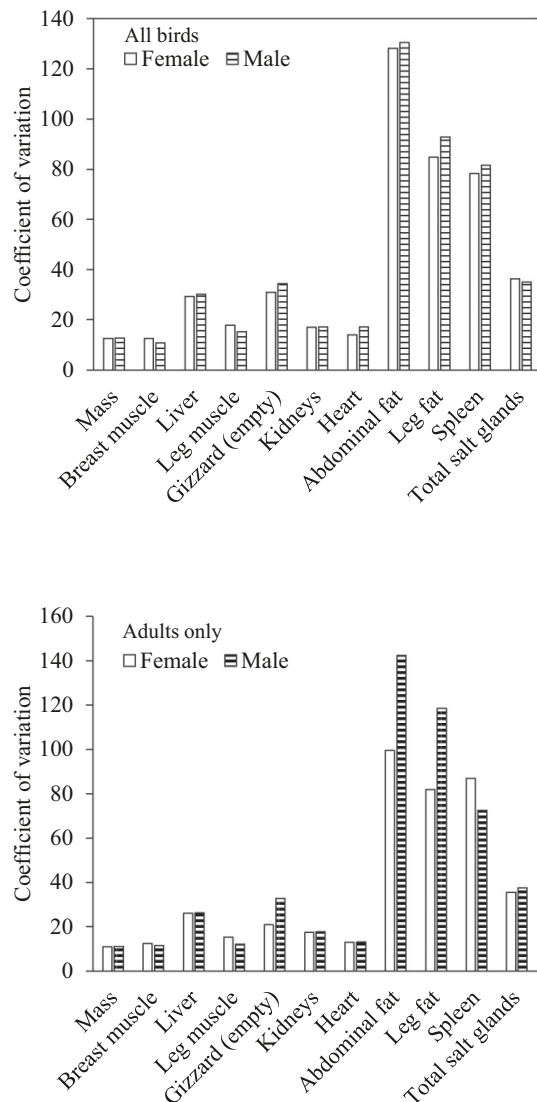
Fig. 2. (concluded).

unknown age birds from analyses did not substantively (<5%) affect results.

As expected, long-tailed duck organs and masses changed substantially during the year (Fig. 2) and, generally, in similar ways for females and males. Body mass gradually increased from February to November. Mass declined from November to February; however, complete dynamics of declines are unknown because we did not obtain birds during the middle of this interval. As general patterns, protein stores (i.e., breast muscle and leg muscle) masses peaked from May to July and remained relatively stable until November when they began to decline. Leg fat and abdominal fat did not fluctuate dramati-

cally until November, when they increased and were highly variable among individuals (Figs. 2, 3). Heart mass was stable over the course of the year. Finally, liver, gizzard, spleen, kidney, and salt gland mass were lowest in June and July (Fig. 2). Most of the organs and tissues we weighed changed synchronously; for example, increases in liver mass corresponded to increases in leg mass and in body mass (i.e., components of the overall bird got larger at the same time). Of 55 possible correlations for females, 43 were positive (binomial test, $P < 0.0001$), 33 significantly so, and only 3 were significantly and negatively correlated (Supplementary Table 2). Equivalent values for males were 37 positives (binomial

Fig. 3. Coefficients of annual variation for temporal changes in mass of various organs and tissues of long-tailed ducks (*Clangula hyemalis*) from Canada shown separately for females and males. Masses proceed from heaviest to lightest on the x-axis. Top figure uses all data; lower panel excludes immatures and unknown age long-tailed ducks.



test, $P = 0.007$), 27 significantly so, with 3 significantly negative. In general, correlations that were significant for females were also significant for males; for instance, in 23 cases, relationships were significantly positive for both sexes (e.g., total mass and breast muscle) (Supplementary Table 2).

Of the tissues and organs we weighed, breast muscle made up the greatest proportion (9.3%) of body mass for both sexes, salt glands the least for females (0.03%), and spleen the least for males (0.1%; Table 1). Coefficients of variation were highest for abdominal fat for both sexes, whether or not we excluded immature and unknown age individuals (Fig. 3). Relationships between the proportion of total body mass made up by a tissue or organ and their coefficients of variation were significantly negative for females ($r_s = -0.67$, $P = 0.03$) and males ($r_s = -0.76$, $P = 0.01$).

Models to predict mass of tissues and organs had R^2 values ranging from 0.06 for total salt glands to 0.55 for total mass (Table 2). Day of the year was a significant predictor for 8 of 10 models, sex for 2 models, and the interaction was not significant in any models. The only overall models that did not detect a significant amount of variation in mass were those for spleen and total salt glands (Table 2).

