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# Rapid environmental degradation in a subarctic ecosystem influences resource use of a keystone avian herbivore

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## Summary

**1.** Environmental degradation can change resource use strategies of animals and thereby affect survival and fitness. Arctic herbivores may be especially susceptible to the effects of such environmental change because their rapid growth rates demand high-quality forage, which may be limited as environmental conditions deteriorate. We studied the consequences of a trophic cascade, driven by Lesser Snow Goose (*Chen caerulescens caerulescens*) overgrazing on the south-west coast of Hudson Bay, Canada, which has caused tidal marsh (TM) degradation and the reduction in high-quality forage plants, on gosling growth and resource use.

**2.** We compared resource use and body size of goslings that inhabited tidal and freshwater marsh (FM) to determine how current foraging strategies influence growth and to test the hypothesis that during early growth goslings require and so consume high-quality TM plants, but that during later growth they may switch to foraging in lower-quality FM.

**3.** To investigate gosling resource use throughout growth, we measured once a week for 28 days the body size of goslings as well as stable isotope ratios ($\delta^{34}S$, $\delta^{15}N$ and $\delta^{13}C$) in multiple tissues of goslings that were collected from both TM and nearby FM. We also measured the stable isotope ratios in forage plants sampled along transects and from gosling foreguts. We used an isotope-mixing model to determine the contribution of FM plants to gosling tissues.

**4.** Contrary to the proposed hypothesis, goslings inhabiting FM or TM primarily consumed FM plants during early growth. Furthermore, goslings that foraged extensively in FM had similar growth rates and grew to a similar size and body mass, as goslings that foraged in the degraded TM. However, goslings that currently inhabit freshwater or TM were significantly smaller than goslings that inhabited TM in the 1980s prior to habitat degradation.

**5.** Consequences of smaller overall body size include decreased survival and fecundity for arctic-nesting geese. The ability of phenotypically plastic responses to sustain persistence is limited by reaction norms and the extent of environmental change. Current research is assessing whether those limits have been reached in this system.

**Key-words:** Arctic herbivores, foraging ecology, gosling growth, stable isotope ecology

## Introduction

Animals can experience rapid environmental changes that often involve habitat degradation (MacMahon *et al.* 1989; Feary *et al.* 2007). As habitat quality declines, individuals may alter their behaviour and density to better exploit degraded habitat (Kohlmann & Risenhoover 1994; Pezzanite *et al.* 2005), they may exploit improved formerly lower-quality habitat (Vickery *et al.* 1995; Nolet *et al.* 2002), or they may modify when they use habitats of different qualities to best satisfy their requirements which may change during, growth or productive periods (McWilliams & Leafloor 2005). Such responses can lessen the negative impacts of environmental change on survival and fitness (Jefferies, Rockwell & Abraham 2004; Inger *et al.* 2006), but they may also reduce growth rates, increase mortality and ultimately lead to population decline (Holt & Kimbrell 2007). Insufficient response of animals to environmental change can lead to temporal and spatial mismatches between when resources are available and when they are required (Post & Forchhammer 2008). Keystone herbivores in Arctic ecosystems are especially susceptible to the effects of environmental change because

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timing of reproduction coincides with maximal availability of high-quality plant tissue that is most nutritious (Sedinger & Raveling 1986; Lepage, Gauthier & Reed 1998).

We investigated the resource use of lesser snow goose goslings (*Chen caerulescens* caerulescens Linnaeus 1758; hereafter LSG) along the south-west coast of Hudson Bay, Canada, where foraging by overabundant geese has caused large-scale degradation of tidal marsh (hereafter TM; Jefferies, Rockwell & Abraham 2004). This trophic cascade provides the opportunity to determine how resource use of extant geese has changed with the degradation of TM and its implications for growth rates of goslings. Prior to the degradation of the TM, LSG adults and goslings foraged almost exclusively in TM especially during early gosling growth (Cooke, Rockwell & Lank 1995). The two sward-forming graminoids in the TM, *Carex subspathacea* and *Puccinellia phryganodes*, are preferred by goslings because they contain more nutrients and less fibre than forage species common in the surrounding freshwater marsh (hereafter FM), such as *Carex aquatilis* (Gadallah & Jefferies 1995a). The importance of the TM graminoids to rapid LSG gosling growth was further revealed in captive trials where goslings fed the dominant FM sedge, *C. aquatilis,* lost or maintained body mass, whereas they gained body mass when fed the preferred *P. phryganodes* and *C. subspathacea* (Gadallah & Jefferies 1995b). Because this population of geese has been monitored for decades, we can compare gosling resource use over time and determine their response to this environmental change.

Recent observations indicate that the reductions in plant quality and quantity in the TM is coincident with family groups increasingly foraging in nearby, FM, although the extent to which this occurs during gosling growth and its consequences for growth is not well understood (Jefferies, Rockwell & Abraham 2004). Given that TM and FM plants eaten by LSG goslings differ in quality, the observed changes may negatively affect gosling growth. In this study, we compared the size of *c.* 28-day-old goslings in 2005 to that of goslings in the 1980s which foraged in high-quality TM prior to the environmental change associated with goose overabundance. We also compared resource use and body size of extant goslings that inhabited TM and FM to determine how current foraging strategies influence gosling growth and to test the hypothesis that during early stages of growth goslings require high-quality TM plants, but that during later stages of growth they may switch to foraging on lower-quality FM plants (Gadallah & Jefferies 1995b).

We used stable isotopes in forage plants and in gosling tissues to determine the extent to which gosling resource use changed with age, and how foraging history and habitat use affected their growth rate and body size. The primary advantages of using stable isotopes in this context are (i) stable isotope values of an individual gosling's tissue are the product of what that individual ate and assimilated and (ii) stable isotope values of tissues with different turnover rates provide a record of an individual's past and present resource use over a range of timescales (Bauchinger & McWilliams 2009; Bauchinger *et al.* 2010).

## Materials and methods

### STUDY AREA

We studied LSG at La Pérouse Bay (henceforth, LPB) during the summer of 2005. LPB is a shallow bay on the south-west coast of Hudson Bay, 25 km east of Churchill in northern Manitoba (58 04′N 94 03′W). In recent decades, an overabundance of LSG has had a progressively negative impact on the coastal marsh at LPB, leading to severe soil degradation and reductions in both vegetation quality and quantity in the TM and to a lesser extent the FM at LPB (Jefferies, Rockwell & Abraham 2004).

#### *Tidal marsh habitat*

The intertidal zone at LPB is currently composed of open mud flats and isolated swards ($< 2$ m$^2$) dominated by a stoloniferous grass, *P. phryganodes*, and a rhizomatous sedge, *C. subspathacea* (nomenclature follows Porslid & Cody 1980). Mud flats have become increasingly more abundant because of hypersaline soil conditions.

