Feedback effects of chronic browsing on life-history traits of a large herbivore

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Summary

1. Increasing ungulate populations are affecting vegetation negatively in many areas, but few studies have assessed the long-term effects of overbrowsing on individual life-history traits of ungulates.

2. Using an insular population of white-tailed deer (*Odocoileus virginianus* Zimmermann; Anticosti, Québec, Canada) introduced in 1896, and whose density has remained high since the first evidence of severe browsing in the 1930s, we investigated potential feedbacks of long-term and heavy browsing on deer life-history traits.

3. We assessed whether chronic browsing contributed to a decline of the quality of deer diet in early autumn during the last 25 years, and evaluated the impacts of reduced diet quality on deer body condition and reproduction.

4. Rumen nitrogen content declined 22% between two time periods, 1977–79 and 2002–04, indicating a reduction in diet quality.

5. After accounting for the effects of year within the time period, age and date of harvest in autumn, peak body mass of both sexes declined between the two time periods. At the end of November, males were on average 12% heavier and adult does 6% heavier in 1977–79 than in 2002–04. Hind foot length did not vary between time periods.

6. The probability of conception increased 15% between the two time periods, but litter size at ovulation declined 7%, resulting in a similar total number of ovulations in 2002–04 and in 1977–79.

7. Our results suggest that following a decline in diet quality, white-tailed deer females modified their life-history strategies to maintain reproduction at the expense of growth.

8. Deer appear to tolerate drastic reductions in diet quality by modifying their life history traits, such as body mass and reproduction, before a reduction in density is observed. Such modifications may contribute to maintain high population density of large herbivores following population irruption.

Key-words: body mass, long-term browsing, phenotypic plasticity, population dynamics, reproduction.

Introduction

Models for irruptive populations suggest that introduced herbivores should peak first at very high density, crash, and ultimately increase to a static equilibrium with reduced food resources, also called carrying capacity (Caughley 1970). Irruptive behaviour has been observed in several ungulate populations (Forsyth & Caley 2006), but many factors may prevent populations from attaining the post-peak equilibrium (McCullough 1997; Forsyth 2006). Factors include a strong influence of environmental stochasticity on plant dynamics (Bayliss & Choquenot 2002), vital rates of ungulates

(Sæther 1997), and diet switching (Coomes *et al.* 2003). Alternative food sources, regulated extrinsically, may also contribute to maintaining populations above carrying capacity even when most vegetation has been depleted (Forsyth 2006). Examples of supplemental food include fruits and flowers, fallen leaves, and litterfall of arboreal lichens (Nugent, Fraser & Sweetapple 2001; Tremblay *et al.* 2005; Ward & Marcum 2005). Agricultural crops may also contribute to maintaining high herbivore densities artificially, potentially devastating natural plant communities (Alverson, Waller & Solheim 1988).

The disappearance of most preferred or palatable plant species under long-term browsing pressure (Côté *et al.* 2004) can potentially induce strong negative feedback effects on

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herbivores' growth, resulting in decreased reproduction and survival (McCullough 1999). Life history theory suggests that decreases in body reserves due to resource shortages are likely to affect juvenile survival first, followed by age at maturity and female reproduction (Eberhardt 2002). Several studies have assessed short-term density-dependent effects on life history traits (reviewed by Fowler 1987), but long-term effects of high density are less documented (Coulson *et al.* 2004). There are only a few empirical studies suggesting that populations facing long-term changes in resource availability are expected to show intergenerational variations in body size and fecundity (e.g. Albon *et al.* 1986 in red deer, *Cervus elaphus;* Skogland 1990 in reindeer, *Rangifer tarandus*; Laider *et al.* 2006 in sea otter, *Enhydra lutris;* Krafft *et al.* 2006 in ringed seal, *Pusa hispida*).

A century after their introduction, white-tailed deer (*Odocoileus virginianus* Zimmermann) on Anticosti Island have maintained high population density (> 20 deer/km^2) without any apparent equilibrium with the boreal plant community. The abundance of preferred deciduous browses has been reduced drastically since the 1950s (Marie-Victorin & Rolland-Germain 1969; Tremblay *et al.* 2005), leading deer to shift their winter diet primarily to balsam fir (*Abies balsamea* L., P. Mill; Lefort *et al.* 2007). The availability of balsam fir browse has declined further during the last 25 years, so that deer now rely mainly on litter fall of arboreal lichens, fir twigs and wind-thrown trees as winter forage (Tremblay *et al.* 2005; Lefort *et al.* 2007). Environmental variations (Sæther 1997), diet adaptability (Coomes *et al.* 2003) and/or supplemental food independent from deer browsing (Tremblay *et al.* 2005) may have favoured the maintenance of high deer density on Anticosti Island despite the scarcity of browses. Another possibility for the success of deer involves their high plasticity and strong tolerance to long-term habitat degradation, as suggested by Skogland (1990) for reindeer.