Correlations among morphological traits ranged from 0.24 (keel and tarsus wrist) to 0.87 (wing chord and 9th primary; Supplementary Table 3). The first PC (hereafter SIZE) captured the majority of variation in morphology (Supplementary Table 3; remaining PCs explained less variation than expected by chance based on the broken stick criterion (Jackson 1993) and were not retained. Because not all variables were measured on all ducks, sample size was reduced to 125 for the PCA, and then because of missing mass variables, was at most 115 (mass, breast muscle, and leg fat), and as little as 60 (kidney). In comparison to the results in Table 2, in models controlling for SIZE, day of the year was no longer significant for breast muscle, leg muscle, or log spleen mass (Table 3). Sex was no longer significant for breast muscle, but became significant for liver, log abdominal fat, and total salt glands (Table 3). The interaction between day of the year and sex remained non-significant for all 11 mass variables (cf. Table 2).

Discussion

As expected, body, tissue, and organ mass fluctuated during the annual cycle of long-tailed ducks (Peterson and Ellarson 1979), as occurs in numerous other taxa (e.g., Scott et al. 1994; Piersma et al. 1999; Jamieson et al. 2006b; McGuire et al. 2013). For the most part, tissues and organs we weighed increased or decreased at similar times. Magnitudes of changes (CVs) were similar for females and males despite differences in ecologies (also see Landys-Ciannelli et al. 2003). Magnitudes of changes in the annual cycle tended to be most extreme for the lightest tissues and organs; we are not aware of previous tests for this pattern. However, it echoes a pattern that occurs interspecifically relative to total body mass: lighter species undergo proportionately greater changes in mass than heavier species (e.g., Moreno 1989). A fuller assessment of this relationship will require a more sophisticated analysis controlling for potential confounding factors (e.g., phylogeny, habitat, altricial vs. precocial, migration strategy). A surprising finding was that there was no interaction between date and sex in mass changes (whether we controlled for SIZE or not); in other words, timing of mass changes was relatively synchronous for the sexes, again despite differences in ecologies (Fleskes et al. 2016; Veon et al. 2023). This may be because breeding seasons are shorter for high-latitude breeders (Winkler et al. 2014) so that greater temporal resolution would be required to detect differences.

Overall annual changes were captured with total body mass, partly driven by changes in fat storage because patterns were similar for abdominal and leg fat. Mass was highest after fall migration, prior to depletion of reserves to fuel migration and prior to times of more restricted food intake, similar to what occurs in many other taxa (Fox et al. 1992; Piersma

Table 2. Tests of sex differences in timing of change in mass of long-tailed duck organs and tissues.

Variable	N	Predictor						Overall model		
		Day of year		Sex		Day of year * sex		R ²	F	P
		F	P	F	P	F	P			
Mass	140	101.6	<0.0001	12.2	0.0007	0.5	0.47	0.55	56.0	<0.0001
Breast muscle	139	7.0	0.01	10.3	0.002	0.1	0.81	0.29	17.8	<0.0001
Liver	134	25.9	<0.0001	3.1	0.08	1.0	0.32	0.18	24.9	<0.0001
Leg muscle	140	17.0	<0.0001	1.8	0.18	0.2	0.65	0.18	9.7	<0.0001
Log(empty gizzard)	137	9.3	0.003	0.4	0.51	0.7	0.41	0.12	5.9	0.0008
Kidneys	72	3.3	0.07	2.4	0.12	<0.1	0.93	0.18	5.0	0.003
Heart	138	<0.1	0.85	2.2	0.14	0.1	0.79	0.08	4.0	0.009
Log(abdominal fat)	139	59.5	<0.0001	0.1	0.77	0.2	0.64	0.32	20.8	<0.0001
Log(leg fat)	134	28.3	<0.0001	0.1	0.72	0.1	0.83	0.18	9.5	<0.0001
Log(spleen)	77	5.5	0.02	0.9	0.36	0.8	0.39	0.09	2.3	0.09
Total salt glands	68	0.4	0.52	3.0	0.09	1.2	0.28	0.06	1.5	0.24

Note: Some variables were not measured for some ducks, so sample sizes vary. Significant associations in bold.

Table 3. Tests of sex differences in timing of change in mass of long-tailed duck organs and tissues controlling for body size (SIZE) using the first PC of a PCA (Supplementary Table 3).