#### *Freshwater marsh habitat*

The TM continues inland for *c.* 0·5–2 km until salt-tolerant graminoid species are replaced by FM species. In these FM communities, pond edges and low-lying areas (flarks) are dominated by *C. aquatilis*, *Kobresia myosuroides*, *Eriophorum angustifolium* and moss species (*Drepanocladus* spp. and *Scorpidium scorpioides*). Elevated ridges in the sedge meadows (*c.* 25–75 cm in height) are dominated by dwarf shrubs (i.e. *Salix arctophila* and *Salix arctica*) and sedge species (i.e. *Carex rariflora* and *Carex scirpoides*).

### VEGETATION SAMPLING

The isotope values of the above-ground tissues of plants growing in the TM and FM surrounding LPB were determined by sampling vegetation along four 5·5-km transects (*c.* 2 km apart). Transect locations were randomly selected and were oriented perpendicular to the coast so that each transect included TM and FM. A total of 12 sampling exclosures (each 1 m$^2$) were placed along each transect in three groups of four exclosures. These sampling exclosures ensured that we collected plants that were not previously grazed.

Vegetation was sampled once in early July, just after peak hatch of LSG goslings. We clipped from each exclosure enough above-ground biomass to ensure we collected about 10 g dry material of each plant species. In the laboratory, samples were rinsed in distilled water, dead plant tissue was removed, and remaining plant tissue was dried for 3 days at 40 °C and then finely ground with a Wiley Mill.

### GOSLING SAMPLING

For the 4 weeks after peak hatch (26 June 2005), we collected *c.* 10 goslings every week from both TM and FM within the same general area of the plant transects, although we did not collect goslings from FM during the third week. Goslings were shot with a 0·17 calibre rifle, and only one gosling per family group was sampled. Collection of LSG goslings was permitted by the Canadian Wildlife Service (permit #: CWS04-M004) and approved by the Institutional Animal Care and Use Committee of the American Museum of Natural History.

Individual goslings were measured and necropsied within *c.* 2 h of collection. Body measurements included body mass, head length, culmen 1, culmen 2 and total tarsus length (Dzubin & Cooch 1992). We removed from each individual *c.* 4 g of liver, leg muscle and leg

cartilage, and we used a capillary tube to collect *c.* 50 μL of blood from the heart. These tissues were selected for stable isotope analysis because their isotopes turn over at different rates from fast to slow: liver, whole blood, leg muscle and cartilage (Bauchinger & McWilliams 2009). In the laboratory, tissues were lyophilized, finely ground with a Wiley Mill and then, except for blood, were placed in cellulose thimbles (10 × 50 mm) and refluxed with petroleum ether for 6 h in a Soxhlet apparatus to remove lipids (Dobush, Ankney & Krementz 1985).

We compared gosling body size in 2005 at LPB to goslings in the 1980s prior to the habitat degradation. Because LSG goslings were not tagged at hatch in 2005, we did not know the exact age of our goslings. We assumed that the oldest goslings collected in 2005 were *c.* 28 days old, the time since peak hatch of the last gosling collected, and that these estimates of age are accurate within *c.* 2–3 days because LSG hatch is highly synchronous (Cooke, Rockwell & Lank 1995). For the comparison of gosling size between the 1980s and 2005, we selected only those goslings measured in 1981–1989 that were of known age, that were 26–30 days old and that were captured in the same general area as those collected in 2005.

### ANALYSIS OF FOREGUT CONTENTS

We measured the relative abundance of plant species in the oesophagus, proventriculus and upper gizzard (hereafter foregut) of goslings. Plant parts in the foregut were removed from goslings during necropsy and stored frozen. Once returned to the laboratory, foregut contents were thawed and rinsed with distilled water. We removed a representative subsample (*c.* 3 g) of foregut contents for stable isotope analysis and then sorted the remaining contents into the following categories: *C. subspathacea* and *Puccinellia phyrganodes*, other Cyperacea, other Gramineae, Equisetaceae and other. Sorted material was then dried at 40 °C and weighed to determine diet composition on a per cent dry mass basis. The representative subsample of the foregut contents was dried at 40 °C and finely ground with a Wiley Mill.

### STABLE ISOTOPE ANALYSIS

Plant and LSG gosling tissue samples were analysed for carbon and nitrogen isotope values using a Carlo-Erba NA 1500 series II elemental analyzer attached to a continuous flow isotope ratio Micromass Optima spectrometer. Sulphur isotope values were determined using an elemental analyzer (Sercon Ltd, Crewe, UK) linked to an isotope ratio mass spectrometer (20-20; Europa Scientific Ltd, Crewe, UK). Stable isotope ratios are reported in δ-notation. One in five samples was run in duplicate as a check for analytical accuracy and precision. Reference material analysed over the course of sample analysis was measured with a ± 0·3‰ precision.

### STABLE ISOTOPE-MIXING MODEL

A Bayesian isotope-mixing model was used to estimate the contribution of TM vs. FM plants to gosling tissues and thus infer the contribution of these food sources to gosling diet (SIAR; Jackson *et al.* 2009; Parnell *et al.* 2010). We only used two of the three measured stable isotopes in the model because sulphur and nitrogen, but not carbon, of forage plants sampled from gosling foreguts were significantly different between FM and TM (see Results). A trophic enrichment value of 3·54 ± 0·74‰ SD was used for $\delta^{15}N$ (Inger *et al.* 2006) and a value of 0·0 ± 0·75‰ SD for $\delta^{34}S$ (McCutchan *et al.* 2003; Florin, Felicetti & Robbins 2011). Isotope values (nitrogen and sulphur) of plant types from gosling foreguts were used as the TM and FM source inputs in our mixing models. We calculated mean and variance in isotope values of plants from all gosling foreguts collected over time in TM and FM and used these values as our source inputs in the mixing models (TM: 2·59 ± 1·06‰ SD for $\delta^{15}N$, 10·69 ± 3·13‰ SD for $\delta^{34}S$; FM: 1·09 ± 1·37‰ SD for $\delta^{15}N$, 6·89 ± 2·83‰ SD for $\delta^{34}S$). The Bayesian mixing models were fitted using R software (R Development Core 2008).

### STATISTICAL ANALYSES

#### *Plant isotope values and the diet of goslings*

We used analysis of variance (ANOVAS) to compare the isotope values (carbon, sulphur and nitrogen) of forage plants sampled from exclosures along the four transects. Only those plant species known to be eaten by LSG (e.g. Gadallah & Jefferies 1995b) were included in this analysis. Isotope values of individual plant samples were averaged across each sampling transect by species and used as our sampling unit within each habitat for the ANOVAS. We used ANOVAS to examine the effect of sampling origin (exclosures vs. gosling foreguts) and habitat on isotope values of LSG gosling forage plants. We also used ANOVA to examine the effect of gosling age and habitat on isotope values of forage plants sampled from gosling foreguts. We used the Kruskal–Wallis test to determine whether the relative abundance of plants in gosling foreguts changed over time. When we detected significant differences in diet over time, we used a Mann–Whitney test with Bonferroni correction to compare means.

