Does organ and muscle plasticity vary by habitat or age in wintering Lesser Snow Geese *Anser caerulescens caerulescens*?

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Abstract

Plasticity in organ and muscle size and function allows individuals to respond to changes in food quality or foraging behaviour, in accordance with cost-benefit hypotheses. Lesser Snow Geese *Anser caerulescens caerulescens* (hereafter Snow Geese) winter in rice-prairie and coastal-marsh habitats in southwest Louisiana, where the time that the birds spend foraging and walking, their composite diets, and associated fibre and energy contents, differ between these two habitats. We therefore hypothesised that: 1) Snow Geese that feed primarily in coastal marshes during winter would have larger digestive organs than those in rice-prairies, to adapt to the higher fibre content of their marsh vegetation diet; and 2) that leg muscles of Snow Geese feeding in rice-prairies would undergo greater hypertrophy and thus be larger than those in coastal marshes, because individuals in rice-prairie habitat spend more time walking while foraging. The first hypothesis applied to adults and juveniles alike, whereas under the second hypothesis, we knew from concurrent studies that juveniles walk more than adults and therefore predicted that they would have relatively larger leg muscles, after adjusting for body size. Seventy juvenile and 40 adult Snow Geese were dissected to test these two hypotheses about plasticity and hypertrophy with respect to habitat and foraging behaviour. Caeca and gizzard lengths were found to be larger for Snow Geese feeding in coastal marshes, where the food ingested is relatively high in fibre compared with the birds' diet in the rice-prairies. Conversely, leg muscles were larger for Snow Geese foraging in rice-prairies, where the juvenile geese spend relatively more time walking. Although not fully grown, juvenile Snow Geese also varied in the length of their digestive system and hypertrophy in muscles in relation to habitat, reinforcing the view that the birds' morphology adapts to different feeding habitats and diets.

Key words: diet, ecological segregation, geese, habitat selection, individual variation, Louisiana.

Plasticity (also termed morphological flexibility) in the length and function of digestive organs allows individuals to respond to variation in food quality or availability, or to respond to variation in foraging behaviour (Ankney & MacInnes 1978; Prop & Vulink 1992; Piersma & Lindström 1997; Starck 1999; Tielemann *et al.* 2003; Fox & Kahlert 2005; Williamson *et al.* 2014). Such changes can occur swiftly and repeatedly, and can also be reversible when needed. These seasonal changes represent trade-offs between the costs and benefits associated with maintaining organs or muscles at particular sizes, which can be explained in terms of prevailing ecological conditions and often expressed as the "cost-benefit hypothesis" (van Gils *et al.* 2003; Fox & Kahlert 2005). The adaptive value of these changes is to allow the organism to respond effectively to changes in ecological conditions (such as food types or food quality), so as to benefit individuals whilst the energetic costs of organ changes (*e.g.* carrying or maintaining larger or more complex organs) are kept to a minimum. Such evolutionary adaptations have been identified to meet specific or seasonal needs of breeding, migration and moult (Moorman *et al.* 1992; Prop & Vulink 1992; Piersma & Lindström 1997; Piersma *et al.* 1999; Starck 1999; van Gils *et al.* 2003; Fox & Kahlert 2005).

Plasticity is most commonly observed for the digestive system in birds, but also occurs for several other internal organs in response to seasonal changes, such as the heart and muscles (Ankney & MacInnes 1978; Piersma *et al.* 1999). Adaptations to changes in foraging conditions have been found to induce plasticity trade-offs in leg muscles, which can undergo atrophy or hypertrophy depending on how much running or walking is required within a season, or in areas with higher predation pressure (Fox & Kahlert 2005). Wild Barnacle Goose *Branta leucopsis* goslings become less active as the goslings mature and prepare to fly south and this decline in activity correlates with decreased aerobic capacity of the leg muscles (Bishop *et al.* 1998). However, it is unclear whether juvenile geese, which are not fully grown until after the first year of life (Davies *et al.* 1988; Cooch *et al.* 1991; Larsson & Forslund 1991), have developed organ systems capable of responding to environmental variation to the extent that adults are able to show organ plasticity. We nevertheless hypothesised that, although body size is not fully formed during the first winter of age in geese, the adaptive value of digestive organ plasticity in relation to habitat would provide benefit to both age groups (adults and juveniles).

Lesser Snow Geese *Anser caerulescens caerulescens* (hereafter Snow Geese) use rice-prairie and coastal-marsh habitats in southwest Louisiana during winter (Alisauskas *et al.* 1988; Alisauskas 1998; Jónsson & Afton 2006, 2015a, 2016; Jónsson *et al.* 2014). The relative costs and benefits to the geese in terms of food intake can vary annually for these two habitats in relation to weather or food availability (Alisauskas 1998; Alisauskas *et al.* 1988; Jónsson & Afton 2006; Jónsson *et al.* 2014). Coastal-marsh Snow Geese feed primarily on tubers of sedges *Scirpus* sp. (48% mean dry weight of vegetation consumed; Alisauskas *et al.* 1988) and on rhizomes of

Saltmeadow Cordgrass *Spartina patens* and Common Saltgrass *Distichlis spicata* (27% mean dry weight of plant vegetation consumed; Alisauskas *et al.* 1988). In contrast, rice-prairie Snow Geese ingest green vegetation, *i.e.* weedy forbs (70% mean dry weight of plant structures consumed) and graminoid leaves of rice plants (28% mean dry weight of plant structures consumed). Forbs comprise 13% crude fibre and 32% crude protein; tubers comprise 12% crude fibre and 7% crude protein; and rhizomes comprise 28% crude fibre and 4% crude protein (Alisauskas *et al.* 1988). Alisauskas *et al.* (1988) therefore defined the composite diets for Snow Geese wintering on the coastal marshes of southwest Louisiana as being of relatively high fibre content (20% dry weight) and low protein (8% dry weight; hereafter coastal-marsh diets). Corresponding values for rice-prairies were 15% and 27% dry weight for fibre and protein contents, respectively (hereafter rice-prairie diets). Digestibility of food, defined as the percentage of a given nutrient taken into the digestive tract that is absorbed into the body, generally is inversely related to fibre content and positively related to protein content (Sedinger & Raveling 1988; Prop & Vulink 1992; Sedinger 1997), and thus the marsh composite diet is less digestible than the corresponding rice-prairie composite diet.

Phenotypic changes to the gizzard or other digestive organs may be advantageous for: 1) improving the ability to grind plant materials that are rich in fibre, low in protein and therefore low in digestibility (Prop & Vulink 1992), such as *Scirpus* tubers in coastal marshes (Alisauskas 1988; Alisauskas *et al.* 1988); or 2) obtaining a higher energy yield from the more fibrous diet, rather than simple physical effects of fibre content on food intake rates or on mechanical (muscular) compensation to fibrous food material (Williamson *et al.* 2014). A longer gut will prolong gut retention time, allowing increased absorption from diets with low digestibility (Prop & Vulink 1992). Accordingly, we hypothesised that Snow Geese (adults and juveniles alike) collected in coastal marshes would have larger digestive organs than those collected in rice-prairies.

Our earlier analysis of the behaviour of Snow Geese in the same study area found that their time-budgets differed between the rice-prairie and coastal marsh habitats, but these differences also varied with the age group of the birds. Adult geese on the rice-prairie spent, on average, 40% of their time feeding and 4.2% in locomotion, compared with 52% and 2% for those in coastal marshes. In contrast, juveniles on rice-prairies spent, on average, 54% of their time feeding and 5.1% in locomotion, compared with 41% and 1% respectively for juveniles in the coastal marshes (Jónsson & Afton 2006). Swimming was included in the locomotion category, but was rarely observed in the marsh where geese walked across vegetation mats. Because Snow Geese mostly actively search whilst feeding, we therefore hypothesised that among juveniles, Snow Geese would walk more in rice-prairies (the habitat where juveniles have to feed and walk for longer periods) than in coastal marshes, and thereby attain larger leg muscles. Although the Jónsson & Afton (2006) time-budget data indicated that adults also walk more when in coastal marsh habitat, the difference was less marked than for juveniles, so we predicted that leg muscles in this study would be of similar size across habitats for the adult geese.