Variable	N	Predictor								Overall model		
		SIZE		Day of year		Sex		Day * Sex		R ²	F	P
		F	P	F	P	F	P	F	P			
Mass	115	0.5	0.48	75.4	<0.0001	3.5	0.06	1.8	0.19	0.58	37.2	<0.0001
Breast muscle	115	20.3	<0.0001	0.1	0.71	<0.1	0.91	2.2	0.14	0.42	20.2	<0.0001
Liver	110	23.9	<0.0001	46.9	<0.0001	8.2	0.005	0.1	0.74	0.34	13.7	<0.0001
Leg muscle	115	42.9	<0.0001	0.8	0.39	1.9	0.17	0.2	0.70	0.40	18.4	<0.0001
Log(empty gizzard)	114	4.2	0.04	15.1	0.0002	1.7	0.20	0.7	0.41	0.17	5.5	0.0004
Kidneys	60	0.2	0.64	3.2	0.08	2.2	0.14	0.2	0.68	0.21	3.6	0.01
Heart	114	1.0	0.33	0.1	0.74	0.4	0.52	1.8	0.18	0.10	3.0	0.02
Log(abdominal fat)	114	0.4	0.54	47.1	<0.0001	0.2	0.66	0.4	0.55	0.33	13.4	<0.0001
Log(leg fat)	115	15.5	0.0001	41.3	<0.0001	2.9	0.09	<0.1	0.83	0.29	11.2	<0.0001
Log(spleen)	66	6.4	0.01	15.0	0.0003	0.1	0.80	2.2	0.15	0.26	5.4	0.0008
Total salt glands	61	2.1	0.15	2.4	0.13	6.3	0.01	1.4	0.24	0.15	2.5	0.05

Note: Some variables were not measured for some ducks, so sample sizes vary. Significant associations in bold.

and Jukema 2002; McWilliams and Karasov 2005). Although the bulk of changes in mass are ascribed to lipids, changes in protein and minerals also contribute (Williams 1996). For example, organs can be protein sources for developing eggs; accordingly, female gizzard masses decrease during oviposition (Raveling 1979; Williams 2005) and breast and leg muscles provide fuel for long distance migration (Bauchinger and Biebach 2001, 2005). The relative importance of various nutrients to specific demands is complex; for example, egg-laying and endocrine functions make greater use of lipids than does immunity (Sturkie 1986).

Consistent with our results, digestive organs (livers, gizzards, intestines) tend to increase as birds near staging intervals, accumulating reserves in preparation for migration (Ankney and MacInnes 1978; Kehoe and Ankney 1985; Ebbinge and Spaans 1995; Piersma et al. 1999). In particular, livers are instrumental in fat metabolism (Newsholme and Start 1973; Rattner and Jehl 1997); it thus also makes sense that their mass decreases when birds fast such as during in-

cubation (Raveling 1979; Jehl 1997). Flightlessness following breeding is associated with increased foraging prior to fall migration, and as expected is associated with enlargement of digestive organs (Jehl 1990). As staging nears completion (i.e., shortly before migration), gizzards and intestines shrink (McWilliams and Karasov 2005). Gizzard size also fluctuates between the pre-breeding and breeding season, likely as a result of decreased foraging during reproduction (Laursen and Møller 2016). The observation of significant variation in liver and gizzard mass supports the hypothesis that organ size is adjusted throughout the annual cycle of long-tailed ducks, and is broadly consistent with previous research (e.g., Piersma and Lindström 1997; McWilliams and Karasov 2005; Sandri 2008).

Breast muscles that are instrumental during migration may become less essential while tending eggs and young (Jehl 1997; Piersma 1998; King et al. 2015). Although breast muscles weighed less in winter before migration, we did not detect substantial changes from once breeding began to early

winter. Because of a lack of sampling from August to October, we may have missed changes in breast muscle mass that have been reported elsewhere. In contrast, leg muscles are probably of limited importance during migration, and more important when foraging becomes paramount, which occurs just before migration and when acquiring nutrients for breeding. These changes in leg muscles were observed in our study.

Heart mass tends to increase before migration in anticipation of higher aerobic capacity needed for flight (Driedzic et al. 1993; Jehl 1997; Piersma et al. 1999), and decrease as a result of reduced aerobic demands (Fox and Kahlert 2005). Although variation in heart mass appeared highest around the two migratory periods in long-tailed ducks, overall, we observed little temporal change through the year. A relatively consistent heart mass suggests that demands on cardiac muscle remain relatively constant throughout the year for long-tailed ducks, perhaps because diving for food requires long-tailed ducks to maintain aerobic capacity (Drabek and Tremblay 2000).

Birds that obtain food or drinking water from saline habitats invest more in salt excretion using their kidneys, and in some cases salt glands, than those in freshwater habitats (Sturkie 1986). Thus, it was expected that when our long-tailed ducks were relying to a greater extent on fresh water at inland breeding sites, smaller kidneys and salt glands would be observed. CVs for salt glands were higher than they were for kidneys, but assuming a direct correlation between size and salt filtering, ranges in kidney mass were ~ 6.5 g whereas for salt glands the range was only ~ 0.4 g. Thus, kidneys in absolute terms contributed greater mass change than did salt glands in responding to changes in salt intake.