#### *Isotope values of tissues from goslings and the estimated contribution of FM and TM plants*

We used ANOVA to examine how sulphur and nitrogen isotope values of gosling tissues (liver, leg muscle, whole blood and cartilage) differed between the two habitats and by gosling age. We used the SIAR output to assess whether the estimated relative contribution of FM plants differed between gosling tissues and between goslings collected from the two habitats. Specifically, we randomly sampled 20 iterations from the 10 000 iterations created by the mixing models that produced the probability distribution of estimated dietary proportions for a certain tissue type from a gosling of known-age class. These values were then used as dependent variables in an ANOVA with gosling tissue, gosling age and habitat type as independent variables.

#### *Comparison of gosling growth over 25 years*

An ANOVA was used to examine the effect of sampling habitat on body mass and head length of goslings collected in 2005. Linear regression was used to determine whether body mass and head length of known-age goslings changed from the 1980s to 2005. We used SAS JMP IN (JMP, Version 5.1. SAS Institute Inc., Cary, NC, 1989-2003) for all statistical analyses.

## Results

### ISOTOPE VALUES OF FORAGE PLANTS SAMPLED FROM EXCLOSURES

Carbon and sulphur isotope values differed between forage plants that we collected from exclosures in FM vs. TM, although there was considerable intraspecific and interspecific variation in the isotope values of plant species collected

in the two habitats (Table S1, Supporting information). Sulphur values were on average more enriched for TM plants (16·84‰) compared to FM plants (9·11‰) ($F_{1,16}$ = 2·17, $P$ = 0·05), and carbon values were on average *c.* 1‰ depleted for TM plants (−25·46‰) compared to FM plants (−24·72‰) ($F_{1,22}$ = 2·64, $P$ = 0·01; Fig. 1). In contrast, nitrogen values of forage plants were similar between the two habitats ($F_{1,22}$ = 0·26, $P$ = 0·79; Fig. 1).

### ISOTOPIC VALUES OF FORAGE PLANTS IN THE FOREGUT OF GOSLINGS

Carbon and sulphur isotope values of forage plants that we sampled from gosling foreguts were depleted compared to some of the same plants that we sampled from exclosures along transects (Sampling origin: $F_{1,85}$ = 56·42, $P$ < 0·01; $F_{1,108}$ = 11·78, $P$ < 0·01, respectively), whereas nitrogen values of forage plants eaten by goslings were enriched compared to forage plants we sampled along transects (Sampling origin: $F_{1,108}$ = 36·04, $P$ < 0·01; Fig. 1). However, carbon, nitrogen and sulphur values of forage plants sampled from exclosures and those sampled directly from gosling foreguts were not the same for FM and TM (Habitat*sampling origin: $F_{1,85}$ = 5·33, $P$ = 0·02; $F_{1,108}$ = 4·18, $P$ = 0·04; $F_{1,108}$ = 4·44, $P$ = 0·04, respectively; Fig. 1). These differences in isotope value between forage plants that we sampled from exclosures and those eaten by goslings occurred in part because goslings selectively foraged so that their foregut contents contained disproportionate amounts and parts of a subset of the available plants. Given this significant interaction between habitat and sampling origin, we assessed how the isotope values of plants sampled directly from gosling foreguts depended on the habitat in which the goslings were collected. Nitrogen values of plants eaten by goslings collected in TM (2·28‰) were more enriched than that of plants eaten by goslings collected in FM (1·09‰) ($F_{1,91}$ = 6·33, $P$ < 0·01; Fig. 1). Sulphur value of plants eaten by goslings collected in TM (10·89‰) were also more enriched than that of plants eaten by goslings collected in FM (6·89‰) ($F_{1,86}$ = 4·38, $P$ < 0·001). Carbon values of plants eaten by goslings collected in TM (−26·28‰) were similar to that of plants eaten by goslings collected in FM (−27·02‰) ($F_{1,65}$ = 1·33, $P$ = 0·19; Fig. 1).

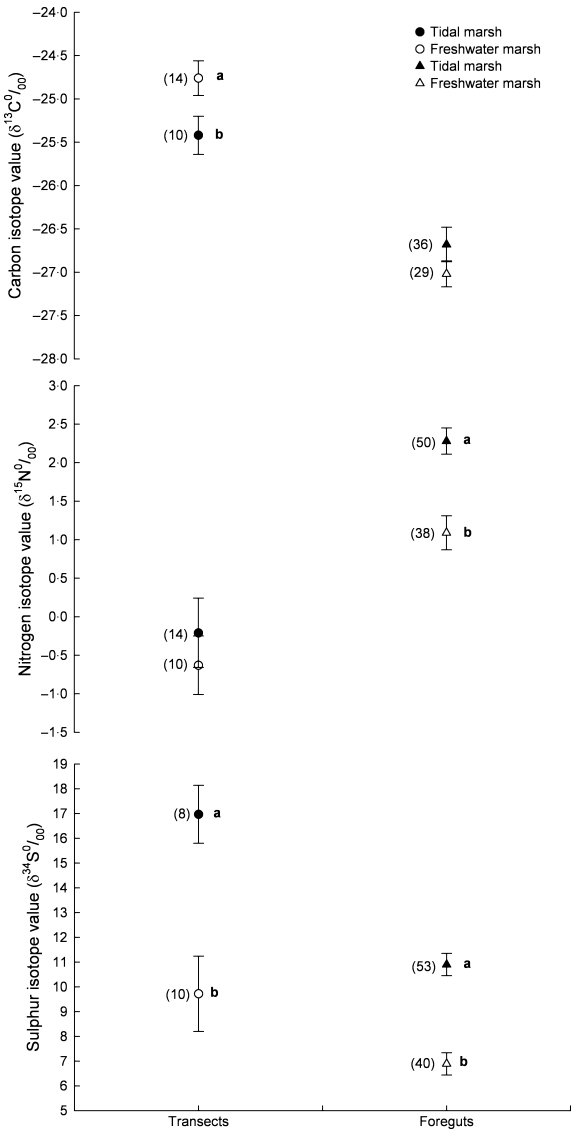


**Fig. 1.** Average (±SE) $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ of forage plants in tidal marsh (solid symbols) and freshwater marsh (open symbols) that we collected in exclosures along transects (circles) or that were in foreguts of collected goslings (triangles). Lower case letters denote significant differences in isotope values between habitats ($P$ < 0·05). Number of goslings collected and number of exclosures in which forage plants were sampled is denoted in parentheses for each habitat.

### ISOTOPIC VALUES OF PLANTS EATEN BY GOSLINGS DURING GROWTH

Isotopic values of plants eaten by goslings changed during gosling growth although the pattern of change depended on habitat (Fig. 2). For goslings collected in TM, carbon values of foregut contents were enriched in the oldest compared to younger goslings ($F_{4,31}$ = 13·48, $P$ < 0·01), whereas nitrogen values were depleted in goslings collected 2·5 weeks after peak hatch ($F_{4,45}$ = 7·41, $P$ < 0·01). We detected no change in carbon or nitrogen values of plants eaten by goslings collected in FM ($F_{3,25}$ = 1·46, $P$ = 0·25; $F_{3,34}$ = 2·34, $P$ = 0·09, respectively). In contrast, sulphur values of plants eaten by goslings changed during growth for goslings collected in FM ($F_{3,36}$ = 11·33, $P$ < 0·01) with foregut contents enriched in the youngest and oldest goslings compared with goslings 2 and 2·5 weeks old but did not change with growth for goslings collected in TM ($F_{4,48}$ = 1·37, $P$ = 0·26; Fig. 2).