A total of 110 Snow Goose specimens were collected and dissected to test the two main hypotheses. Firstly, that the digestive organs would differ in length by habitat, with habitat plasticity being evident for both age categories (*i.e.* adults and juveniles), and secondly that habitat-induced mobility would affect the size of leg muscles in waterfowl dependent on age, in that it would be evident in juveniles but not in adult birds.

Methods

Study area

Our study area (10,764 km^2) in southwest Louisiana was bordered by Sabine National Wildlife Refuge (29°53'N, 93°23'W) on the west; Lake Charles and Highway 383 on the northwest; Highway 190 on the north; Highway 387 and Interstate 10 on the northeast; Highway 35 on the east, and the Gulf Coast on the south (see map in Jónsson *et al.* 2014). The Intra-coastal Canal generally separates the coastal marsh from the rice-prairies in southwest Louisiana (Bateman *et al.* 1988). Coastal marshes are comprised of fresh, intermediate, brackish or saline wetlands, but fresh and intermediate wetlands are not used frequently by Snow Geese. The coastal brackish and saline wetlands of the coastal marshes are about 32 km from the rice-prairies, which also are used by Snow Geese (Bateman *et al.* 1988). Rice-prairies are former tall-grass prairies that have been extensively cultivated, mostly for rice, but also as pastures for cattle (Alisauskas 1988; Alisauskas *et al.* 1988; Bateman *et al.* 1988).

As with previous studies of Snow Geese in this area (Alisauskas *et al.* 1988, 1998; Jónsson & Afton 2016), we acknowledge that the birds may move between habitats and that, rather than staying in rice-prairies or coastal marshes for prolonged time periods, geese included in the study could have moved between habitats prior to collection. Our concurrent banding study however demonstrated that movements between habitats occurred only occasionally (Jónsson *et al.* 2014), and we therefore remain confident that, overall, the two groups were segregated and consistently exposed to diets of different fibre contents for a sufficiently long period to warrant a comparison of digestive organs between habitats. Despite these occasional movements, variation in skeletal morphology indicative of habitat segregation, first reported by Alisauskas (1998), was also evident during our 2002–2004 study (Jónsson 2005).

Collection of Snow Goose specimens

We examined gut and muscle samples from 70 juvenile and 40 adult Snow Goose specimens collected from 20 November to 17 February in the winters of 2001/02, 2002/03 and 2003/04, using 0.22 rifles and 12 gauge shotguns. The samples were collected within a 13 week period over the three different winters; variation in measurements attributable to collection date (measured as the number of days from 20 November each year) therefore was assessed in the subsequent analyses. These comprised 70 geese (21 adult females, 15 adult males, 15 juvenile females and 19 juvenile males) from the rice-prairies of Sweet Lake (8–16 km north of the Cameron Prairie National Wildlife Refuge; 29°51'N, 93°13'W) or in the vicinity of the towns of Lake Arthur at Oak Island (30°00'N, 92°04'W) and Thornwell (30°10'N, 92°80'W), and 40 geese (2 adult females, 2 adult males, 21 juvenile females and 15 juvenile males) from coastal marshes at Rockefeller State Wildlife Refuge (29°40'N, 92°55'W).

Collected specimens were individually double-bagged and frozen, and subsequently stored in a walk-in freezer at Louisiana State University. Collected specimens were sexed *post mortem* by cloacal examination (see Hochbaum 1942) and age was confirmed by plumage colour as either juvenile (hatch-year) or adult (see Baldassarre 2014). The geese were collected under the U.S. Fish and Wildlife Service's scientific collection permit MB048372-0, the Louisiana Department of Wildlife and Fisheries' scientific collection permit LNHP-01-052, and Louisiana State University Agricultural Center Institutional Animal Care and Use Committee's (LSU AgCenter IACUC) protocol number A01-09.

Digestive organ measurements

All specimens were thawed and measured, weighed and dissected (see Jónsson & Afton 2016). Specifically, we opened the abdominal cavity on the left side of each specimen, and carefully pulled out the alimentary tract. The gizzard was excised and measured with calipers (± 0.1 mm). The lengths of the following segments were disentangled, straightened and measured with a ruler (± 1 mm): 1) the upper digestive tract from the tip of the bill to the entrance to the gizzard, including the oesophagus and proventriculus (this approach provided reliable and repeatable start and end points for this measurement); 2) gizzard length; 3) the small intestine from the exit of the gizzard to the caecum; 4) both caeca; and 5) the large intestine.

Leg muscle measurements

We measured and weighed the paired gastrocnemius and tibialis anterior muscles (hereafter collectively termed "leg muscles"), which were cut from their attachment sites on the tibio-tarsus of the leg. These muscles were selected because others are more difficult to remove intact, and use of intact muscles ensures that the measurements are repeatable. Muscles were weighed with a digital scale to ± 0.1 g and measured immediately after excision. The muscles were then laid on a flat surface for measurement of muscle diameter (the response variable for leg hypertrophy), which was measured once, at the widest point of each muscle with digital calipers (± 0.1 mm).

Standardising data for body size effects

On analysing variation in digestive organ measurements, we included as response variables in linear mixed models the length of the upper digestive tract, the gizzard, the small and large intestines, and also the averaged lengths of the two caeca. For leg measurements, we included the weights and diameters of the gastrocnemius and tibialis muscles (4 measurements in total) as response variables in the analyses.

Researchers typically standardise measurements to some value representative of body size, particularly for species where there is known to be variation in body size across individuals that may influence the hypotheses being tested in the study (Relya 2005). We had good reasons to expect that overall body size would influence the sizes of our response variables (*i.e.* the length of the digestive organs or leg muscle diameters) for the Snow Geese. We therefore initially explored variation in body size in relation to age and sex, because we knew *a priori* that: 1) males are larger than females (Cooch *et al.* 1991; Alisauskas 1998; Jónsson 2005); 2) adults are larger than juveniles (Cooch *et al.* 1991; Jónsson 2005); and 3) that habitat can be related to body size in at least some years (Alisauskas 1998). We used a principal components analysis (PCA) on nine morphological measurements (skeletal morphology) to index body size (Alisauskas 1998; Jónsson & Afton 2016), using one PCA for all age and sex groups, so that PC1 would include body size variation attributable to sex, age, habitat and individual variability. The first principle component (PC1) of these nine morphological measurements explained 60.9% of the overall variation in this dataset and, thus, is a useful index of body size. We also considered the approach of Meixell *et al.* (2016) who used a segregated PCA to remove body size variation due to sex and age, but the results did not differ between the two PCA approaches, perhaps because in both analyses the effects of the PC1 were apparent only for upper digestive tract and (weakly) for gizzard length. Here, we therefore present findings using the one PCA for all age and sex groups approach.

When PC1 was compared among adults and juveniles of each sex, adult males were larger than females in both age groups, females were similar in body size regardless of age, and juvenile males were intermediate between adult males and the two female groups (Appendix 1). We therefore standardised the organ measurements for body size effects by regressing PC1 on each of the digestive organ and leg muscle measurements to obtain residual values for each measurement for each individual. We then added the residual value to the overall mean measurement to obtain standardised individual size-adjusted values (mean + residual) (see Ankney & Afton 1988; Afton & Ankney 1991).

