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Contributions of digestive plasticity to the ability of white-tailed deer to cope with a low-quality diet

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Many herbivores exhibit phenotypic variations of their digestive system in response to changes in quality of food resources. This digestive plasticity is considered an adaptive trait for individuals to help them cope with variation in food resources and to fulfill nutritional needs. We investigated whether digestive phenotypic variations could contribute to sustain the population of introduced white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Québec, Canada) facing a winter diet of low-quality forage. We compared digestive morphology and in vitro digestibility of winter forage to that of deer from the original mainland population. Deer on Anticosti Island had a higher ruminal volume and digesta load (43% and 62%, respectively), greater absorption surface of the ruminal papillae, and greater relative mass of all forestomachs than deer from the mainland. Woody forage digestibility was similar between the 2 populations, even though faster kinetic digestion may occur for deer on Anticosti Island. Digestive plasticity appears to play a central role in sustaining high deer densities facing harsh forage conditions on Anticosti Island. Comparisons of digestive morphology and digestibility between populations that have access to forage of variable quality contribute to our understanding of the digestive response and the role of digestive plasticity for individuals facing a decline in diet quality.

Key words: balsam fir, digestive morphology, in vitro digestibility, *Odocoileus virginianus*

Individuals rarely face optimal diet quality, and natural selection thus should favor behavioral or physiological traits that improve energy acquisition. Such traits often increase food intake or size components of the digestive tract for diverse species facing lower quality diet conditions (Olsson et al. 2007; Serrano Ferron et al. 2011). The optimal digestion theory (Sibly 1981) suggests that the digestive morphology of individuals can be adjusted in response to diet quality to optimize energy intake. The theory predicts that a herbivore facing a low-quality diet should increase the global length of its digestive tract to allow for more complete digestion of plants and higher energy acquisition. As diet quality decreases, individuals commonly increase food intake, a process known as the instantaneous response strategy (Meyer et al. 2010).

Digestive plasticity refers to the ability to exhibit changes in the shape of digestive organs in response to external conditions such as variation in diet quality, and it allows an individual to maintain itself under conditions of unpredictable food quality and availability (Piersma and Lindström 1995). Although digestive plasticity is recognized as a key driver of individual acclimatization following diet shifts, evidence of such plasticity, particularly in large herbivores such as ruminants, is still relatively rare under natural conditions. Many studies examining the digestive responses of ruminants focus on interspecific comparisons (Fraser 1996; Clauss et al. 2006; Zimmerman et al. 2006) or on relations between life-history traits (i.e., body mass, age, or sex) and digestive morphology (Veiberg et al. 2009; Duarte et al. 2011; Parra et al. 2014), with fewer studies questioning the role of the digestive response at the intraspecific level (Weckerly 1989; Serrano Ferron et al. 2011).

The rumen–reticulum complex is probably the most studied digestive organ in ruminants (Hofmann 1989; Codron and Clauss 2010; Luna et al. 2012) because of its importance for food intake and retention time and because it plays a central role for energetic inputs through byproducts of microbial anaerobic

fermentation (Van Soest 1996). Digestive morphology of the rumen–reticulum (i.e., its capacity and size) varies due to individual body size, sex, age, reproductive status, diel period, and diet quality (Jenks et al. 1994; Veiberg et al. 2009; Duarte et al. 2011; Aiken et al. 2014). Following a shift in diet, morphological variation in ruminal papillae, which are responsible for absorption of digestible energy within the rumen–reticulum (Van Soest 1996), has been interpreted as a mechanism to cope with variations in the nutritive quality of the diet in some species (Jiang et al. 2003; Zimmerman et al. 2006).

Some indicators, e.g., the surface enlargement factor (SEF), provide quantitative values of the ruminal papillation level. These values are based on how much the absorptive rumen mucosa surface is influenced by papillae density and shape and signify the ruminal absorption capacity (Zimmerman et al. 2006). Other morphological traits of the forestomach, such as the omasal laminar surface area (OLSA), also have been used as indicators of absorption capacity at the forestomach level (Clauss et al. 2006). Other organs, e.g., salivary glands and liver, also may respond to shifts in diet quality, even if they are not part of the digestive tract directly. Parotid and liver mass of ruminant species increase following a decrease in diet quality (Jiang et al. 2003; Luna and Weckerly 2013). In addition to digestive plasticity, composition of the ruminal microbiome, which provides digestible energy, is dynamic and can change to maintain adequate energy acquisition following shifts in diet (Van Soest 1994). Red deer (*Cervus elaphus*) exhibit such modifications when fed low- and high-quality diets (Gordon et al. 2002).