### ISOTOPIC VALUES OF GOSLING TISSUES

Sulphur and nitrogen values of gosling tissues differed by gosling collection habitat ($F_{1,347}$ = 90·72, $P$ < 0·01, $F_{1,350}$ = 53·00, $P$ < 0·01, respectively; Table 1), so results below are described based on the habitat where goslings were sampled.

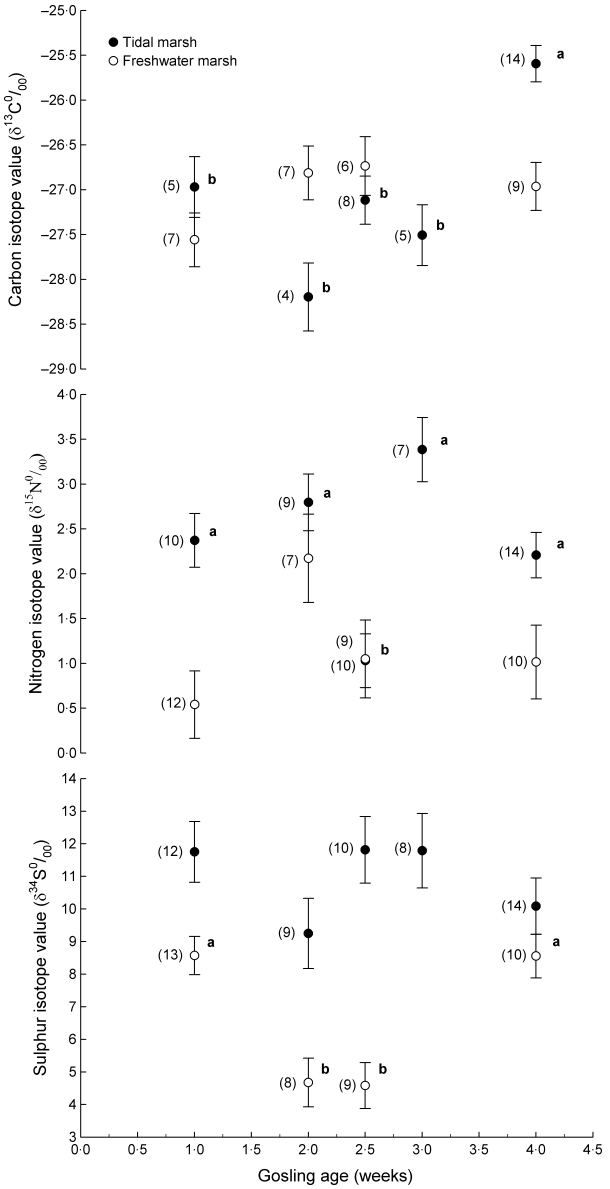


**Fig. 2.** Average (±SE) $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ of plants in the foregut of goslings collected within 4 weeks of peak hatch in tidal marsh (solid symbols) and freshwater marsh (open symbols). Lower case letters denote significant differences in isotope values between collection times for a given habitat type ($P < 0{\cdot}05$). Habitat types without letters were not significantly different through time. Number of goslings collected of each age and in each habitat is denoted in parentheses.

### *Goslings inhabiting TM*

Sulphur values of tissues from goslings collected in TM differed with gosling age (Gosling age: $F_{4,135} = 6{\cdot}03$, $P < 0{\cdot}01$; Tissue*gosling age: $F_{8,135} = 1{\cdot}05$, $P = 0{\cdot}41$), with tissues being more depleted at 2·5 and 4 weeks of age (Table 1). Sulphur values of faster turnover rate tissues (liver and leg muscle) were also similar to that of slower turnover rate tissue such as cartilage ($F_{2,135} = 2{\cdot}53$, $P = 0{\cdot}08$, Table 1).

Nitrogen values of liver, leg muscle and cartilage from goslings collected in TM were more depleted during

**Table 1.** Sulphur and nitrogen isotope values of tissues (mean ± SE) from goslings ($n$ = 7–14 individuals depending on gosling age) collected in tidal marsh (TM) and freshwater marsh (FM)

| | Approximate gosling age | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 week old | | | 2 weeks old | | | 2·5 weeks old | | | 3 weeks old | | | 4 weeks old | | | |
| | $n$ | S (‰) | N (‰) | $n$ | S (‰) | N (‰) | $n$ | S (‰) | N (‰) | $n$ | S (‰) | N (‰) | $n$ | S (‰) | N (‰) |
| TM | | | | | | | | | | | | | | | | |
| Liver | 10 | 11·13 ± 1·26 | 5·37 ± 0·28 | 8 | 7·49 ± 0·93 | 4·63 ± 0·23 | 8 | 8·35 ± 0·47 | 4·46 ± 0·22 | 10 | 10·66 ± 0·27 | 5·80 ± 0·46 | 14 | 5·86 ± 0·17 | 8·45 ± 0·36 |
| Leg muscle | 9 | 8·28 ± 0·97 | 4·52 ± 0·17 | 10 | 10·58 ± 1·03 | 4·25 ± 0·23 | 9 | 8·43 ± 0·41 | 3·57 ± 0·05 | 9 | 10·59 ± 0·48 | 5·72 ± 0·21 | 13 | 5·17 ± 0·18 | 7·91 ± 0·56 |
| Whole blood | | NA | NA | 10 | 9·60 ± 0·66 | 4·28 ± 0·08 | 7 | 8·33 ± 0·47 | 3·45 ± 0·17 | 8 | 10·03 ± 0·41 | 5·15 ± 0·39 | 11 | 5·37 ± 0·28 | 9·45 ± 0·91 |
| Cartilage | 10 | 7·55 ± 1·28 | 5·60 ± 0·87 | 9 | 9·74 ± 0·93 | 4·44 ± 0·13 | 8 | 8·46 ± 0·41 | 3·68 ± 0·08 | 10 | 9·93 ± 0·45 | 5·20 ± 0·27 | 14 | 4·87 ± 0·19 | 7·16 ± 0·58 |
| FM | | | | | | | | | | | | | | | | |
| Liver | 10 | 7·92 ± 1·01 | 4·74 ± 0·24 | 9 | 9·93 ± 1·05 | 5·00 ± 1·11 | 10 | 5·39 ± 0·51 | 4·28 ± 0·18 | | NA | NA | 11 | 4·19 ± 0·11 | 6·09 ± 0·25 |
| Leg muscle | 10 | 7·38 ± 0·98 | 4·84 ± 0·16 | 8 | 6·81 ± 0·61 | 4·47 ± 0·16 | 10 | 6·15 ± 1·00 | 3·99 ± 0·23 | | NA | NA | 11 | 3·71 ± 0·11 | 5·05 ± 0·69 |
| Whole blood | 10 | 6·73 ± 1·15 | 4·54 ± 0·28 | 9 | 6·23 ± 0·86 | 4·30 ± 0·14 | 9 | 5·26 ± 0·83 | 3·47 ± 0·36 | | NA | NA | 7 | 3·58 ± 0·09 | 7·77 ± 2·33 |
| Cartilage | 10 | 5·58 ± 1·23 | 4·97 ± 0·22 | 10 | 5·56 ± 0·65 | 4·47 ± 0·13 | 10 | 5·05 ± 0·87 | 3·92 ± 0·22 | | NA | NA | 10 | 3·39 ± 0·13 | 3·74 ± 0·62 |