Here, we expand the knowledge of the relationships between chronic browsing and life history traits of large herbivores by examining variations of diet quality, body mass, hind foot length and reproduction indices during a 25-year time period. First we document that, since 1977–79, chronic browsing has decreased diet quality in early autumn, similar to the situation that occurred with winter browse (Tremblay *et al.* 2005). Because autumn diet quality declined and deer density remained high, we hypothesized that autumn body mass and fertility would have declined further in the last 25 years (Albon, Mitchell & Staines 1983), even if they were already low in the late 1970s (Goudreault 1980). We also measured skeletal growth, as it is expected to change more slowly than body mass (Klein, Meldgaard & Fancy 1987). Alternatively, Skogland (1990) suggested that long-term reduction in resources would have enhanced the tolerance of deer to adverse conditions, i.e. that deer on Anticosti that have already acclimated to several years of forage limitation since 1977–79 would not be affected strongly by a further decline in diet quality. Selection for high-quality individuals may have generated similar body mass and reproduction, as in 1977–79.

Methods

STUDY AREA

We conducted this study on western Anticosti Island (49° N, 62° W; 7943 km^2), located in the Gulf of St Lawrence (Québec, Canada). Anticosti has a maritime subboreal climate with short summers, long winters and abundant rainfall (630 mm year^{-1}) and snowfall (406 cm year^{-1}; Environment Canada 1982). Average snow sinking depth for deer in winter is 27 cm, with sinking depth above 50 cm for about 40 days year^{-1} (A. Gingras, unpublished data). The vegetation on Anticosti belongs to the eastern balsam fir–white birch bioclimatic forest region, characterized by balsam fir, white spruce [*Picea glauca* (Moench) Voss] and black spruce [*P. mariana* (P. Mill.) BSP]. As a consequence of severe deer browsing, white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) are now present only sporadically, and many other shrubs and trees have been almost extirpated (e.g. *Acer spicatum* Lam., *Cornus stolonifera* Michx., *Taxus canadensis* Marsh; Tremblay *et al.* 2005). Strong diet selection of deer for balsam fir (Sauvé & Côté 2007) is leading to a progressive conversion of balsam fir stands into white spruce stands (Potvin, Beaupré & Laprise 2003).

There are no predators on Anticosti and annual harvest rates < 8% appear too low to regulate or limit the deer population (Gingras 2002). Indices suggest that the abundance of deer has remained similarly high during the last 25 years and that deer browsing pressure, based on fir sapling demography, has also remained high (Chouinard & Filion 2005). Hunting success and sex ratio of harvested deer were similar in 1977–79 (1·64 deer per hunter for a maximum of two and 63% males) and 2002–04 (1·67 deer per hunter and 64% males), although it varied annually from 1·50 to 1·86 deer per hunter and 57–69% males (A. Gingras, unpublished data). We have no data on the sex ratio of the live population. The number of harvested deer per km^2 has also been relatively stable since 1975, ranging from one to 1·4 deer per km^2 (Gingras 2002). Exponential growth rate of white-tailed deer on Anticosti Island from 1980 to 2005 was estimated at $\lambda = 1·06 \pm 0·10$ [standard error (SE); Simard *et al.* unpublished data], suggesting a relatively stable population considering the error term. Adult survival rate was estimated at $0·77 \pm 0·06$ with strong annual variations (Simard *et al.* unpublished data).