We investigated digestive responses of white-tailed deer (*Odocoileus virginianus* Zimmermann 1780) to contrasting diets using 2 related populations. Deer on Anticosti Island (Québec, Canada) were introduced in the late 1800s from a mainland population (Potvin et al. 2000). Following the introduction of approximately 200 individuals, the Anticosti deer population rapidly reached high densities (Potvin et al. 2000). Intense browsing modified the vegetation structure, primarily through eradication of the most palatable deciduous species and reduction of balsam fir (*Abies balsamea* Mill. 1768) regeneration to the benefit of white spruce (*Picea glauca* Voss. 1907—Potvin et al. 2003). These changes impacted the diet of deer on Anticosti Island, especially during winter, when their diet is composed of approximately 70% balsam fir, 20% white spruce, and 10% lichens for at least the last 3 decades (Lefort et al. 2007). This situation is unusual for white-tailed deer because balsam fir, although present in the winter diet on the mainland, represents only a small percentage of the diet compared to deciduous twigs (hobblebush, *Viburnum lantanoides* Michx. 1803, red osier dogwood, *Cornus stolonifera* L. 1753, *Betula* spp., and *Acer* spp.—Dumont et al. 2005). Sauvé and Côté (2007) found that both balsam fir and white spruce were poor nutritional resources for deer on Anticosti Island. However, deer on Anticosti Island remained at high density, even though individual body size decreased (Lesage et al. 2001), presumably through a negative feedback loop involving plant–deer interactions (Simard et al. 2008).

For the main objective, we used a morphological description of the digestive tract and in vitro digestibility trials to assess whether digestive changes in response to consumption of a coniferous diet may explain, at least in part, the maintenance of high white-tailed deer densities on Anticosti Island. First, we compared digestive morphology of deer on Anticosti Island with deer from the original mainland population (Chaudières-Appalaches, Québec, Canada). We predicted that deer on Anticosti Island have heavier, longer, or larger digestive organs than mainland deer to allow for higher food intake and to enhance absorption and digesta processing through the digestive tract. We also predicted heavier livers and parotid masses in Anticosti deer to meet higher demands for detoxification. Second, we assessed whether deer from Anticosti Island, with a diet dominated by conifers, had a higher capacity to digest balsam fir and white spruce than deer from the mainland population.

Materials and Methods

Study area.—This study took place in 2 areas: Anticosti Island (49°28′N, 63°00′W; 7,943 km^2), located in the Gulf of St. Lawrence, and the mainland region (46°59′N, 70°33′W), Québec, Canada. Following deer browsing, vegetation on Anticosti Island is now mainly composed of white spruce, balsam fir, and black spruce (*Picea mariana* Mill., Britton 1879—Potvin et al. 2000). Mean deer density is estimated at > 20 deer/km^2, with local densities reaching > 50 deer/km^2 in some areas on the Island (Tremblay et al. 2007). Vegetation type in the mainland region corresponds to the sugar maple-yellow birch and the balsam fir-yellow birch bioclimatic regions, and mean deer density is estimated at 1.6 deer/km^2 (Huot and Lebel 2012).

Collection of digestive tracts.—We collected digestive tracts during the 2012 and 2013 deer hunting seasons in collaboration with local hunters. We also collected digestive tracts of 2 road-killed females from the mainland region. Harvested individuals spread across a wide range of body size (Anticosti Island: 25.0–73.0 kg; mainland: 47.5–104.5 kg). Over the 2 field seasons, we collected digestive tracts from 41 (20 females and 21 males with mean ± *SE* eviscerated body mass of 37.5 ± 1.3 kg and 50.0 ± 3.1 kg, respectively) adult deer (≥ 1.5 years) on Anticosti Island and 53 adult deer (4 females and 49 males with mean eviscerated body mass of 56.8 ± 3.8 kg and 64.4 ± 1.7 kg, respectively) from the mainland population. In both years, sample collection occurred mostly during October on Anticosti Island and in the 1st 2 weeks of November in the mainland region. The mating season takes place in late November in both populations (Simard et al. 2013), reducing the potential effect of rut on male digestive morphology (Mysterud et al. 2008).