mid-growth (Gosling age: $F_{4,139} = 27{\cdot}51$, $P < 0{\cdot}01$) and were different between tissues ($F_{2,139} = 10{\cdot}68$, $P < 0{\cdot}01$; Table 1). Nitrogen value of whole blood also changed over time ($F_{3,35} = 11{\cdot}36$, $P < 0{\cdot}01$). The pattern of change in nitrogen value of liver, leg muscle and cartilage over time was different between tissues (Tissue*gosling age: $F_{8,139} = 2{\cdot}01$, $P = 0{\cdot}05$) with liver changing less through time than the other tissues (Table 1).

### *Goslings inhabiting FM*

Sulphur tissue values did not change with collection week ($F_{3,143} = 2{\cdot}19$, $P = 0{\cdot}09$), and there were no differences between the sampled tissues ($F_{3,143} = 2{\cdot}63$, $P = 0{\cdot}05$; Table 1). Sulphur values of faster turnover rate tissues (liver and leg muscle) were consistently similar to slower turnover rate tissue (cartilage) throughout gosling growth (Tissue*gosling age: $F_{9,146} = 0{\cdot}60$, $P = 0{\cdot}79$; Table 1).

Nitrogen isotope values differed between tissues and with gosling growth. Nitrogen value of the fastest turnover rate tissue (liver) was on average more enriched than the slowest turnover rate tissue (cartilage) throughout growth (Tissue: $F_{3,143} = 3{\cdot}79$, $P = 0{\cdot}01$; Table 1). The pattern of nitrogen depletion over time was similar for all tissues (Tissue*gosling age: $F_{9,143} = 1{\cdot}60$, $P = 0{\cdot}12$). Nitrogen values of tissues from goslings collected in FM became more depleted with gosling growth (Gosling age: $F_{3,143} = 19{\cdot}22$, $P < 0{\cdot}01$; Table 1).

## MIXING MODEL RESULTS

### *Goslings inhabiting TM*

Mixing models revealed that sulphur and nitrogen in tissues of goslings from TM were on average predominately from FM plants (63% average across all collection weeks). Proportional contribution of FM plants to gosling diet differed with gosling age (Gosling age: $F_{3,380} = 77{\cdot}02$, $P < 0{\cdot}01$) and by tissue (Tissue: $F_{2,380} = 20{\cdot}51$, $P < 0{\cdot}01$; Tissue*Gosling age: $F_{11,380} = 10{\cdot}08$, $P < 0{\cdot}01$; Fig. 3). Proportional contribution of FM plants to gosling liver, leg muscle, whole blood and cartilage increased until goslings were 2·5 weeks old (*c*. 70–85%), decreased at 3 weeks of age (*c*. 40–55%) and then slightly increased at 4 weeks of age (*c*. 50–80%; Fig. 3).

### *Goslings inhabiting FM*

Mixing models indicated that sulphur and nitrogen in tissues of goslings from FM were on average predominately from FM plants (81% average across all collection weeks). Proportional contribution of FM plants to gosling diet did not change with gosling age (Gosling age: $F_{3,319} = 38{\cdot}49$, $P = 0{\cdot}08$), but differed by tissue ($F_{3,319} = 2{\cdot}32$, $P < 0{\cdot}01$; Tissue*Gosling age: $F_{9,319} = 1{\cdot}88$, $P = 0{\cdot}05$; Fig. 3). Proportional contribution of FM plants to gosling liver, leg muscle, whole blood and cartilage was similar between tissues throughout growth and consistently increased during growth (*c*. 90% contribution of FM plants in 2·5-week-old goslings) in all tissues except whole blood.

## RELATIVE ABUNDANCE OF PLANTS IN GOSLING FOREGUTS

Gosling diet changed during growth and differed between individuals that were collected in TM and FM. Total dry mass of foregut contents was greater in older goslings and in goslings collected in FM ($F_{3,66} = 10{\cdot}43$, $P < 0{\cdot}01$; $F_{1,66} = 17{\cdot}50$, $P < 0{\cdot}01$, respectively; Tables 2 and 3). In general, goslings collected *c*. 1 week after peak hatch in TM mostly ate *P. phryganodes* and *C. subspathacea* whereas older goslings collected in TM usually ate these plants plus a variety of lower nutritional quality grasses (Other Graminеae) and sedges (Other Cyperacea) that were present at the bases of willow patches in the supratidal zone at LPB (Table 2). Goslings collected in TM ate different amounts of *P. phryganodes* and *C. subspathacea* over time ($Z = 8{\cdot}79$, $P = 0{\cdot}03$) as well as other sedges (Other Cyperacea) over time ($Z = 11{\cdot}35$, $P = 0{\cdot}01$), whereas the amount goslings ate of the other plant species did not change through time (Table 2.). Goslings collected *c*. 1 week after peak hatch in FM mostly ate sedges and some grasses, and then when older mostly ate a variety of sedges (Cyperacea) and horsetails (Equistaceae) (Table 3). Goslings collected in FM ate more sedge over time ($Z = 25{\cdot}66$, $P < 0{\cdot}01$), whereas the amount goslings ate of the other plant species did not change with gosling growth ($P > 0{\cdot}05$; Table 3).

## GOSLING GROWTH

In general, head length and body mass of goslings collected in 2005 from the two habitats were similar (TM: $F_{1,68} = 0{\cdot}99$, $P = 0{\cdot}32$; FM: $F_{1,67} = 0{\cdot}48$, $P = 0{\cdot}49$; Fig. 4). Goslings in 2005 were significantly smaller at *c*. 4 weeks old (24–28 days) compared with goslings measured in the early 1980s, prior to severe habitat degradation. Head length and body mass significantly declined across years ($R^2 = 0{\cdot}18$, $P < 0{\cdot}01$; $R^2 = 0{\cdot}12$, $P < 0{\cdot}01$, respectively; Fig. 5). Average head length in 2005 was 9% less than head length measured in the 1980s (79·6mm ± 0·9 SE vs. 83·1mm ± 0·1 SE, respectively), and average body mass in 2005 was 15% less than average gosling body mass in the 1980s (1015·0 g ± 32·8 SE vs. 880·0 g ± 5·4 SE, respectively) (Fig. 5).