DIET QUALITY

Deer diet quality in early autumn was estimated using the nitrogen content of rumen samples from deer killed by hunters (Lewis 1994). Rumen samples (500 mL) were collected in 1976–78 ($n = 28$), 2003 ($n = 18$) and 2004 ($n = 17$) at the end of September, and preserved with formalin. All samples were unwashed (Huot 1982), except in 2003 when samples were rinsed with water in a 500 μ sieve. The relation of nitrogen content (N) between washed and unwashed samples $\{R^2 = 0·73, F_{2,47} = 130·1, P < 0·001, n = 49; N = 0·86 [\pm 0·23 \text{ (SE)}] + 0·87 [\pm 0·07] \text{ N}_{washed}\}$ was estimated with aliquots of the same samples in 2004 and applied to washed samples from 2003. Total N content was determined using an automated Macro Kjeldahl analysis (Kjell-Foss Automatic 16200, Foss Electric, Hillerød, Denmark).

BODY MASS AND SIZE

Dressed body mass (minus viscera and bleedable blood) of adult deer ($\geq 1·5$ years old) was obtained during the hunting season for three time periods: 1966–70 (all years but 1968), 1977–79 and 2002–04

Table 1. Sample sizes for body mass, hind foot length, and number of pairs of ovaries, of white-tailed deer harvested on Anticosti Island

| Years | Sexes | | Pairs of ovaries |
	Males	Females	
1966	134	94	–
1967	498	450	–
1969	134	183	–
1970	650	596	–
Total	**1416**	**1323**	**–**
1975	–	–	63
1976[1]	162	155	118
1977	379	196	86
1978	65	156	90
1979	137	102	37
Total	**743**	**609**	**394**
2002	108	267	100
2003	207	212	141
2004	299	266	149
Total	**614**	**745**	**390**

[1]There were no data on harvest date in 1976, therefore 1976 was included only in the analyses of female hind foot length (no effect of harvest date) and reproduction.

(Table 1). Deer were weighed using a spring scale (± 0.25 kg). Hind foot length was measured from the calcaneum to the edge of the hoof (± 0.2 cm) and we verified the reliability of multiple observers ($n = 12$) in 2002–04 by comparing their measurements with one control observer. Between-observer error was less than 2·5% (average difference $\pm$ SE of 0.50 ± 0.12 cm). Deer age was estimated using tooth wear in 1966–70, possibly under-estimating the age of some old deer (Hoye 2006), and using cementum layers in incisor teeth from 1976 to 2004 (Hamlin *et al.* 2000). In 1966–70, only mean dressed mass (without variance) and sample sizes per age and sex classes were available. Data from 1977–79 and 2002–04 were divided into six harvest periods of 15 days (from 1 September to 30 November) to take into account the effect of harvest date on mass.

Because body masses were collected from harvested deer, hunter selectivity may have influenced the sample: hunters are likely to select large males (trophy) or large females, although to a lesser extent (Nilsen & Solberg 2006). Hunter selectivity is expected to have remained similar during the whole study, as hunting statistics and sex structure did not vary (see above). Because we controlled for age and sex in all models, selectivity should not be an issue in our analyses (Solberg *et al.* 2004).

FEMALE REPRODUCTION

Ovaries from does of known age were collected during 1975–79 and 2002–04 (Table 1). Ovaries were preserved in 10% formalin for 10 days, then in 70% ethanol until they were embedded in paraffin and prepared for histological analyses (Goudreault 1980). Ovaries were cut into thin slices (10 µm) that were coloured with a Masson trichrome stain and examined at a magnification of 10×. Following ovulation, *Corpus luteum* of pregnancy are formed (one for singleton and two for twins) and regress slowly after parturition into white scars named *Corpus rubrum* (CR) when they are less than 6 months old (Langvatn 1992). Corpus rubrum are identified in ovaries based on size and texture and their occurrence is a reliable criterion for assessing age-specific fertility rate (Langvatn, Bakke & Engen 1994).

STATISTICAL ANALYSES

The difference in diet quality between time periods was assessed using a Z-test on N content of rumen samples from 1976 to 1978 and 2003 to 2004. Rumen N contents in 2003 (3.2 ± 0.3%) and 2004 (3.1 ± 0.1%) did not differ ($t_{21} = 0.30$, $P = 0.8$), and were pooled for comparisons with data from 1976 to 1978 that were pooled previously by Huot (1982).