In addition to the habitat and age explanatory variables, we considered the effects of sex because males are larger than females (Alisauskas 1998; Jónsson & Afton 2016), and sex effects are commonly considered in studies of organ plasticity (Fox & Kahlert 2005; Laursen & Møller 2016). Sex, age and habitat were considered explanatory fixed effects because we included all possible groups of each variable. Adjusting our response variables with PC1 (overall body size) may conceivably have removed some of the variation associated with sex and age, but we chose to retain age and sex in the analyses because PC1 represents 49–61% of overall variation in the morphological measurements of wintering Snow Geese (Alisauskas 1998; Jónsson *et al.* 2014; Jónsson & Afton 2016; this study), and some of the body size variation therefore may not by represented by PC1 but rather by PC2, PC3, *etc*. We considered age in particular to be important, because juvenile Snow Geese are not fully grown until after 1 year of age (Cooch *et al.* 1991) and their internal organs may not be fully developed during the first winter of life. Age therefore was included in the analysis despite sample sizes being low for adults in the coastal marshes (*n* = 4), albeit higher for adults on rice-prairies (*n* = 36), because the data were obtained initially for a study on foraging by juvenile Snow Geese (Jónsson & Afton 2016). Comparisons of adult and juvenile morphologies in relation to habitat are consequently interpreted with consideration to these sample size restrictions in the current study.

Sampling effort also was not evenly distributed across the three winters (2001/02–2003/04 inclusive), with 2002/03 accounting for 67% of our collected specimens (23 adults; 51 juveniles). It therefore was not feasible to include winter as an explanatory variable in the model, especially not in relation to sex or age. Given that most of the birds were collected in a single winter, and that within-winter effects may be more important than annual variation in influencing gut and muscle measurements (because of the length of time that the birds have been on the two habitats since the start of the winter), we considered temporal variation by including collection date as a random effect and assumed that effects of collection date were independent of winter. We know from our sample of neck-collared Snow Geese (Jónsson & Afton 2014) that their mean (± s.d.) duration of stay in Louisiana was 57.3 (± 32.3) days (J.E. Jónsson & A. Afton, unpubl. data), and that collection date can serve as an index of how long each specimen had been in southwest Louisiana. We compared standardised regression coefficients (*i.e.* betas from z-scored variables) for meaningful correlations (indicated by AIC) between collection date and each measurement, to evaluate which measurement was mostly influenced by collection date.

Linear mixed model analysis

The body size adjusted measurements for each digestive organ were used as response variables in linear mixed model analysis. A second PCA was used to reduce the dimensions of the body size adjusted muscle measurements from four dimensions to one before running the linear mixed models. Here, the first PC score (hereafter termed leg muscles) explained 62.3% of the overall variation in the four muscle measurements.

AIC model selection (Anderson 2008) was used to compare linear mixed models for the PC scores between sex (male or female) and habitats (rice-prairies *versus* coastal marshes), using the AICcmodavg package in the R system (Mazerolle 2015). We followed Burnham and Anderson (2002) and Anderson (2008), in considering that models which make no biological sense need not be tested. We therefore included only interactions relating to the study hypotheses in our models, in particular the habitat * age interaction to test the hypothesis that organ plasticity by habitat is independent of age, although the low sample size for adults in coastal marshes requires careful interpretation of this interaction for this dataset. We did not include the habitat * sex interaction because we had no biological reasons to believe that sex effects would depend on habitat, or *vice versa* (*i.e.* that one sex would be affected by habitat differences and not the other). Most adult birds are paired, so the sexes generally do not segregate by habitat, and males and females therefore should respond to habitat variation independently of sex. The age * sex interaction was included because data inspection suggested that age effects were dependent on sex (*i.e.* adult males were larger in overall body size than juvenile males), whereas adult and juvenile females were similar in overall body size (Appendix 1).

Model building followed a four-step process: 1) we commenced with a model which included all of the fixed explanatory variables (Habitat + Sex + Age), and then added all nested models, including the single effects models for each of these variables; 2) collection date was included as a random effect in all models and calculation of AIC values were repeated; 3) the age * sex interaction was added to all models that included both age and sex, and the habitat * age interaction was added to all models that included both habitat and age; and lastly 4) we ran null models (models with intercept only) for all analyses, resulting in 26 models.

Following Anderson (2008), we identified pretender variables as follows: candidate models which are within ΔAIC $\leq$ 2.0 of the top-ranked model but differ from the top-ranked model by the inclusion of 1–2 additional variables, yet their log-likelihood values are almost the same as those of the top-ranked model (see also Jónsson & Afton 2016). Since we were running six model selections on six response variables, we also examined cumulative weights of variables to compare the relative importance of habitat, sex, age, and collection date relative to one another. Cumulative weights were calculated prior to running the last models, which contained the age * sex or habitat * age interactions, to ensure an even number of models for each variable.

Results

Generally, there were varying degrees of support for the explanatory variables among the six analyses (Tables 1a–1f), with only two analyses sharing the same top-ranked model, *i.e.* the model containing all five explanatory variables for small intestine and gizzard length. Effects of collection date and habitat or habitat * age were supported in four analyses and effects of sex * age were supported in three analyses. Of the correlations with collection date, caeca length had the highest beta (0.158) whereas small intestine, large intestine and gizzard length had similar betas of 0.021, 0.036, and 0.046, respectively.

The best supported model for upper digestive tract was sex + age + sex * age, whereas there was no support for other models except habitat + sex + age + sex * age (ΔAIC = 1.3) and sex + age (ΔAIC = 1.7, Table 1a). However, we identified habitat as a pretender variable because of the small change in LogL (0.4) between habitat + sex + age + sex * age and the top-ranked model sex + age + sex * age. Cumulative weights for sex and age were both 1.00, compared to 0.30 and 0.06 for

Table 1. The top ten of 26 linear mixed models testing effects of sex, habitat, age, sampling date and collection date on the length of the digestive organs and leg muscles from 110 Snow Geese, collected in southwest Louisiana in winters 2002/03–2003/4. Models used for interpretation are shown in bold, see text for details.

(a) Length of the upper digestive tract

Rank	Model	K	AIC	ΔAIC	Wi	LogL
1	**Sex + Age + S * A**	**5**	**406.0**	**0.0**	**0.393**	**–197.7**
2	Habitat + Sex + Age + S * A	6	407.4	1.3	0.204	–197.3
3	Sex + Age	4	407.8	1.7	0.165	–199.7
4	Habitat + Sex + Age	5	409.4	3.4	0.073	–199.4
5	Habitat + Sex + Age + H * A + S * A	7	409.6	3.6	0.065	–197.3
6	Sex + Age + Collection date + S * A	6	410.9	4.8	0.035	–199.0
7	Habitat + Sex + Age + H * A	6	411.6	5.6	0.024	–199.4
8	Habitat + Sex + Age + Collection date + S * A	7	412.7	6.6	0.014	–198.8
9	Sex + Age + Collection date	5	413.3	7.2	0.011	–201.3
10	Habitat + Sex + Age + Coll. date + H * A + S * A	8	413.4	7.4	0.010	–198.0

(b) Length of caeca

Rank	Model	K	AIC	ΔAIC	Wi	LogL
1	**Habitat + Age + Collection date + H * A**	**6**	**544.2**	**0.0**	**0.213**	**–265.7**
2	Habitat + Sex + Age + Coll. date + H * A	7	545.9	1.7	0.092	–265.4
3	Habitat + Sex + Age + Coll. date + H * A + S * A	8	546.0	1.8	0.088	–264.3
4	Habitat	3	546.2	2.0	0.077	–270.0
5	Habitat + Collection date	4	546.5	2.3	0.068	–269.1
6	Habitat + Age + Collection date	5	546.5	2.3	0.067	–268.0
7	Habitat + Age	4	546.9	2.6	0.057	–269.2
8	Habitat + Sex + Age + H * A + S * A	7	547.0	2.8	0.053	–268.3
9	Habitat + Age + H * A	5	547.5	3.3	0.041	–268.5
10	Habitat + Sex + Collection date	5	548.0	3.7	0.033	–268.7

Table 1 (*continued*).