## Discussion

Our results do not support the hypothesis that during early stages of growth LSG goslings require high-quality TM plants and so inhabit TM and that during later stages of growth they may switch to foraging in lower-quality FM. We found that goslings were relatively consistent in their habitat use and did not show the predicted switch from foraging in higher-quality TM when youngest and then foraging predominantly in lower-quality FM when older. We also found

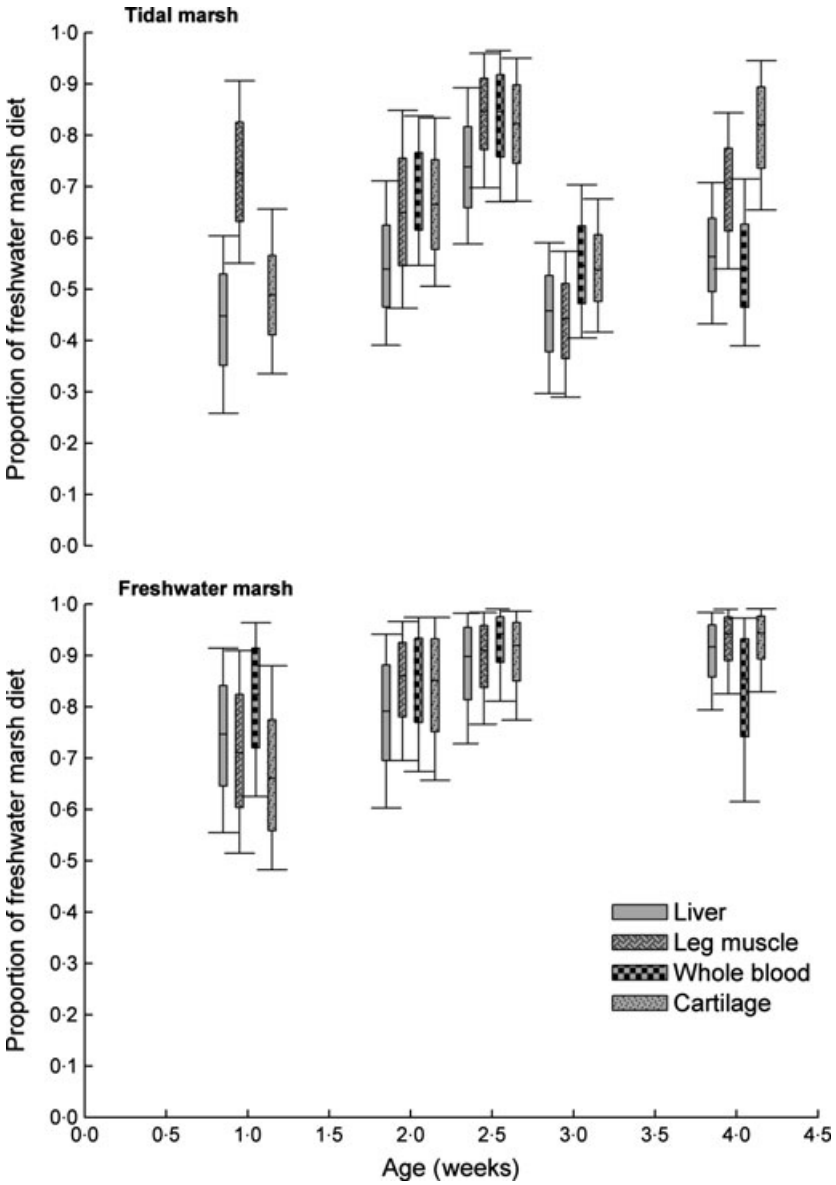


**Fig. 3.** Results of mixing models showing estimated contribution of freshwater marsh (FM) plants to liver, leg muscle, whole blood and cartilage of goslings collected in tidal marsh and freshwater marsh at 1–4 weeks of age. Whiskers represent 95% credibility intervals, boxes the 75% credibility intervals and the line is the median value.

that goslings that foraged extensively in FM had similar growth rates, and grew to a similar size and body mass, as goslings that foraged in the degraded TM. These similar growth rates of goslings occurred even though resource use of goslings inhabiting FM or TM was different. Our comparisons of size and body mass of goslings that currently inhabit FM or TM with that of goslings that inhabited TM in the 1980s prior to habitat degradation suggest that LSG goslings no longer benefit from foraging in TM.

### DIET SELECTIVITY AND THE STABLE ISOTOPE VALUES USED TO EVALUATE RESOURCE USE

Most studies that use stable isotopes to track an organism's dietary history measure the stable isotope values of all known foods in the environment based on previous gut content and observational studies (Felicetti *et al*. 2003; Gauthier, Bety & Hobson 2003). These isotopic values are then assumed to accurately represent all isotopic diet sources for the organism. In most studies, this is the only realistic approach because of the difficulty of collecting gut contents without sacrificing individuals. We used this approach in our study, but we also directly measured stable isotope values of foregut contents to obtain isotopic values of plant parts eaten by goslings. For highly selective foragers such as geese, isotope values of the plant parts directly eaten by goslings provide a more accurate estimate of the resources used by consumers.

Stable isotope value of plants eaten by LSG goslings successfully delineated TM and FM as found in previous studies (McClelland, Valiela & Michener 1997; Rubenstein & Hobson 2004), although these values were different than values for forage plants that we sampled along transects (Fig. 2). Differences in isotopic value of plants eaten by goslings compared to the forage plants that we sampled along transects

**Table 2.** Frequency (% of goslings that ate a given plant species) and relative abundance (mean % ± SE by dry mass) of plant material in the foregut of goslings collected in tidal marsh at La Pérouse Bay in 2005

| Gosling age[a] | *n* | Plant spp. | Frequency (%) | Relative abundance (%) |
|---|---|---|---|---|
| 1 week | 6 | *Carex subspathacea/Puccinellia phryganodes* | 83 | 83·3 ± 17·1 |
| | | Cyperacea[b] | 0 | 0 |
| | | Graminae[c] | 0 | 0 |
| | | *Plantago juncoides* | 0 | 0 |
| | | Other[d] | 17 | 16·7 ± 16·7 |
| 2 weeks | 10 | *C. subspathacea/P. phryganodes* | 50 | 50·0 ± 16·8 |
| | | Cyperacea[b] | 10 | 10·0 ± 10·1 |
| | | Graminae[c] | 30 | 30·0 ± 15·2 |
| | | *Plantago juncoides* | 0 | 0 |
| | | Other[d] | 10 | 10·0 ± 10·1 |
| 2·5 weeks | 9 | *C. subspathacea/P. phryganodes* | 0 | 0 |
| | | Cyperacea[b] | 44 | 44·4 ± 17·6 |
| | | Graminae[c] | 22 | 22·2 ± 14·7 |
| | | *Plantago juncoides* | 0 | 0 |
| | | Other[d] | 33 | 33·3 ± 16·7 |
| 4 weeks | 14 | *C. subspathacea/P. phryganodes* | 35 | 28·5 ± 12·4 |
| | | Cyperacea[b] | 0 | 0 |
| | | Graminae[c] | 50 | 46·4 ± 13·2 |
| | | *Plantago juncoides* | 29 | 3·3 ± 2·8 |
| | | Other[d] | 43 | 21·8 ± 11·3 |

[a]Indicates week since peak hatch of lesser snow goose goslings in 2005.
[b]Species in the family Cyperacea included *Carex ambylorhyncha*, *Carex aquatilis* and *Carex saxatalis*.
[c]Species included *Poa arctica*, *Festuca rubra*, *Dupontia fisheri* and *Calamagrostis* spp.
[d]Included *Salix* spp. and *Potentilla* spp. Also included plant material that was difficult to categorize because it was digested or too small.