Hind foot lengths between 1977–79 and 2002–04 were compared using a general linear model (GLM procedure in SAS version 9·1; SAS Institute 2003). For body mass (log-transformed), we used a model allowing us to take annual heterogeneous variances into account (mixed procedure in SAS; Diggle, Liang & Zeger 1994). Because males and females may respond differently to environmental conditions (Toïgo *et al.* 2006), they were modelled separately. The effect of 'year' was included as a nested factor in the time period, and we used age, age^2 (non-linear effect) and the harvest period as covariates. We used the backward stepwise method to verify the statistical hypothesis that body mass had changed between time periods. We tested all two-way and three-way interactions, although none of the three-way interactions were significant. In the hind foot length model, all deer ≥ 5.5-year-olds were pooled, because asymptotic hind foot length is then reached for deer on Anticosti (this study and Lesage *et al.* 2001). Although deer hind foot length is not expected to grow significantly during autumn, we tested the effect of the harvest period on hind foot length to verify whether hunters select larger individuals as the rut approaches (B.-E. Sæther, personal communication). We used least squared means (lsmeans; SAS version 9·1; SAS Institute Inc. 2003) to conduct a posteriori comparisons at each value of the covariates age and harvest date in autumn.

We used a Z-test to compare body mass from 1977 to 1979 and 2002 to 2004 (lsmeans and SE produced by the previous models) with means from 1966 to 1970. To be conservative, we applied the largest SE found in the previous models (always from 1977 to 1979) to the data of 1966–70. We grouped all deer ≥ 6.5-year-olds in the same age class to reduce possible bias associated with different ageing methods (Hoye 2006). Because the sample sizes per age class were large and taken during the whole autumn during 1966–70, we believe that the comparisons of average body mass between the three time periods are appropriate.

Variations in female reproduction between time periods were assessed using three different indices: the probability of conception (0 or 1 based on the observation of ≥ 1 CR), the number of ovulations for each ovulating doe (i.e. litter size at ovulation, 1 or 2 CR) and the total annual number of ovulations (0, 1 or 2 CR), an integrative index of overall doe productivity. For the first two indices, we used generalized linear models (Genmod procedure; SAS Institute Inc. 2003) with a binomial error distribution and a logit link. For the last index, because it had three levels, we used a multinomial ordinal logistic regression with a cumulative logit link (Logistic procedure; SAS Institute Inc. 2003); lsmeans were calculated from model parameter estimates and compared a *posteriori* by the least squares difference (LSD) method. For logistic regressions, the SE of lsmeans were calculated using bootstraps with 1000 replications (Efron & Tibshirani 2000). All models included the time period, the year nested into it, and age at ovulation (1·5, 2·5 and ≥ 3.5-year-olds). Again, we verified the statistical hypothesis that reproduction changed between time periods using a backward stepwise approach. All two-way interactions were tested. As fawns do not reproduce on Anticosti, they were not included in the analyses.

All results are presented as means or lsmeans $\pm$ SE, unless stated otherwise. The threshold for statistical significance was fixed at $\alpha = 0.05$.

Table 2. Main effects retained in general models to predict changes of white-tailed deer body mass (a) and hind foot length (b) between 1977–1979 and 2002–2004 for males (d.f.$_{den}$ = 1175 for mass and 1186 for hind foot length) and females (d.f.$_{den}$ = 1187 for mass and 1348 for hind foot length) on Anticosti Island

	Males			Females		
Effects	d.f.$_{num}$	F	P	d.f.$_{num}$	F	P
(a) Log body mass						
TP	1	0·8	0·4	1	2·4	0·1
Years (TP[1])	4	10·2	< 0·001	4	34·1	< 0·001
HD	1	15·2	0·001	1	69·7	< 0·001
Age	1	332·5	< 0·001	1	155·0	< 0·001
Age^2	1	98·8	< 0·001	1	80·4	< 0·001
HD × age	1	6·0	0·01	1	12·0	< 0·001
Age × TP	1	5·0	0·03			
Age × years (TP)	4	4·2	0·002			
HD × TP				1	5·7	0·02
HD × years (TP)	4	4·8	00008			
(b) Hind foot length						
TP	1	11·8	< 0·001	1	1·7	0·47
Years (TP)	4	8·1	< 0·001	5	37·3	< 0·001
Age	1	292·8	< 0·001	1	623·0	< 0·001
HD	1	7·6	0·006			
HD × TP	1	7·2	0·008			
HD × years (TP)	4	4·7	< 0·001			

[1]TP: time period, i.e. 1977–79 vs. 2002–04; HD: harvest date in autumn; Years (TP): years nested into time period.