(c) Length of small intestines

Rank	Model	K	AIC	ΔAIC	Wi	LogL
1	**Habitat + Sex + Age + Coll. date + H * A + S * A**	**8**	**868.8**	**0.0**	**0.673**	**–425.7**
2	Habitat + Sex + Age + Coll. date + H * A	7	871.8	3.0	0.147	–428.3
3	Habitat + Sex + Age + Collection date + S * A	7	872.6	3.8	0.099	–428.7
4	Sex + Age + Collection date + S * A	6	875.4	6.7	0.024	–431.3
5	Habitat + Age + Collection date + H * A	6	875.5	6.8	0.023	–431.3
6	Habitat + Sex + Age + Collection date	6	875.7	6.9	0.021	–434.4
7	Sex + Age + Collection date	5	878.7	9.9	0.005	–434.0
8	Habitat + Age + Collection date	5	879.5	10.8	0.003	–433.1
9	Habitat + Sex + Collection date	5	880.1	11.3	0.002	–434.8
10	Sex + Collection date	4	882.2	13.4	0.001	–436.9

(d) Length of large intestines

Rank	Model	K	AIC	ΔAIC	Wi	LogL
1	**Collection date**	**3**	**393.3**	**0.0**	**0.226**	**–193.5**
2	Age + Collection date	4	393.6	0.3	0.192	–192.6
3	Habitat + Collection date	4	395.2	1.9	0.086	–193.4
4	Habitat + Age + Collection date	5	395.7	2.5	0.065	–192.6
5	Sex + Collection date	4	396.1	2.8	0.056	–193.8
6	Habitat + Age + Collection date + H * A	6	396.3	3.0	0.050	–191.7
7	Age	3	396.4	3.1	0.048	–195.1
8	Sex + Age + Collection date	5	396.6	3.3	0.044	–193.0
9	Habitat	3	397.1	3.9	0.033	–195.5
10	Habitat + Age	4	397.6	4.3	0.026	–194.6

Table 1 (*continued*).

(e) Gizzard lengths

Rank	Model	K	AIC	ΔAIC	Wi	LogL
1	**Habitat + Sex + Age + Coll. date + H * A + S * A**	**8**	**687.8**	**0.0**	**0.607**	**–335.2**
2	Habitat + Sex + Age + Collection date + S * A	7	690.1	2.3	0.188	–337.5
3	Habitat + Sex + Age + Collection date + H * A	7	691.4	3.6	0.098	–338.2
4	Habitat + Age + Collection date + H * A	6	693.6	5.8	0.033	–340.4
5	Habitat + Sex + Age + Collection date	6	693.8	6.0	0.030	–340.5
6	Habitat + Sex + Collection date	5	695.5	7.7	0.013	–342.5
7	Habitat + Age + Collection date	5	695.9	8.1	0.011	–342.6
8	Habitat + Collection date	4	697.2	9.5	0.005	–344.4
9	Habitat	3	698.2	10.5	0.003	–346.0
10	Habitat + Sex	4	698.4	10.6	0.003	–345.0

(f) Length of leg muscles

Rank	Model	K	AIC	ΔAIC	Wi	LogL
1	**Habitat + Age**	**4**	**359.6**	**0.0**	**0.433**	**–175.6**
2	Habitat + Sex + Age	5	361.5	1.9	0.165	–175.5
3	Habitat + Age + H * A	5	361.7	2.1	0.155	–175.5
4	Habitat + Sex + Age + S * A	6	363.6	4.0	0.059	–175.4
5	Habitat + Sex + Age + H * A	6	363.6	4.0	0.059	–175.4
6	Habitat + Age + Collection date	5	365.1	5.5	0.028	–177.3
7	Age	3	365.3	5.7	0.025	–179.5
8	Habitat + Sex + Age + H * A + S * A	7	365.8	6.1	0.020	–175.3
9	Habitat + Age + Collection date + H * A	6	366.1	6.5	0.017	–176.6
10	Sex + Age	4	366.9	7.3	0.011	–179.3

habitat and collection date, respectively. Adult males had longer upper digestive tracts than the other age and sex groups, there was more overlap between the age groups within females than males, and juvenile males were larger than juvenile females and similar to the larger 50% among adult females (Fig. 1).

The analysis for caeca supported effects of habitat * age and collection date (Table 1b). We identified sex and sex * age as pretender variables, with a cumulative weight of 0.29 for sex and small difference in LogL values (0.3 and 1.4) between the highest ranked model habitat * age + collection date and the corresponding models (ΔAIC = 1.7 and 1.8) that also included sex or sex * age. Specimens from coastal marshes had larger caeca than those from rice-prairies, and among rice-prairie specimens, caeca length was smaller in adults than juveniles, while there was no age effect in coastal marshes (Fig. 2a). Caeca length increased with collection date (Fig. 2b).

The model containing all five explanatory variables was best supported for small intestine (Table 1c). However, cumulative weights were 0.99, 0.89, 0.87, and 0.80 for collection date, age, sex, and habitat, respectively, indicating a varying degree of support for of them. Small intestine length was positively correlated with collection date (Fig. 3a). Adults of both sexes were larger but also more variable than juveniles, whereas there was little size difference by sex in juveniles compared to that in adults (Fig. 3b). Small intestines from rice-prairies generally were more variable than those from coastal marshes, and adult coastal marsh specimens were larger than the other age and habitat groups (Fig. 3c).

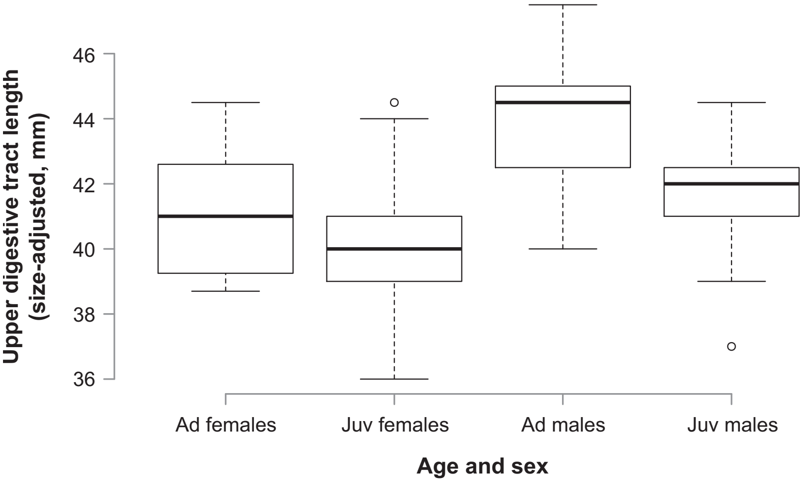

Figure 1. Differences between the sexes and age groups in length of upper digestive tracts (mm) for adult (n = 40) and juvenile (n = 70) Snow Geese collected in southwest Louisiana during winters 2001/02–2003/04. Tukey boxplots: the length of the box is the interquartile range; whiskers are drawn to the largest observations within 1.5 interquartile lengths from the top and bottom.