**Table 3.** Frequency (% of goslings that ate a given plant species) and relative abundance (mean ± SE) of plant material in the foregut of goslings collected in freshwater marsh at La Pérouse Bay in 2005

| Gosling age[a] | *n* | Plant spp. | Frequency (%) | Relative abundance (%) |
|---|---|---|---|---|
| 1 week | 9 | Cyperacea[b] | 78 | 75 ± 14·4 |
| | | Graminae[c] | 11 | 11·1 ± 11·1 |
| | | *Equisetum variegatum* | 0 | 0 |
| | | Other[d] | 22 | 13·9 ± 11·1 |
| 2 weeks | 14 | Cyperacea[b] | 93 | 80·0 ± 8·6 |
| | | Graminae[c] | 0 | 0 |
| | | *Equisetum variegatum* | 35 | 11·6 ± 5·2 |
| | | Other[d] | 14 | 8·4 ± 6·9 |
| 2·5 weeks | 14 | Cyperacea[b] | 93 | 50·4 ± 8·6 |
| | | Graminae[c] | 0 | 0 |
| | | *Equisetum variegatum* | 50 | 45·5 ± 8·3 |
| | | Other[d] | 21 | 4·1 ± 3·1 |
| 4 weeks | 14 | Cyperacea[b] | 100 | 98·7 ± 8·6 |
| | | Graminae[c] | 0 | 0 |
| | | *Equisetum variegatum* | 36 | 1·3 ± 0·2 |
| | | Other[d] | 0 | 0 |

[a]Indicates week since peak hatch of lesser snow goose goslings in 2005.
[b]Species in the family Cyperacea included *Carex aquatilis*, *Carex bigelowii*, *Carex capillaris*, *Carex gynocrates*, *Carex microglochin*, *Carex rariflora*, *Carex arctogena*, *Carex vaginata*, *Eriophorum vaginatum*, *Kobresia myosuroides* and *Scirpus caespitosus*.
[c]Species included *Poa arctica* and other *Graminae* spp.
[d]Included scarce amounts of *Triglochin palustris* and *Salix* spp. Also included plant material that was difficult to categorize because it was digested or too small.

were likely because of differences in (i) plant species composition, (ii) isotope values of the whole plant compared to plant parts selected by goslings (Evans 2001; Dawson *et al*. 2002) and (iii) within-species variation in isotope value of plants over time and space. Future studies that use stable isotopes as a tool to determine dietary history must carefully consider the most appropriate source inputs into isotope-mixing models, especially when studying organisms that are selective consumers such as herbivorous geese (Parnell *et al*. 2010; Ward, Semmens & Schindler 2010).

### RESOURCE USE OF GOSLINGS IN TM AND FM AS DETERMINED BY MIXING MODELS

The isotope-mixing models revealed that sulphur and nitrogen in tissues of 1-week-old goslings sampled from FM was predominately from FM forage plants. In contrast, goslings sampled from TM at 1-week-old had a lower proportion of their diet from FM forage plants, but on average their diet consisted of more FM forage plants than TM forage plants, and this continued throughout growth.

Isotope values of young animal tissues are derived from the endogenous reserves supplied by their mother (Pilgrim 2007; Olin *et al*. 2011), and as they grow there is rapid incorporation of exogenous nutrients into their tissues (Gladbach, McGill & Quillfeldt 2007). Our results suggest that endogenous resources did not strongly contribute to tissues in 1-week-old goslings from TM and FM because their tissue isotope values were already quite distinct. If endogenous resources were primarily influencing tissue isotope values of

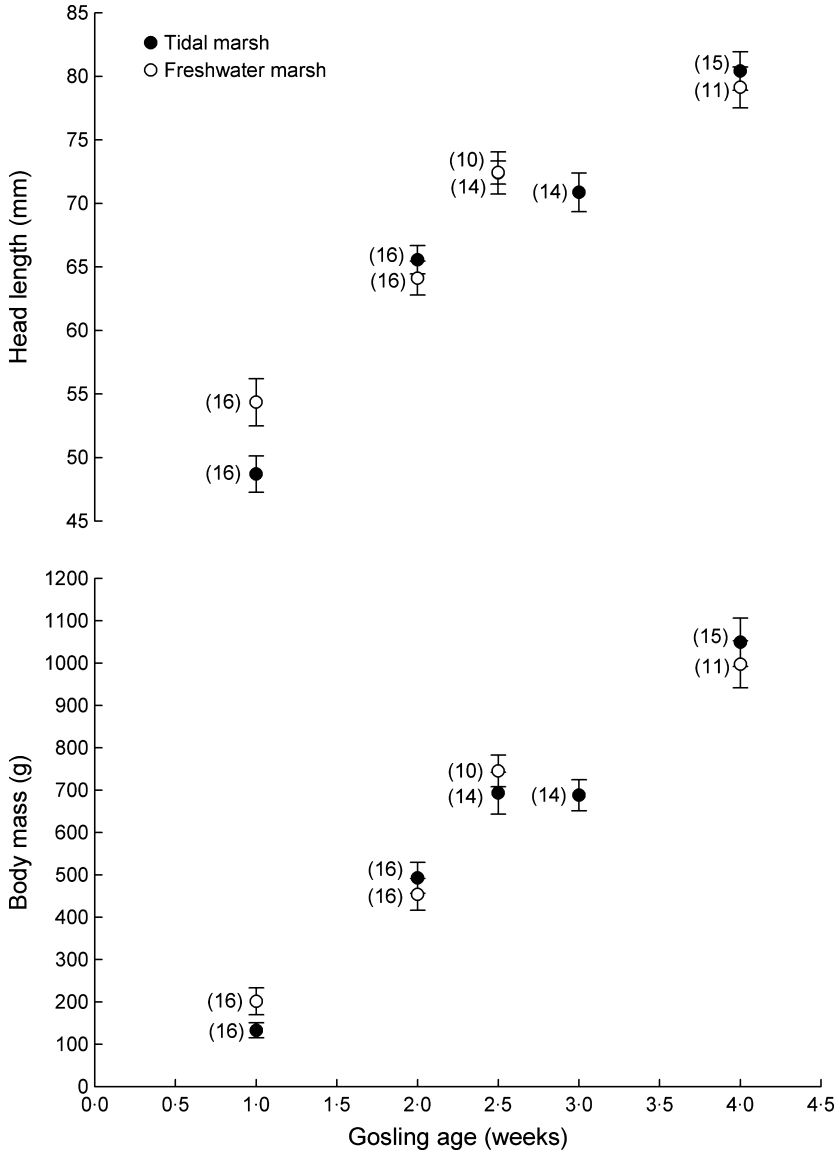


**Fig. 4.** Head length (mm) (mean ± SE) and body mass (grams) (mean ± SE) of goslings collected in tidal marsh (solid symbols) and freshwater marsh (open symbols) during the first 4 weeks of gosling growth at La Pérouse Bay in 2005. Number of goslings collected of each age and in each habitat is denoted in parentheses.