Results

DIET QUALITY

Rumen N content was 22% higher in 1976–78 (3·9 ± 0·1%) than in 2002–04 (3·2 ± 0·2%; Z = 3·12, d.f. = 56, P = 0·003), indicating that diet quality in early autumn has declined between the two time periods.

BODY MASS

The model for male body mass (Table 2a) indicated that body mass increased with age (model parameter estimate ± SE in log scale; age = 0·205 ± 0·013), but non-linearly as differences in mass between young age classes were larger than between older age classes (age^2 = – 0·013 ± 0·001; Fig. 1a). Males accumulated mass throughout autumn (harvest date = 0·029 ± 0·009; Fig. 1b), but younger deer gained more mass than older ones (harvest date × age = – 0·004 ± 0·002). Interestingly, we observed that body mass decreased between the two time periods, but particularly for older males, as shown by the interaction of time period with age (1977–79 minus 2002–04 = 0·024 ± 0·008; Table 2a, Fig. 1a). There was an 8% decline in average body mass (3·5-year-olds in mid-October) between 1977 and 1979 (47·6 ± 0·6 kg) and 2002 and 2004 (44·1 ± 0·3 kg, t_{1175} = 5·64, P < 0·001). Differences in body mass between time periods were larger in late November (at 3·5-year-olds: 5·9 ± 0·2 kg, t_{1175} = 2·47, P = 0·01) than in September (2·1 ± 0·04 kg, t_{1175} = 2·47, P = 0·01), the slope of mass gain in autumn being steeper in 1977–79 than in 2002–04 (Fig. 1b). This effect is explained by the interaction of harvest date and the factor year nested into the time period. The model also revealed the importance of annual variability in body mass (significant nested year effect and interactions with age and harvest date; Table 2a).

The model for female body mass (Table 2a) also indicated that body mass increased with age (model parameter estimate ± SE in log scale; age: 0·090 ± 0·007), but non-linearly as differences in mass between ages were larger in young deer (age^2: –0·005 ± 0·001; Fig. 1a). Adult females accumulated mass during autumn (harvest date = 0·042 ± 0·007; Fig. 1b), but younger females gained more mass than older ones (age × harvest date = – 0·004 ± 0·001; Table 2a). Females were smaller in 2002–04 than 25 years ago, but only from October onwards, as harvest date interacted with time period (1977–79 minus 2002–04 = 0·016 ± 0·007; Fig. 1b). Average body mass (4·5 years old) in mid-October decreased between 1977 and 1979 (37·6 ± 0·6 kg) and 2002 and 2004 (37·0 ± 0·2 kg, t_{1187} = 1·96, P = 0·05), but differences were greater in late November (1977–79 = 44·0 ± 0·9 kg and 2002–04 = 41·3 ± 0·5 kg, t_{1187} = 2·73, P = 0·006). Year within each time period was significant, again underlying the influence of annual factors on body mass (Table 2a).

Deer were heavier in 1966–70 than in 1976–79 and 2002–04 for all age–sex classes (Fig. 1a). Average male body mass declined from 56·8 ± 0·6 kg in 1966–70 to 50·2 ± 0·6 kg in 1976–79 (Z_{3272} = 14·1, P < 0·001) and 45·9 ± 0·3 kg in 2002–04 (Z_{3480} = 22·5, P < 0·001). Similarly, females were heavier on average in 1966–70 (45·1 ± 0·6 kg) than in either 1976–79 (37·0 ± 0·6 kg, Z_{1350} = 14·6, P < 0·001) or 2002–04 (36·3 ± 0·2 kg, Z_{1237} = 16·9, P < 0·001).

HIND FOOT LENGTH

The models for hind foot length (Table 2b) included a significant effect of year (nested in the time period) and age for both males (model parameter estimate for age ± SE; 0·73 ± 0·04) and females (0·76 ± 0·04). The model for males suggested that, in 1977–79, larger males of each age class were harvested earlier in the season (hind foot length: September = 49·3 ± 0·2 cm, November = 48·1 ± 0·2 cm, t_{1186} = 3·65, P = 0·0002), but not in 2002–04 (September = 48·4 ± 0·2 cm, November = 48·5 ± 0·2 cm, t_{1186} = 0·39, P = 0·70), as revealed by the interaction of harvest date and time period (1977–79 minus 2002–04 = –0·68 ± 0·23; Fig. 1d). Male hind foot length in 1977–79 was therefore greater than in 2002–04 (1977–79 minus 2002–04 = 2·78 ± 0·50), but possibly because of hunter selectivity early in autumn. Hind foot length of females did not change from 1976–79 to 2002–04 (Table 2b, Fig. 1c) and was not affected by harvest date (Fig. 1d).