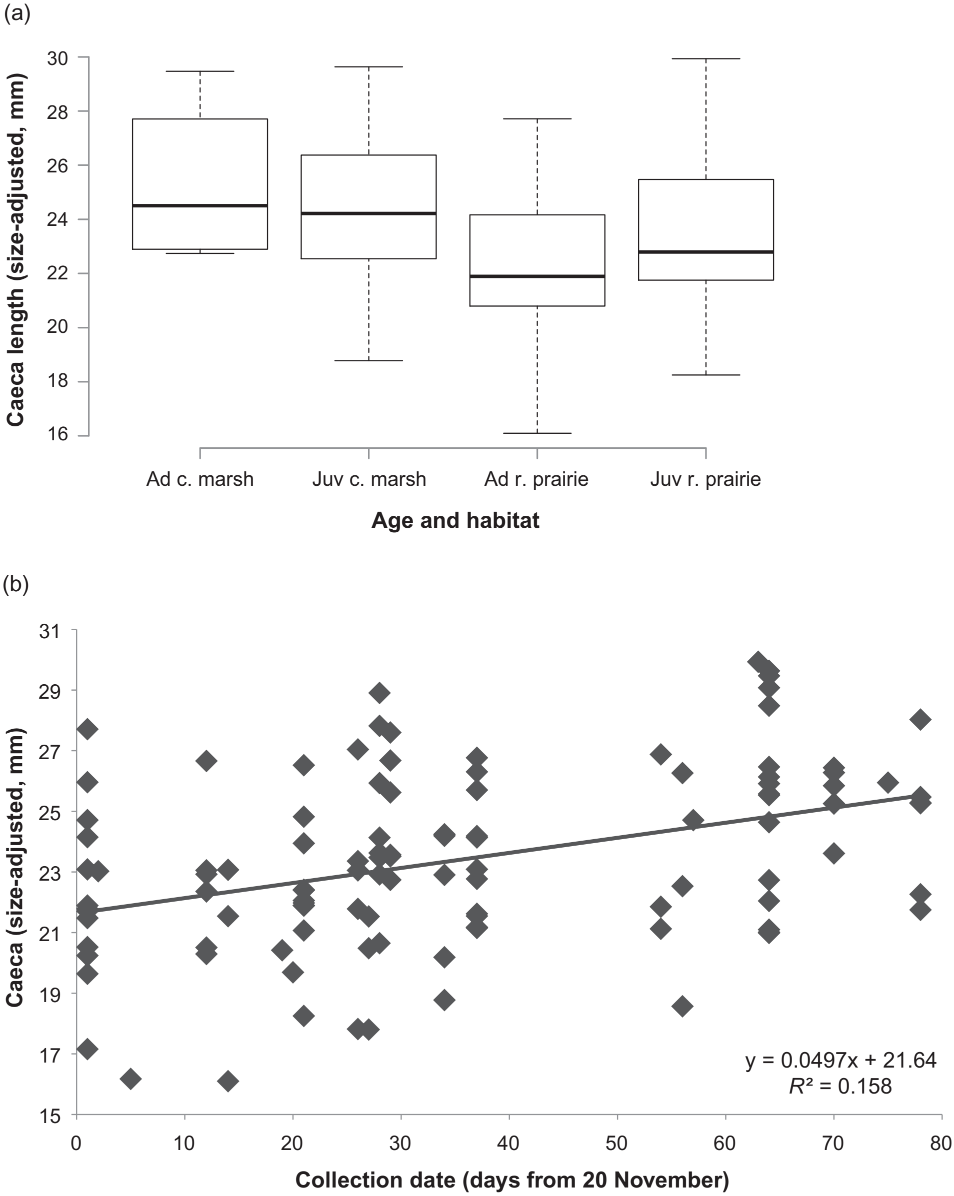

Figure 2. Differences in length of caeca (mm): a) between the habitats (coastal marshes and rice-prairies) and age groups, and b) by collection date, for adult (n = 40) and juvenile (n = 70) Snow Geese collected in southwest Louisiana during winters 2001/02–2003/04. Tukey boxplots: the length of the box is the interquartile range; whiskers are drawn to the largest observations within 1.5 interquartile lengths from the top and bottom.

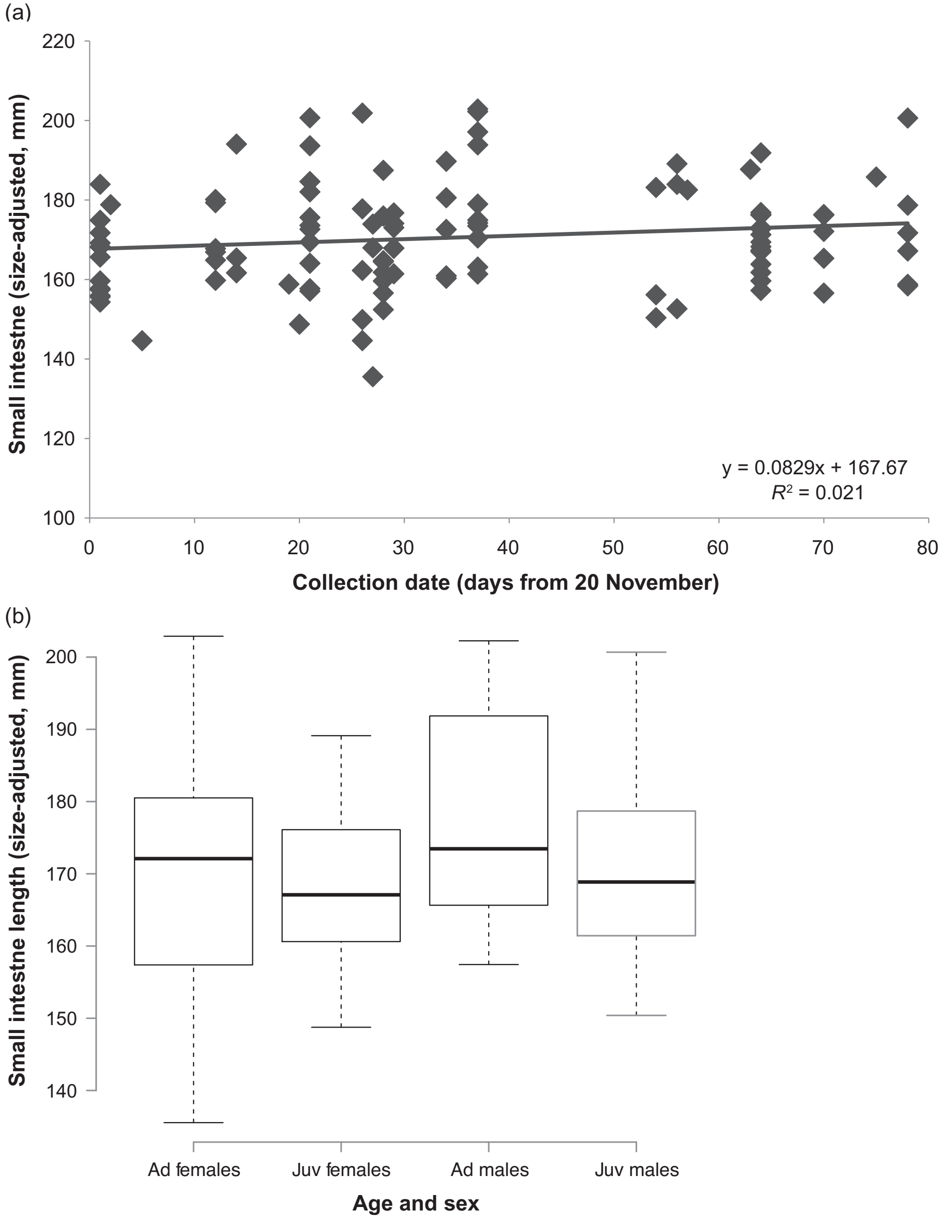

Figure 3. The relationship between the length of small intestine (mm) and: a) collection date, b) age and sex categories, and c) age groups and habitats (coastal marshes and rice-prairies), based on specimens of adult ($n = 40$) and juvenile ($n = 70$) Snow Geese collected in southwest Louisiana during winters 2001/02–2003/04. Tukey boxplots: the length of the box is the interquartile range; whiskers are drawn to the largest observations within 1.5 interquartile lengths from the top and bottom.