We recorded the diel period of death for each deer (hereafter referred to as harvest period, i.e., AM or PM): 16 and 27 deer were shot during AM and 25 and 26 deer during PM on Anticosti Island and the mainland, respectively. Within 2 h postmortem, the whole digestive tract and internal organs were removed from the abdominal cavity and either measured or frozen for later analysis.

We estimated age using counts of cementum annuli in incisor teeth (Hamlin et al. 2000). Mean age was 5.5 years for females and 4.5 years for males on Anticosti Island, and 3.5 years for both females and males in the mainland population.

Forestomach, liver, and parotid gland.—We used digesta load and water holding capacity (hereafter referred as volume) to determine rumen–reticulum capacity. We determined digesta load of each forestomach compartment by measuring the difference between the mass of each organ with and without its contents to the nearest 0.1 kg with an electronic scale (Salter Brecknell CS2000, Brecknell, Fairmont, Minnesota) in 2013 only. We determined the rumen–reticulum relative volume (2012 and 2013 data set) by pouring water into the emptied rumen–reticulum and recording the amount of water that it held to the nearest 0.1 liter. Our protocol followed methods outlined by Ramzinski and Weckerly (2007). We dissected and weighed the left parotid gland to the nearest 0.1 g using an electronic scale (Mettler Toledo SB16000, Mettler-Toledo International Inc., Columbus, Ohio). We weighed the liver to the nearest 1 g.

Omasal laminar surface area.—We classified and counted omasum laminae based on size: 1st (≥ 3 cm), 2nd (≥ 1 and < 3 cm), and 3rd orders (< 1 cm). We measured the central height of 3 randomly chosen lamina of each order to the nearest 0.1 cm. We used the equation (equation 1) developed by Lentle et al. (1998) to estimate OLSA:

$$\mathrm{OLSA} = \sum_{i=1}^{n} m_i \times h_i$$

where m corresponds to the number of laminae for each order i, and h corresponds to the mean laminae central height for each order i (Lentle et al. 1998).

Ruminal papillae.—We cut approximately 5 cm^2 of rumen wall tissue from 5 ruminal indicative regions: ventral rumen wall, dorsal rumen wall, *atrium ruminis*, caudoventral blindsac, and caudodorsal blindsac (2013 only) that provided a good characterization of overall ruminal absorption capacity (Fraser 1996). We subsampled 1 cm^2 of tissue in the middle of each rumen sample and measured papillae density and shape (e.g., central width and length to the nearest 0.1 mm) of 10 randomly selected and dissected papillae (Supporting Information S1 and S2) under a stereoscopic microscope (Fraser 1996). We calculated SEF for each ruminal region based on the equation from Zimmerman et al. (2006):

$$\mathrm{SEF} = \frac{[\mathrm{density} \times (2 \times \mathrm{mean\ length} \times \mathrm{mean\ central\ width}) + \mathrm{base\ surface}]}{\mathrm{base\ surface}}$$

Hindgut.—We separated the hindgut segments (i.e., small intestine, cecum, and large intestine) and measured length to the nearest 1 cm according to Weckerly (1989). We kept cecum content intact by ligating the ileocecal junctions. In 2013, we recorded digesta load and volume of the cecum to the nearest 0.1 liter using the same method previously described for the rumen–reticulum.

In vitro true digestibility on dry matter basis (%IVTD$_{DM}$).—We selected 11 browse species: balsam fir, white spruce, eastern larch (*Larix laricina* K. Koch 1873), white cedar (*Thuja occidentalis* L. 1753), red maple (*Acer rubrum* L. 1753), striped maple (*Acer pensylvani*cum L. 1753), mountain maple (*Acer spicatum* Lam. 1786), hobblebush, red osier dogwood, yellow birch (*Betula alleghaniensis* Britton 1904), and white birch (*Betula papyrifera* Marshall 1785), because they represented the winter diet of deer from both populations (Dumont et al. 2005; Lefort et al. 2007). We sampled terminal twigs (1–5 cm long and mean diameter of 4 mm) between 0.5 and 2 m from the ground in late September 2012 and 2013. We removed the leaves for deciduous species when present because only twigs are available for deer in winter. We dried samples at 50°C for 48 h and ground them separately with a centrifuge mill (1-mm particle size, Ultra Centrifugal Mill, Type ZM200, RETSCH) before placing 0.50 ± 0.01 g of ground tissues in filter bags (F57 ANKOM size 5 × 5 cm; pore size 25 µm).