REPRODUCTION

For all three parameters of reproduction we found significant effects of annual variations within each time period. Not surprisingly, all reproductive parameters increased with female
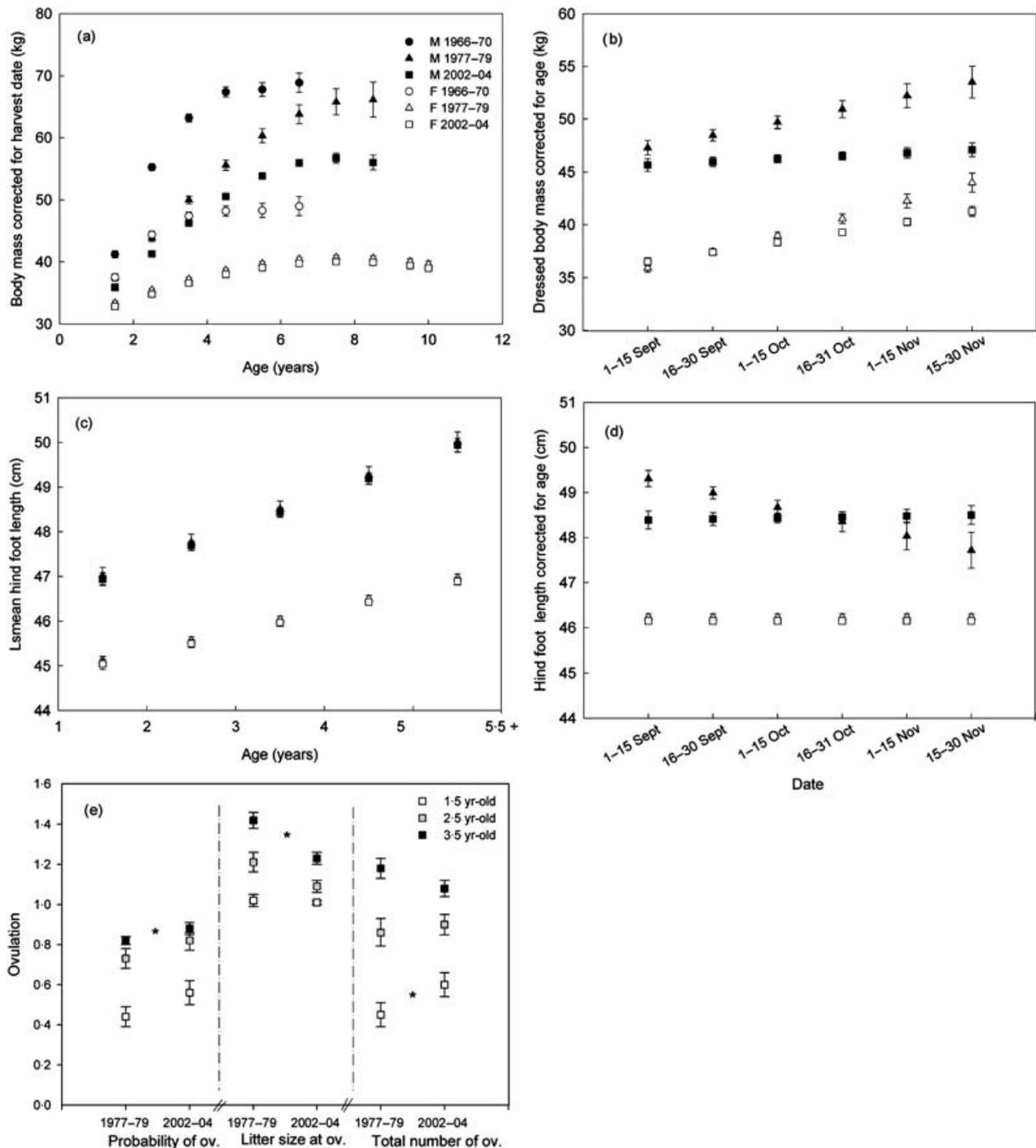
Fig. 1. Dressed body mass (kg) (a, b), hind foot length (cm) (c, d) and reproduction indices (e) in 1966–70 (only for mass), 1977–79 and 2002–04, for male (M) and female (F) white-tailed deer on Anticosti Island according to age corrected for harvest date (a, c), the harvest date in autumn corrected for age (b, d) and age at ovulation (e). Data from 1977 to 79 and 2002–04 are lsmeans (± standard error) estimated from models, data from 1966 to 1970 are raw data to which the largest standard error of 1977–79 for each age class was applied. In (e), the three indices of female reproduction are the probability of conception, litter size at ovulation and the total number of ovulations and significant differences between time periods for each age class are indicated by *.