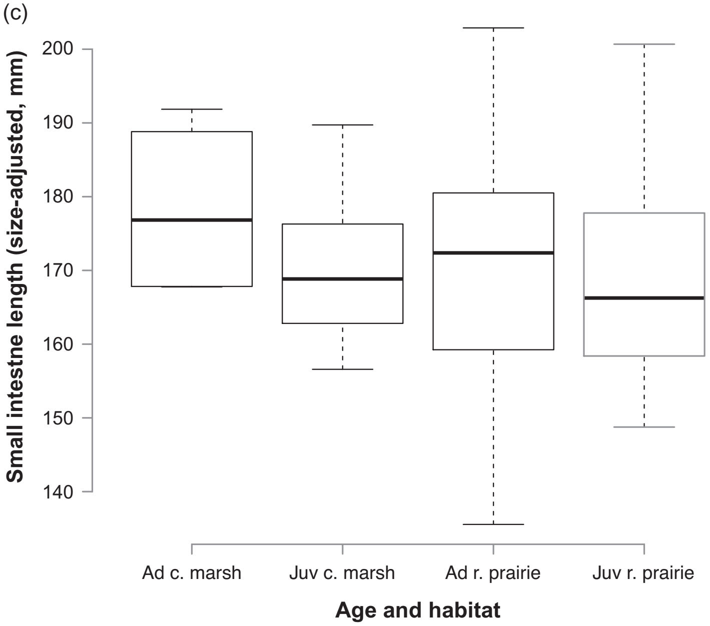

Figure 3 (*continued*).

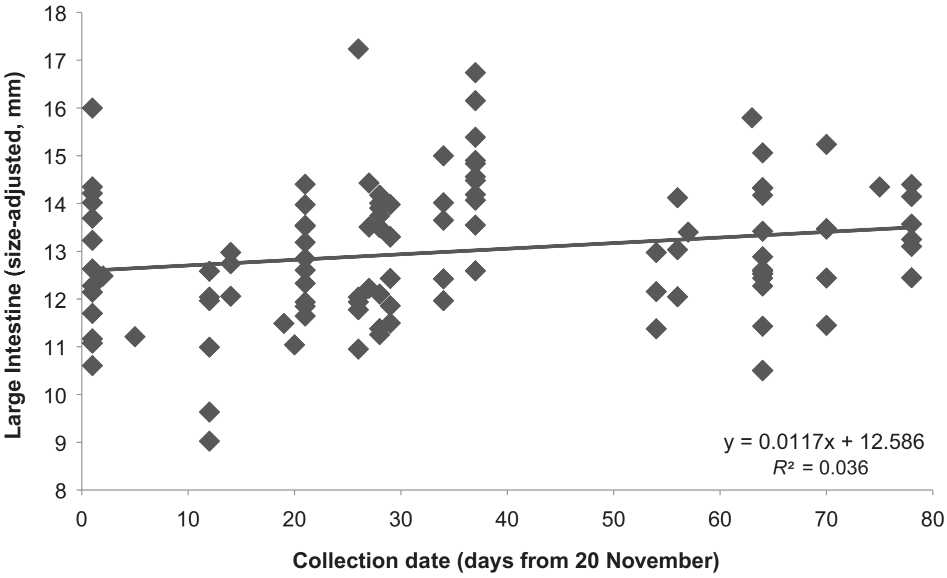

Figure 4. Relationship between collection date and the length of large intestine (mm) for adult (n = 40) and juvenile (n = 70) Snow Geese collected in southwest Louisiana during winters 2001/02–2003/04.

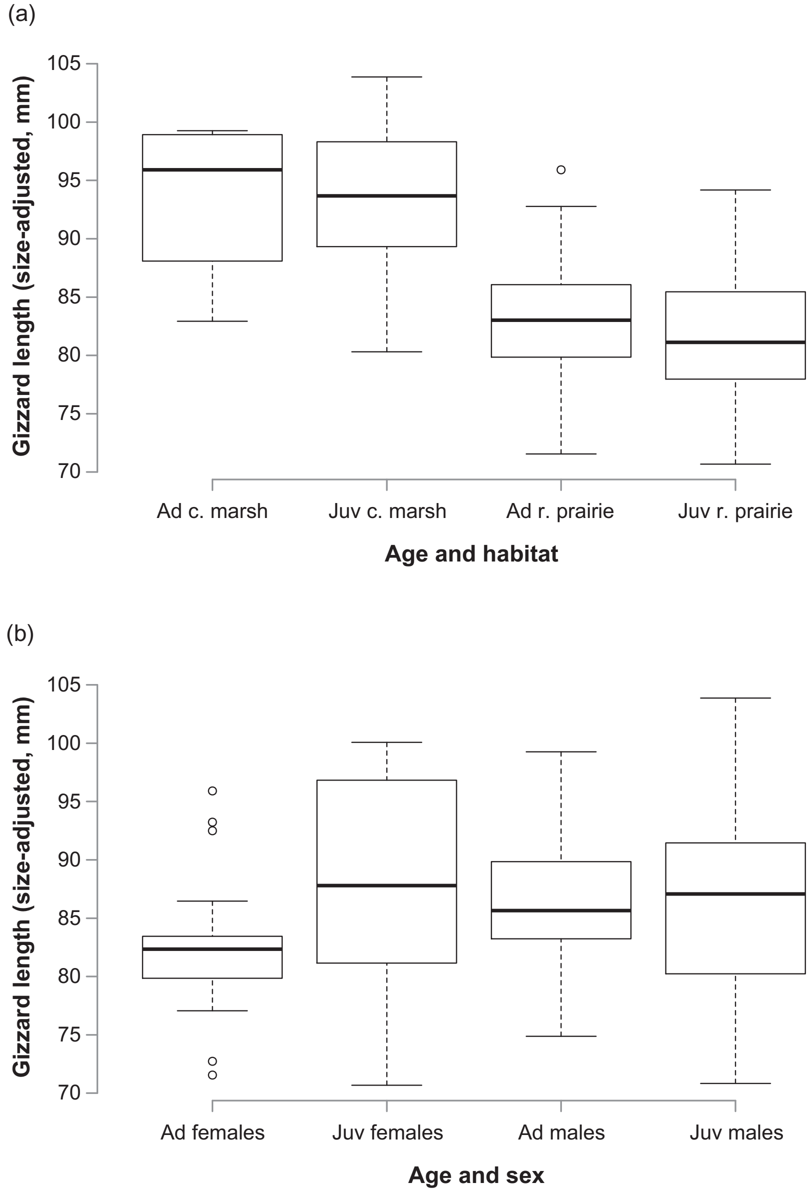

Figure 5. Differences in the length of gizzards (mm): a) between age groups and habitats (coastal marshes and rice-prairies); (b) between sexes and age groups, and c) in relation to collection date, for adult (*n* = 40) and juvenile (*n* = 70) Snow Geese collected in southwest Louisiana during winters 2001/02–2003/04. Tukey boxplots: the length of the box is the interquartile range; whiskers are drawn to the largest observations within 1.5 interquartile lengths from the top and bottom.