We sampled inoculum only from adult males (≥ 1.5 years) to reduce potential age or sex effects on digestibility. For 2012 trials, we used the inocula of 3 and 2 adult males from Anticosti Island and from the mainland population, respectively. For 2013 trials, we used inocula from 3 adult males in each population. Shortly after death (< 1 h), we closed the esophagus and the pyloric sphincter to prevent gas exchange and deterioration of the ruminal microbiome, and we kept the digestive tract in a plastic bag placed in hot water during transport. Handling time between sampling and the beginning of trials varied between 1 and 2.5 h, which should not affect digestion efficiency of the inoculum under these conditions (Milchunas and Baker 1982). We obtained inoculum through an incision in the rumen wall, and we strained the material through cheesecloth under a CO_2 flux.

We obtained %IVTD$_{DM}$ using a *Daisy^{II}* Incubator 200 (ANKOM Technology, Macedon, New York) following the filter bags procedure (Operator's manual, *Daisy^{II}* Incubator, ANKOM Technology). The incubator consisted of four 5-liter jars maintained at constant temperature (39 ± 0.5°C) and rotated. The contents of each jar consisted of 2 sample bags by browse species, a blank bag, 400 ml of deer inoculum, and a buffer solution (ANKOM Technology). We calculated %IVTD$_{DM}$ for each species based on ANKOM procedure (ANKOM Technology).

Statistical analyses.—We compared digestive morphology between populations with linear mixed models for each digestive variable separately. We included population (i.e., Anticosti Island and mainland), sex, and harvest period (AM–PM; for forestomach attributes) as fixed effects and eviscerated body mass and age as covariates for each digestive attribute to control for their potential scaling relationship with digestive variables (Ramzinski and Weckerly 2007; Duarte et al. 2011; Luna et al. 2012; Parra et al. 2014). Using only the data set for Anticosti Island deer, we determined the scalar between rumen–reticulum digesta load and eviscerated body mass using a linear model and adjusting for sex and harvest time (Duarte et al. 2014). Year was included as a random effect in each model for which measurements were taken in > 1 year. We applied a

natural logarithm transformation to all rumen–reticulum and abomasum variables and eviscerated body mass to meet model assumptions for variance homogeneity and normality. We tested for the assumptions for homogeneity of slopes of covariates. We pooled data for SEF values because we detected no significant effect of age and sex for SEF values of each ruminal region. We examined population differences for SEF values using a Student's *t*-test.

We compared $\%IVTD_{DM}$ between populations for each incubation time and each species using analyses of variance with linear mixed-effect models. We added year and individual inoculum as random effects. To prevent type I errors, we applied sequential Bonferroni corrections (Holm 1979) on population comparisons for digestibility of each species (24 and 48 h). Statistical analyses were performed with the R program (R Development Core Team 2013), and the significance level was set at $\alpha = 0.05$.

Results

Morphology of digestive organs.—Deer on Anticosti Island had a relative rumen–reticulum volume and mass that was 43% and 32% higher, respectively, than deer from the mainland population (Table 1). Relative rumen–reticulum digesta load of deer from Anticosti Island was more than twice the load than deer from the mainland (Table 1). The estimated scalar for Anticosti deer between the natural logarithm of rumen–reticulum digesta load and eviscerated body mass was allometric (0.64 ± 0.19, $t_{16} = 3.3$, $P = 0.004$).

Relative mass and digesta load of the omasum, abomasum, and cecum were higher for deer from Anticosti Island compared to the mainland (Table 1). We found a trend for higher OLSA ($F_{1,28} = 3.07$, $P = 0.09$) for deer on Anticosti Island ($685 \pm 34\ cm^2$) compared to deer from the mainland population ($550 \pm 63\ cm^2$). We observed no significant effects of sex or harvest period on forestomach measurements (Table 1).

Relative length of the small intestine was 14% longer for deer from the mainland compared to Anticosti Island (Table 1). However, the large intestine was 7% longer in deer on Anticosti than from the mainland (Table 1). We observed a significant effect of sex on relative length of the large intestine, with females having longer and larger intestines than males (Table 1). Relative cecum length did not differ between the 2 populations (Table 1). Liver mass did not differ between populations, but males had heavier livers than females did (Table 1). Relative mass of the parotid gland was 19% higher for deer harvested on Anticosti Island than for deer from the mainland (Table 1).