We expected to find a significant interaction between sex and time of year in affecting variation in tissue and organ mass. It may be that temporal differences in demand have limited time to shift in compressed long-tailed duck breeding seasons, so that sex differences in timing are less pronounced than they might be for species or populations breeding at lower latitudes. Another possibility is that the temporal gaps in our sample collections obscured sex differences in timing of mass changes. Although 153 is a reasonable sample size, it was spread over an entire year, which likely limited our power to detect differences.

No data were collected from August to October or in January, so we can only infer how masses fluctuated during these periods (but see Peterson and Ellarson 1979). Schummer et al. (2012) sampled long-tailed ducks in the winter on the Great Lakes and showed declines in fat reserves from December through March, which corresponds to the pattern we observed in body mass. We note carcasses spent different amounts of time stored frozen before processing so that masses were not precisely comparable. In addition, sampling relied on volunteers and was partly opportunistic. Imperfect sampling is common in ecological research, and it does require us to be cautious in our interpretations. Nonetheless, our sample size was relatively healthy, and we have no reason to suspect significant bias as a consequence of our sampling design.

At high latitudes, resource availability increases and decreases more rapidly than at lower latitudes, attendant with the rate of changes in daylight hours and primary productivity (Alerstam 1990; Winkler et al. 2014). One of our intentions was to evaluate effects of breeding latitude in an interspecific comparison, but we discovered that the necessary information was largely unavailable from the published literature (Ray Alisauskas pers. comm). We encourage future work to address this by providing CVs for mass change to enable such tests.

Larger species have lower proportional, but higher absolute, capacities to store fat (e.g., Raveling 1979; English et al. 2018). Based on CVs, the same also appears to be true for individual tissues, as would be expected given that whole animals are the sums of their parts. However, the pattern is not precisely linear (e.g., abdominal fat had the greatest CV, but was not the lightest item we weighed), and it may be instructive to evaluate the patterns reported here in other species to more rigorously determine reasons for this nonlinearity (Jamieson et al. 2006b). Whereas we attempted to control for some measurement error by having the same investigator do all the laboratory work, measurement error may have contributed to the greater CVs in smaller tissues and organs simply because smaller organ can be challenging to excise precisely.

Ideally, individual ducks would have been followed throughout the year and sampled repeatedly for at least total body mass. Moreover, a more even sample size from each study location may have altered our interpretation of annual patterns in atrophy and hypertrophy. Finally, it would have been useful to know the breeding provenance of long-tailed ducks collected between November and May. It is important to recognize these issues, but we believe more important to have access to the data we present.

We have only considered effects of seasonal changes on tissues and organs. Many other factors, such as anthropogenic stressors (e.g., hunting pressure, contaminants, climate change, encroachment of humans) and parasites are woven into these patterns (e.g., Pfister et al. 1992; Shutler et al. 1999, 2012). For example, the liver performs a critical role in immunity by filtering blood to eliminate pathogens and hepatomegaly can result from infection (Grant 1991; Jenne and Kubes 2013). Because the aforementioned stressors are temporally dynamic, and particularly so in recent decades (e.g., Halpern et al. 2015), patterns we report here may not reflect historical patterns or selection pressures that produced phenotypes we are currently measuring, nor will they reflect impending selection pressures or future phenotypes. Only compilations of historical data will permit us to evaluate consequences to these patterns for long-tailed ducks and other species.

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Data availability

Data generated or analyzed during this study are available in the Dryad repository, (DOI): doi:[10.5061/dryad.t1g1jwttb](https://doi.org/10.5061/dryad.t1g1jwttb).

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Competing interests

The authors have no competing interests that could have influenced the work reported in this paper. Mark Mallory served as Co-Editor-in-Chief at the time of manuscript review and acceptance but did not handle peer review or editorial decisions regarding this manuscript.

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Ethical statement

Our research used ethically harvested carcasses obtained as described in the paper. Inuit organizations in NU, such as the Iqaluit Hunters and Trappers Organization and Hunters and Trappers Association hold the legal right to hunt and process long-tailed ducks within their respective quotas. We recognize the importance of obtaining ethical permits for animal-based research when necessary. However, the Canadian Department of Fisheries and Oceans and Environment and Climate Change Canada do not require ethical waivers or approvals for the use of Inuit-harvested samples in this circumstance.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/as-2024-0010>.

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