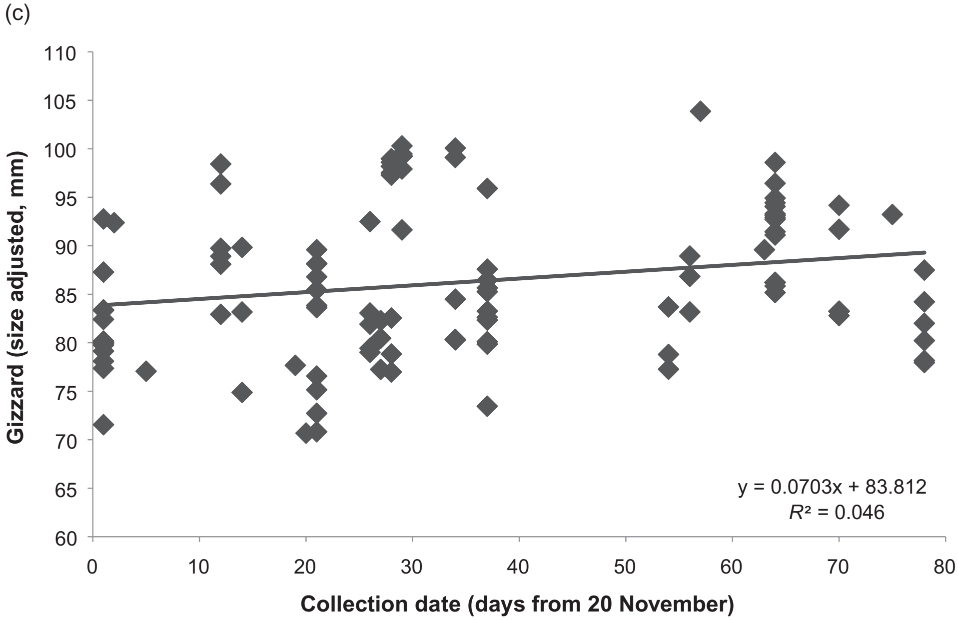

Figure 5 (*continued*).

For the large intestine, the highest-ranked models were collection date (single effects model) and age + collection date (ΔAIC = 0.3; Table 1d). However, the LogL difference between the two models was 0.9, suggesting that age was a pretender variable. Furthermore, collection date had the highest cumulative weight of 0.80, whereas age had cumulative weights of 0.47, indicating poor support for the effects of age. Similarly, the cumulative weights of habitat and sex indicated no support for those variables; 0.30 and 0.21, respectively. Length of the large intestine was positively correlated with collection date (Fig. 4).

The model containing all five explanatory variables was best supported for gizzard length (Table 1e) and the cumulative weights were 1.00, 0.85, 0.69, and 0.65 for habitat, collection date, sex and age, respectively. Habitat was by far the best supported variable; all models containing habitat (ranks 1–16) had ΔAIC ≤ 13.6, whereas all models without habitat (ranks 17–26) had ΔAIC ≥ 46.7 (Table 1e). Specimens from coastal marshes had larger gizzards than those from rice-prairies (Fig. 5a). Gizzard length in coastal marshes was also more variable than that in rice-prairies and adults were slightly larger within both habitats, although our sample size may not have been sufficient to detect statistically an age effect within coastal marshes (Fig 5a). The sex * age interaction suggested that adult females had smaller gizzards than other age and sex groups, and that gizzard length was more variable within juveniles of both sexes than for adults (Fig. 5b). Collection date was well supported (cumulative weight 0.85) and present in the eight top-ranked models

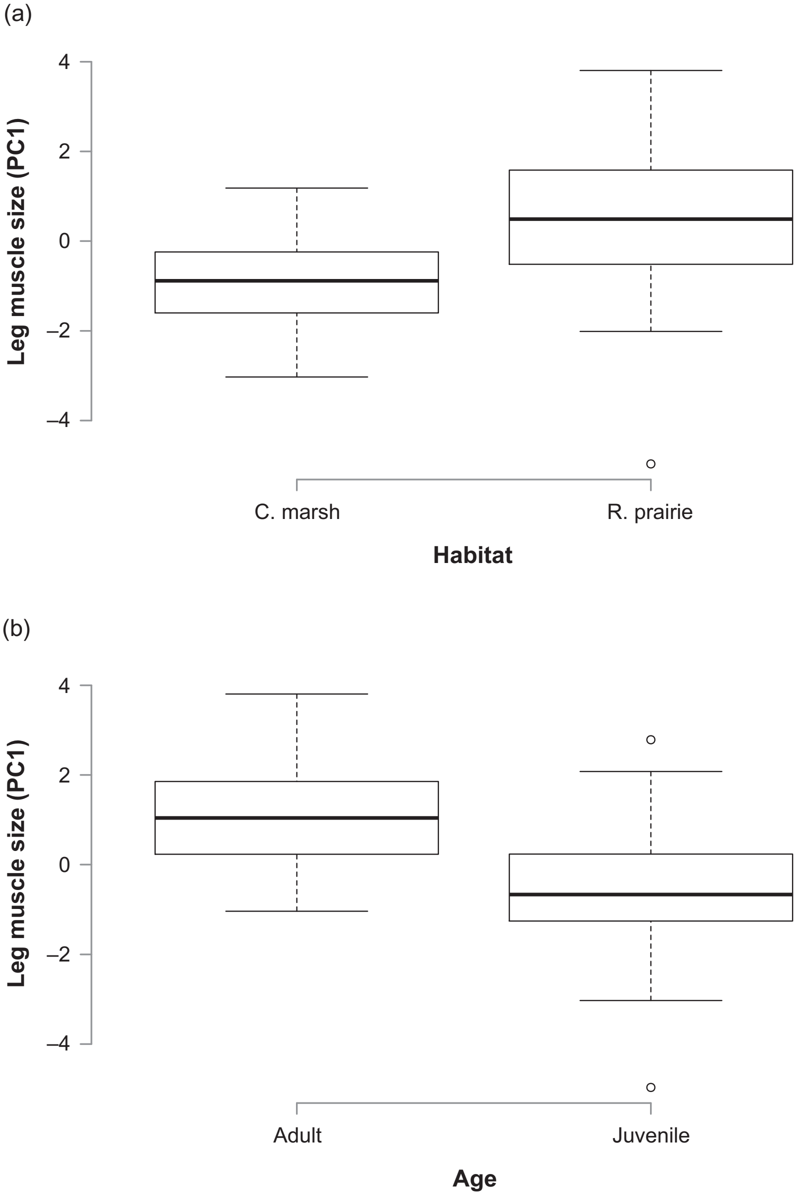

Figure 6. Differences in leg muscle size (PC1 from leg muscle measurements) between: a) habitats (coastal marshes and rice-prairies), and b) age groups, for adult (*n* = 40) and juvenile (*n* = 70) Snow Geese collected in southwest Louisiana during winters 2001/02–2003/04. Tukey boxplots: the length of the box is the interquartile range; whiskers are drawn to the largest observations within 1.5 interquartile lengths from the top and bottom.

(ΔAIC ≤ 8.1); gizzard length was positively correlated with collection date (Fig. 5c).

For leg muscles, the habitat + age model was the lone best supported model (Table 1f) and cumulative weights for habitat and age were 0.94 and 1.00, respectively. There was no support for effects of sex or collection date, where the cumulative weights were 0.27 and 0.06, respectively. Specimens from rice-prairies had larger leg muscles than those from coastal marshes (Fig. 6a) and adults had larger leg muscles than juveniles (Fig. 6b) but effects of habitat and age were independent of each other.

Discussion

The results of our study indicated that the digestive organ morphology of juvenile Snow Geese differed between habitats, as shown previously for adult Snow Geese (see also Alisauskas 1988; Alisauskas *et al.* 1988). Digestive organs were larger in coastal marshes, whereas leg muscles were larger in rice-prairies (*i.e.* the habitat that required more mobility), which was consistent with our hypothesis. However, contrary to our prediction, the habitat effect on leg muscles was independent of age. Caeca, small intestine, large intestine and gizzard length were all related to collection date. Of those, caeca seemed to have the strongest relationship to collection date, suggesting that caeca respond more strongly to the winter diet than the other digestive organs.