White-tailed deer on Anticosti Island had significantly greater SEFs for ventral rumen wall (20% higher), *atrium ruminis* (16% higher), and caudodorsal blindsac (16% higher) ruminal regions than deer from the mainland (Table 2). SEF values for caudoventral blindsac tended to be higher for deer on Anticosti compared to the mainland, but that difference was not statistically significant (Table 2). Dorsal rumen wall SEF values did not differ between populations (Table 2).

In vitro digestibility.—In vitro digestibility on dry matter basis values for balsam fir, white cedar, and yellow birch were higher when digested with inocula from deer harvested on Anticosti Island for a 24-h incubation period than with inocula from deer from the mainland (Fig. 1). Mean digestibility values did not differ statistically for the 48-h trials; however, eastern larch tended to have slightly higher digestibility with inocula from Anticosti deer compared with inocula from the mainland (Fig. 1). Although means were not statistically significant after Bonferroni corrections, we observed a constant trend of higher digestibility for browse species for deer from Anticosti Island compared to deer from the mainland (Fig. 1). See Supporting Information S3 for mean $\%IVTD_{DM}$ of each species for 24- and 48-h incubations.

Discussion

Attributes of the digestive tracts of deer on Anticosti Island, particularly at the forestomach level, were larger than those from mainland individuals, potentially allowing higher digestive efficiency under a poor quality diet (Sibly 1981). We observed slightly higher digestibility of coniferous species on Anticosti Island over 24 h that evened out over 48 h of incubation in deer ruminal inoculum, suggesting that digestibility efficiency did not differ clearly between deer populations. Our results suggest that digestive morphology is a key factor sustaining high deer densities on Anticosti Island.

All forestomach compartments showed higher mass and digesta load on Anticosti Island than on the mainland. These differences suggest that digestive adjustments promoting higher food intake or higher retention time and better processing of the digesta might contribute to improve the digestive efficiency of Anticosti deer facing a low-quality diet. Increases in rumen–reticulum digesta load previously have been linked to consumption of low-quality forages for deer species (Jenks et al. 1994; Zimmerman et al. 2006). Contrary to results for reindeer (*Rangifer tarandus tarandus*—Veiberg et al. 2009) and for black-tailed deer (*Odocoileus hemionus columbianus*—Duarte et al. 2011), we did not find a significant effect of age on rumen–reticulum capacity. This discrepancy might be explained by the few individuals older than 8.5 years in our data set or by individual body mass having a greater influence on rumen–reticulum capacity.

The biological advantages resulting from an increase in rumen–reticulum capacity could have further implications for deer over the long term because individuals may be forced to include higher amounts of white spruce in their winter diet as balsam fir stands are converted into white spruce stands (Barrette et al. 2014). Taillon et al. (2006) suggested that white-tailed deer on Anticosti Island could maintain high population densities with increasing amounts of white spruce in their diet (i.e., 20% to < 40%) by increasing food intake as long as forage availability and digestive morphology are not limiting factors (Duarte et al. 2014). Similar to Duarte et al. (2014) for white-tailed deer, we observed an allometric scalar between rumen–reticulum digesta load and body mass for Anticosti deer. Such

Table 1.—Estimates of fixed terms and covariates from the analysis of covariance explaining variance attributable to population (Pop), sex, age, eviscerated body mass (BM), and harvest period (HP) on digestive morphology of white-tailed deer (*Odocoileus virginianus*) from Anticosti Island and the mainland. Values in bold indicate a significant effect of the population term on the digestive attribute of deer at $\alpha = 0.05$ level. R–R = rumen–reticulum.