1-week-old goslings, then we expected these values to be more consistent between individuals sampled in the two habitats.

### RESOURCE USE OF GOSLINGS IN TM AND FM AS DETERMINED BY FOREGUT ANALYSIS

Both the plants identified in the foreguts of goslings and the stable isotope analysis of gosling tissue and foregut contents suggested that goslings foraged in different ways when inhabiting FM vs. TM. Goslings in FM ate mostly sedge species and to a lesser extent *Equisetum variegatum*, and the isotopic values of tissues with different turnover rates were similar suggesting that they foraged consistently in FM throughout growth. In contrast, goslings in TM initially ate almost exclusively *C. subspathacea* and *P. phryganodes* (TM species) and then when older ate a wider variety of plant species that were common around the bases of willow patches, and the isotope values of their tissues and mixing model results indicated this variability in their diet during growth. This foraging strategy of goslings inhabiting degraded TM is different than documented during the early 1980s, when goslings primarily ate the two dominant TM graminoids, *C. subspathacea* and *P. phryganodes* (Ruess, Hik & Jefferies 1989).

### GOSLING GROWTH AND SIZE IN RELATION TO HABITAT QUALITY

Our results indicate that FM plants may be adequate for LSG goslings to survive, grow and successfully fledge, although they may not be adequate for maximal growth of goslings. The FM carices and Equisetum spp., commonly found in the adjacent FM, both have high protein content and a balance of amino acids and minerals especially in younger plant tissues that may satisfy the requirements of growing gosling (Thomas & Prevett 1982; Ngai & Jefferies 2004). However, our results from 2005 document for the first time that LSG goslings collected in FM were similar in size and mass compared to goslings collected in TM, yet these goslings

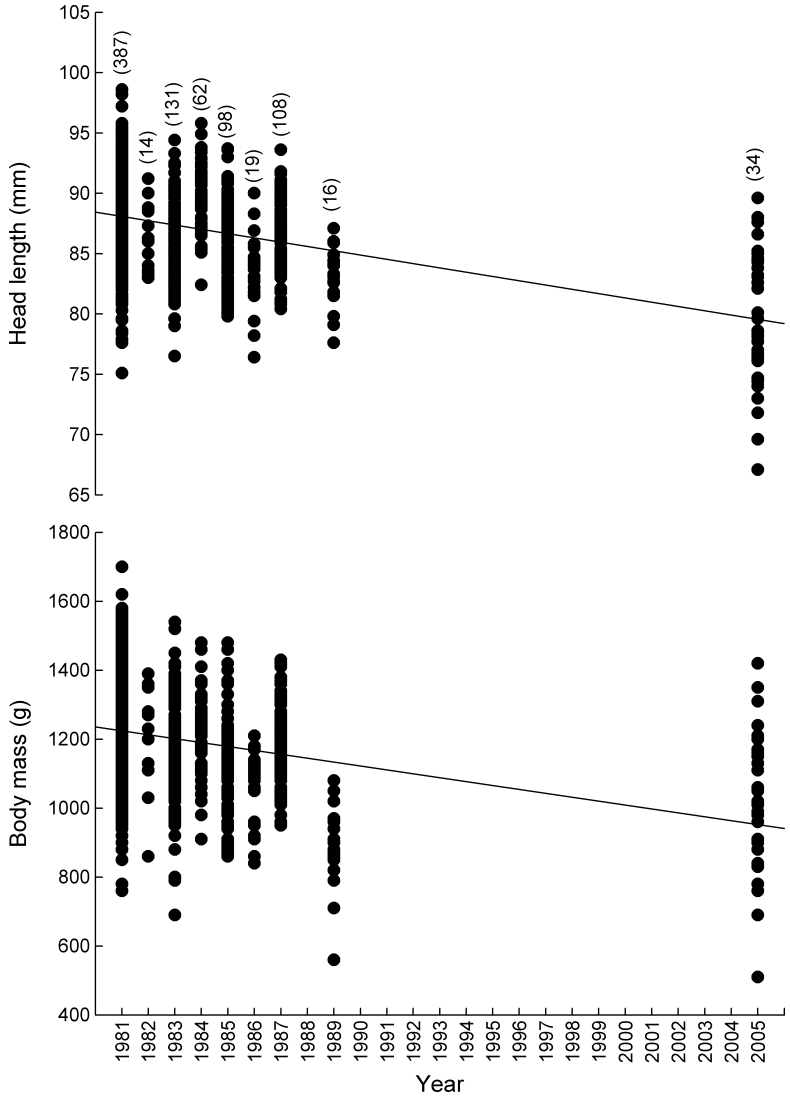


**Fig. 5.** Head length (mm) (mean ± SE) and body mass (grams) (mean ± SE) of goslings collected at La Pérouse Bay during the 1980s and in 2005. Goslings in 1981 to 1989 were known-age goslings between 25 and 30 days old. Goslings collected in 2005 were *c*. 28 days old. Individual goslings represent by circles with total number of goslings measured per year denoted in parentheses.

were significantly smaller than goslings prior to habitat degradation. This indicates that in 2005 higher-quality forage plants in the TM were not available in quantities for goslings to achieve maximal growth rates. We suggest that the degraded condition of the current TM limits gosling growth that a similar limitation occurs for goslings in FM, and this may have longer-term consequences for this population of LSG. Reduction in LSG gosling growth and smaller adult body size are associated with decreased gosling survival and reduced fecundity (Cooch *et al*. 1991b).

### RESPONSE TO RAPID ENVIRONMENTAL CHANGE

Comparisons between our results and those of earlier studies (Gadallah & Jefferies 1995b) reveal that LSG responded to rapid environmental change by broadening their diet to include lower-quality plants while inhabiting TM, and by more extensively foraging on FM plants very early during growth. Our results suggest that LSG goslings and their parent(s) have responded by utilizing both habitats during gosling growth and that FM plants currently contribute more to gosling tissue growth and development than TM plants.

Large-scale changes predicted in Arctic ecosystems because of global warming, and elevated $CO_2$ will result in reduced plant quality and quantity that likely will have profound impacts on many Arctic species if they are unable to adjust their foraging strategies and behaviour (McWilliams & Leafloor 2005). Our results reveal that one such herbivore, the LSG, responds to rapid environmental change by modifying its foraging strategy, growth rates, and overall body size. However, the ability of such phenotypic plasticity to sustain adaptive responses is ultimately limited by reaction norms and the extent of environmental change (Visser 2008). Current research is examining whether that limit has been reached by assessing whether the observed shifts in behaviour, growth rate and size are associated with reduced survival or reproductive success.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Sulphur, carbon and nitrogen isotope values (‰, Mean ± SD) of tidal and freshwater marsh plant species eaten by LSG goslings, during July 2005.

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