We found that coastal-marsh specimens had larger caeca and gizzards than did those from rice-prairies. This difference in the length of the gizzards seemingly is related to the differences in the protein and fibre contents and digestibility of the composite diets between habitats (Alisauskas *et al.* 1988). A larger gizzard in birds on a high-fibre diet can be interpreted as an adaptation towards increased digestibility of dietary fibre (Williamson *et al.* 2014). Digestive organs of waterfowl generally increase in size in response to increased fibre contents (Miller 1975; Paulus 1982; Halse 1984; Thompson & Drobney 1996), but such changes in Snow Geese seem more prominent in the caeca and gizzard than in the remainder of the digestive tract. Such a difference in gizzard length requires prolonged exposure to high-fibre diets in coastal marshes, as empirical data suggests that short-term exposure to high-fibre diets does not necessarily cause an increase in gizzard length (Jones *et al.* 2013).

The smaller caeca of adult specimens in rice-prairies, compared to that of juveniles in both habitats and adults in coastal marshes, were somewhat surprising but may have resulted from years of low fibre diets for these adult specimens, causing their caeca to become regressed from their first winter of life until the date they were collected. Alternatively, juveniles are inexperienced foragers and may be less adept than adults in maximising low fibre food when foraging, and therefore may develop larger caeca in response to the high fibre intake that results from their less effective selection of low fibre foods which adults are more adept at finding. Like other herbivorous waterfowl, geese have limited capacity to digest cellulose to a certain extent, via bacterial flora within the caeca. Generally, the overall contribution to total energy intake from cellulose digestion is small, mostly because of the fast throughput time of food (*c.* 70–120 min) through the alimentary canal (Mattocks 1971; Buchsbaum *et al.* 1986; Prop & Vulink 1992). Conversely, the caeca occasionally may function in some storage capacity until their contents are used to supplement the diet. This relative unimportance of cellulose for nutrition may explain why caeca in our coastal marsh specimens were not enlarged as much as the gizzard in response to a more fibre rich diet in the coastal marshes. Lastly, caeca are notably shorter in geese than in grouse (which also are predominantly herbivorous but often relatively non-migratory birds), which could be explained by energetic costs of carrying large caeca (or perhaps a cost of maintaining them via the circulatory or endocrine systems) during the long migrations undertaken by geese (Sedinger 1997).

The interactive terms habitat * age and sex * age did not provide additional explanatory information for variation in the length of the large intestine or leg muscles. Conversely, the habitat * age interaction was found to influence caeca length, sex * age influenced the upper digestive tract, and both interactions added information to the analyses of small intestine and gizzard lengths. Our data suggests that coastal marsh Snow Geese have larger gizzards and small intestines than those in rice-prairies, but these differences may not be independent of age in that: 1) adults in rice-prairies have slightly larger gizzards than juveniles (after adjusting for age differences in body size) but that gizzard length in coastal marshes is more variable and possibly independent of age; 2) adults have longer small intestines than juveniles but either the greater variation among rice-prairie specimens may blur age effects within that habitat, or our small sample size among adults may do that in coastal marshes; 3) the sex * age effect on gizzard length may be a result of our sample being biased towards smaller gizzards in adults found in rice-prairies (where 90% of our adults were collected); and 4) our habitat * age findings could come from the analysis failing to find an age effect in coastal marshes but finding it in rice-prairies.

Waterfowl do not have a specialised crop or a comparable storage organ but the oesophagus is capable of expanding to accumulate substantial amounts of food, especially during short feeding bouts, allowing geese to store food to subsequently digest at roost sites (Owen 1980). Effects of age * sex were the only plausible explanatory variables for variation in the length of the upper digestive tract, which was larger in males within both age groups, but more interestingly, juvenile males had longer upper digestive tracts than did the majority of the adult females. We interpret these differences as an enhanced sexual dimorphism particular to neck length, which is not represented by the sex difference in overall body size (PC1), *i.e.* a sexually selected size difference in addition to differences overall body size. Male geese generally spend more time alert than females or juveniles (Gauthier & Tardif 1991; Fowler & Ely 1997; Flint *et al.* 1997). Thus, we hypothesise that males have evolved longer necks (and concurrently, longer upper digestive tracts) as a result of sexual selection. These benefits of higher posture and greater visibility, or improved ability to appear more threatening during aggressive displays have had value for reproductive success throughout the evolutionary history of Snow Geese. As a result of greater vigilance, males may feed less for long periods and also use shorter feeding bouts as a result of their time investment spent alert. Thus, there is another potential benefit of longer necks that relates to food ingestion or possibly digestion: the longer neck and upper digestive tract may allow males to ingest more food quickly when it is superabundant. This adaptation also could lengthen food throughput time by lengthening the digestive tract to enhance digestive capacity (*cf.* Prop & Vulink 1992). Somewhat surprisingly, this sexual dimorphism is already evident in juveniles but perhaps it is costly to grow the neck tissues, and thus, the process begins early and extends over a couple of years until a longer neck conveys a competitive advantage as the juvenile males become mature and obtain mates and subsequently families.

Gizzards of herbivorous birds often contain grit (gastroliths) which aid the breakdown of tough plant material (Williamsson *et al.* 2014). Snow Geese in the study area are heavily dependent on grit sites (patches of sand and gravel, commonly created by managers for gizzard-grit consumption by waterfowl), which are located within both rice-prairies and coastal marshes (Harris 1990). We did not analyse gizzard contents or attempt to measure grit in our Snow Goose samples because the bulk of these "gastroliths" was merely sand from these grit sites. Snow Geese in coastal marshes may consume more sand from grit sites than those in rice-prairies but there is no reason to expect different types of gastroliths between gizzards from the two habitats. Thus, gizzard length probably is not affected much by gastrolith types but rather the different composite diets, possibly their different energy contents (Alisauskas *et al.* 1988).

In conclusion, the analyses found that Snow Geese in coastal marshes had larger gizzards and caeca than those on rice-prairie habitat, which may be attributable to the fibre contents of the different composite diets (Alisauskas *et al.* 1988). Our findings for juveniles indicate that organ plasticity in relation to habitat begins during the first winter of life, despite the fact that juveniles have not attained full growth. This provides a useful baseline for exploring in further detail the effects of different habitat types on organ and muscle plasticity, as expressed by differential muscular exertion and different energy and fibre content of composite diets. These findings could also prove important in the face of the continued northward expansion of the Snow Goose wintering range (Jónsson & Afton 2015b), which could decrease the need for organ plasticity among adult or juvenile Snow Geese.

Acknowledgements

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Appendix 1. Overall body size (indexed by PC1 from a principal components analysis), for adult (*n* = 17 males, 23 females) and juvenile (*n* = 34 males, 36 females) Snow Goose specimens collected in southwest Louisiana, USA, during winters 2001–2004. Least Squares Means test for an age * sex interaction effect on the PC1 values found that adult males were significantly larger in size (lsmean ± s.e. = 3.12 ± 0.44, $P < 0.0001$ for all group comparisons) in comparison with the other groups (lsmean = –1.09 ± 0.37 for adult females, –1.23 ± 0.30 for juvenile females, and 0.48 ± 0.31 for juvenile males). Juvenile males were intermediate between adult males and the two female groups ($P < 0.002$ on comparison with adult females, $P < 0.0001$ on comparison with adult males, and $P = 0.0001$ on comparison with juvenile females). The two female groups did not differ from each other ($P = 0.77$, n.s.).