Digestive organ	*d.f.*	Anticosti		Mainland		Pop		Sex		Age		BM		HP	
		$\bar{X}$	*SE*	$\bar{X}$	*SE*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
R–R volume (L)[a]	1,50	14.7	1.9	8.4	1.9	20.0	**< 0.0001**	0	0.86	0.4	0.52	24.0	< 0.0001	0.1	0.71
R–R digesta load (kg)	1,36	8.6	0.4	3.3	0.4	51.9	**< 0.0001**	0.5	0.47	0.1	0.81	8.6	0.01	0.2	0.66
R–R mass (kg)	1,36	1.9	0.1	1.3	0.1	20.9	**< 0.0001**	3.2	0.08	0.4	0.55	6.1	0.02	2.7	0.11
Omasum digesta load (g)	1,39	207.8	17.1	82.5	18.9	16.6	**< 0.0001**	0.03	0.86	0.2	0.66	2.5	0.11	0.3	0.57
Omasum mass (g)	1,40	136.4	8.2	95.6	8.8	7.9	**0.01**	0.8	0.38	1.3	0.25	0.6	0.45	0	0.91
Abomasum digesta load (g)	1,37	437.4	29.1	147.4	30.1	32.5	**< 0.0001**	3.2	0.08	0.4	0.55	5.5	0.02	1.8	0.19
Abomasum mass (g)	1,39	206.8	7.3	119.6	7.1	55.5	**< 0.0001**	2.3	0.13	1.9	< 0.0001	19.9	< 0.0001	2.4	0.13
Small intestine length (m)[a]	1,62	13.8	1.1	16	1.0	4.9	**0.03**	0	0.99	0.4	0.52	2.6	0.11		
Large intestine length (m)[a]	1,69	8.3	0.3	7.7	0.3	4.1	**0.05**	4.4	0.04	1.1	0.30	9.1	0.004		
cecum length (m)[a]	1,70	0.44	0.02	0.45	0.02	0	0.91	0.04	0.84	6.0	0.02	0.3	0.57		
cecum volume (L)[a]	1,62	1.0	0.07	0.9	0.06	0.8	0.39	0.5	0.50	7.6	0.008	0.1	0.70	0.8	0.38
cecum digesta load (g)	1,40	57	39	300	41	17.0	**< 0.0001**	0.1	0.82	8.2	0.007	2.3	0.14	0.3	0.61
cecum mass (g)[a]	1,68	92.4	4.4	59.1	3.6	24.4	**< 0.0001**	0.2	0.69	12.5	0.001	1.1	0.29		
Liver mass (g)[a]	1,39	1,425	64	1,343	81	0.4	0.52	5.1	0.03	4.4	0.04	9.9	0.003		
Parotid mass (g)[a]	1,64	32.7	2.7	26.5	2.7	5.7	**0.02**	1.0	0.32	0.4	0.51	13.8	< 0.0001		

[a] Year (2012 and 2013) was included as a random term in the model.

Table 2.—Mean ± *SE* papillae density (per cm^2) and surface enlargement factor (SEFs) for each of 5 ruminal indicative regions of white-tailed deer (*Odocoileus virginianus*) on Anticosti Island and from the mainland population with corresponding results of the Student's *t*-test for SEFs population comparisons of each ruminal regions.

	Papillae density(per cm^2)		SEFs		SEFs population comparisons		
Ruminal regions	Anticosti	Mainland	Anticosti	Mainland	*d.f.*	*t*	*P*
Ventral wall[a]	59.1 ± 3.7	53.3 ± 2.3	11.4 ± 1.3	9.1 ± 1.3	1,75	–3.42	0.001
Dorsal wall[a]	59.2 ± 3.6	53.5 ± 2.2	9.1 ± 1.1	8.0 ± 1.1	1,76	–1.74	0.10
Atrium ruminis[a]	61.4 ± 3.4	66.9 ± 2.8	11.3 ± 1.6	9.5 ± 1.6	1,68	–2.07	0.04
Caudoventral blindsac[a]	59.5 ± 2.5	61.3 ± 2.5	10.2 ± 1.2	9.1 ± 1.2	1,73	–1.84	0.07
Caudodorsal blindsac	54.1 ± 3.1	47.3 ± 3.0	9.2 ± 0.5	7.7 ± 0.5	1,39	–2.12	0.04

[a] Year (2012 and 2013) was included as a random term in the model.

a scalar suggests that individuals are not at the physical limit of rumen–reticulum capacity (Allen 1996). Our results suggest that deer on the Island might accommodate a potential further increase in food intake resulting from an increase in white spruce consumption. Because we did not directly measure food intake rates and rumen–reticulum retention time, we cannot determine which of these mechanisms better explains the higher forestomach attributes.

We detected higher omasum mass and a trend for higher OLSA values for deer on Anticosti Island compared to deer from the mainland population. Increases in omasum mass have been linked to consumption of low-quality forage during winter for reindeer (Mathiesen et al. 2000). However, OLSA values need to be interpreted with caution because they fall within the reported range for white-tailed deer (Clauss et al. 2006) and might be a morphological consequence resulting from the increase in ruminal digesta load rather than a plastic adjustment directly linked to diet quality.

As predicted, Anticosti deer exhibited higher SEF values than mainland deer. Such results were observed in Mongolian gazelles (*Procapra gutturosa*—Jiang et al. 2003) but disagree with other findings (Hofmann et al. 1988; Zimmerman et al. 2006) where a low-quality diet led to a decrease in papillae development. Higher SEF values (Jiang et al. 2003), coupled with increasing size of both foregut and hindgut fermentation chambers (Jiang et al. 2002), were observed for gazelles during winters of low food quality conditions. These variations were interpreted as an adaptive response to maintain energetic balance under harsh nutritional conditions (Jiang et al. 2003). Enhancement of the ruminal surface available for absorption could lead to higher intake of digestible energy products (Hofmann 1989). This digestive trait, coupled with higher rumen–reticulum capacity, may play a crucial role for sustaining high deer densities on Anticosti Island. In Norwegian reindeer (*Rangifer tarandus*), lichen consumption influences rumen papillation patterns during late winter, and lichen intake is correlated with a significant increase in global SEF (Mathiesen et al. 2000). Because arboreal lichens contribute to at least 10% of the winter diet of deer on Anticosti Island (Lefort et al. 2007), their contribution to papillae development needs to be tested.

Morphological changes in hindgut length in relation to forage quality in ruminants are difficult to interpret because ruminants

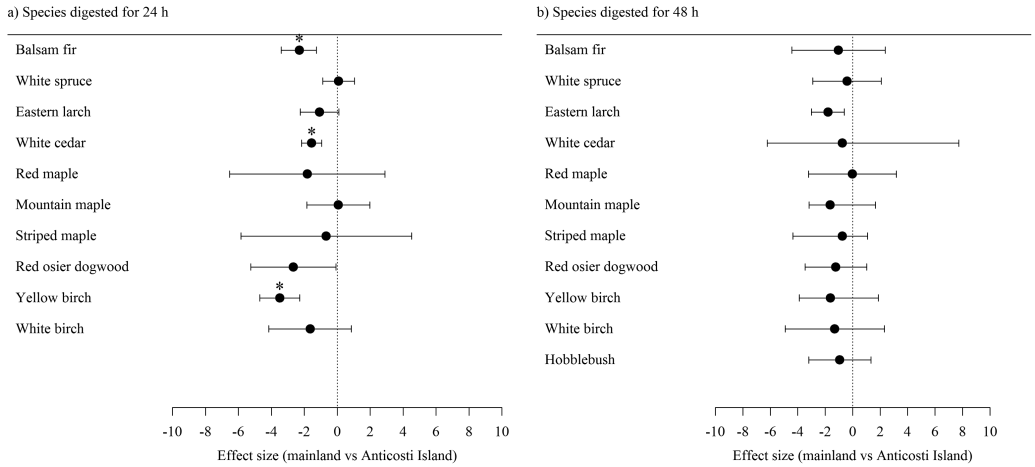

Fig. 1.—Difference in mean in vitro true digestibility of dry matter (%IVTD$_{DM}$) for selected browse species digested for a) 24 h (2013 data set, hobblebush was not included in the 24-h trials) with inocula from adult male deer (> 1.5 years) harvested on the mainland (n = 3) or on Anticosti Island (n = 3) and b) 48 h (2012 and 2013 data sets) with inocula from white-tailed deer (*Odocoileus virginianus*) harvested on the mainland (n = 5) or on Anticosti Island (n = 6). Results are presented as the difference (effect size) of %IVTD$_{DM}$ between populations with corresponding 95% confidence intervals (*CI*s) for each plant species. Negative and positive values correspond to lower and higher %IVTD$_{DM}$ values, respectively, obtained when using inocula from the mainland population over inocula from Anticosti Island. Effect size of plant species digestibility accompanied by an asterisk (*) and for which *CI* do not include 0 are statistically different after sequential Bonferroni correction.

mostly rely on the forestomach for digestible energy acquisition (Van Soest 1994) and because conflicting results have been reported about the effect of food quality on hindgut length (Weckerly 1989; Jiang et al. 2002; Zimmerman et al. 2006). Contrary to Weckerly (1989) and Zimmerman et al. (2006), we found a significant effect of population on hindgut length for white-tailed deer, possibly stemming from an overall decline of diet quality over the last 3 decades on Anticosti Island (Simard et al. 2008). Longer large intestines are linked to the digestive strategy of Sika deer (*Cervus nippon*) exploiting low-quality habitat (Jiang et al. 2006). The larger cecum attributes (i.e., digesta load and organ mass) and higher large intestine length on Anticosti Island presumably highlight the role played by the hindgut fermentation process under a low-quality diet (Staaland and White 1991; Holand 1992). Serrano Ferron et al. (2011) observed an increase of the mass of the cecum in roe deer that foraged in low-quality landscapes and interpreted this increase as a plastic response to maintain energy acquisition under a low-quality diet. We found a significant scaling relationship between age and all cecum attributes, suggesting that cecum fermentation might be more important for older than younger individuals. Similar age-related effects on digesta load and mass were observed at the rumen–reticulum level for reindeer (Veiberg et al. 2009) and black-tailed deer (Duarte et al. 2011) and were related to an increase in food particle size due to a reduction of mastication efficiency. The relationship between age and cecum morphological attributes might be explained indirectly through an increase in particle size in the hindgut at advanced age for white-tailed deer, but this idea remains to be tested.

The higher relative mass of the parotid of deer from Anticosti Island reflects a morphological adjustment linked to diet quality because individuals must feed on rich tanniferous plant species (Sauvé and Côté 2007). Deer might tolerate consumption of high amounts of tannins due to high production of proline-rich tannin-binding proteins by the parotid glands (Jones et al. 2010). Contrary to the mass of the parotid, liver mass did not vary between populations. Similar to results of Parra et al. (2014) for white-tailed deer, males had heavier livers than females did. In our study areas, liver mass of deer was mainly explained by individual condition rather than a correlation with diet quality as observed elsewhere (Verme and Ozoga 1980; Luna and Weckerly 2013).

Higher rumen–reticulum capacity for deer on Anticosti Island presumably promotes longer contact time between digesta particles and microbes. Our findings suggest that some food fractions could be digested more rapidly within the first 24 h of digesta processing through the digestive tract of deer on Anticosti Island compared to deer from the mainland. However, general digestibility efficiency remained similar between the 2 populations as %IVTD$_{DM}$ of balsam fir and white spruce digested with inocula from Anticosti deer were not significantly higher than values for the mainland (for 48-h trials). The ruminal microbiome of deer from northern temperate regions is probably adjusted for a variety of forage types (Gruninger et al. 2014). Some browse species consumed by deer in the mainland region, such as birch, are rich in plant secondary compounds and fibers (Palo 1985). Consumption of these species might maintain a ruminal microbiome acclimatized to high polyphenols and fiber contents, thus explaining the overall similar results between populations.

Our study suggests that digestive plasticity plays a key role in the maintenance of high deer densities on Anticosti Island and contributes to our understanding of digestive plasticity among individuals experiencing different environments. Deer seem to have developed morphological adjustments of the digestive system allowing them to cope with the low quality of their main alimentary resources. Despite some evidence for higher digestibility of conifer on Anticosti Island that would need to be addressed further, our results mostly support the

hypothesis that digestive morphological adjustments may be necessary for deer on Anticosti Island to meet their energetic needs. Our results and previous evidence of digestive plasticity for cervids (Holand 1992; Serrano Ferron et al. 2011) suggest that acclimatization is the key mechanism explaining the ability of deer on Anticosti Island to cope with a low-quality diet.

The persistence of high deer density on Anticosti Island despite a low-quality winter diet is not only the result of digestive plasticity, but also a combination of several factors such as pre-winter body mass gain (Taillon et al. 2006), availability of food resources during summer (Simard et al. 2014), and adjustments of life-history traits such as body size and reproductive rate (Simard et al. 2008). Still, we conclude that enhancement of digestive efficiency through enlargement of both rumen–reticulum capacity and absorptive surface are plastic traits highly linked to the ability of deer to cope with low forage quality.

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Supporting Information

Supporting Information S1.—Central width of ruminal papillae of white-tailed deer on Anticosti Island and from the mainland population. These values were used to determine surface enlargement factor (SEF) values for each ruminal region.

Supporting Information S2.—Length of ruminal papillae of white-tailed deer on Anticosti Island and from the mainland population. These values were used to determine surface enlargement factor (SEF) values for each ruminal region.

Supporting Information S3.—In vitro true digestibility on dry matter basis (% $IVTD_{DM}$) after 24 and 48 h of incubation for species representative of the winter diet of white-tailed deer.

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