age but no interactions were significant (Table 3). The probability of conception was 15% lower in 1975–79 (0·68 ± 0·03) than in 2002–04 (0·78 ± 0·03, $Z = 2·3$, $P = 0·02$; model parameter estimate: 1975–79 minus 2002–04 = –0·93 ± 0·54; Table 3). Litter size, however, was 7% larger in 1975–79

(1·14 ± 0·04) than in 2002–04 (1·07 ± 0·02, $Z = 1·9$, $P = 0·05$; 1975–79 minus 2002–04 = 0·13 ± 0·43; Table 3). The total number of ovulations did not change significantly between 1975–79 (0·75 ± 0·05) and 2002–04 (0·82 ± 0·04, $Z = 1·3$, $P = 0·2$), although the distribution of the three factors in the

Table 3. Main effects selected in models to predict changes in the probability of conception (d.f.$_{den}$ = 774), litter size at ovulation (d.f.$_{den}$ = 597) and total number of ovulations (d.f.$_{den}$ = 784) using analyses of ovaries of female white-tailed deer on Anticosti Island between 1975–79 and 2002–04

Model parameters	Probability of conception			Litter size at ovulation			Total number of ovulations		
	d.f.	χ^2	P	d.f.	χ^2	P	d.f.	χ^2	P
TP	1	5·7	0·02	1	15·5	< 0·001	2	21·3	< 0·001
Year (TP[1])	6	38·0	< 0·001	6	44·8	< 0·001	12	69·5	< 0·001
Age at ovulation	2	60·6	< 0·001	2	52·0	< 0·001	4	66·0	< 0·001

[1]TP: time period, i.e. 1975–79 vs. 2002–04; Year (TP) = year nested into time period.

multinomial model (probability of 0, 1 or 2 ovulations; Table 3) varied with the time period, confirming the results obtained in the two previous models. Differences between time periods were variable and depended on age at ovulation (Fig. 1e). Prime-aged does, i.e. ≥ 3·5 years, showed a significant increase in the probability of conception ($Z = 2·1$, $P = 0·04$) and a decrease in litter size at ovulation ($Z = 3·9$, $P < 0·001$). Only yearlings showed a significant increase in the total number of ovulations ($Z = 2·0$, $P = 0·05$), but the reproduction of 2·5-year-olds did not change.

Discussion

On Anticosti Island, 70 years of chronic browsing have generated severe impacts on the vegetation. Consequently, we found a decline in autumn diet quality over the last 25 years, which concurs with the observed decline in winter browse abundance during the same period (Tremblay *et al.* 2005; Fig. 2). Deer density appeared to have remained high since 1975, therefore the decline in body mass for both sexes has probably been generated by a decline in diet quality or abundance, although we cannot rule out fully a possible role of density. Our results confirmed the expected mass decline following resource limitation (Sæther *et al.* 1996), but other data seemed to support the hypothesis of a strong tolerance of deer to long-term resource limitations (Skogland 1990). For example, hind foot length and total number of ovulations were similar between the two time periods (Fig. 2). Reproductive strategies, however, have appeared to change, as the probability of ovulation increased and litter size at ovulation decreased during the last 25 years. Surprisingly, our results do not support some of the predictions of life history theory (Eberhardt 2002), as body mass and reproduction were affected more negatively in adults than in yearlings, suggesting strong selection for high-quality fawns (Taillon, Sauvé & Côté 2006).

DIET QUALITY

The situation of moose (*Alces alces*) in Sweden is similar to what we observed with deer on Anticosti Island; in both places herbivores have affected plant size and quality profoundly, as well as species composition and abundance (Danell *et al.* 2003). The first observations of deer effects on the boreal vegetation of Anticosti occurred in the 1930s (Marie-Victorin & Rolland-Germain 1969), but habitat degradation continued as density remained high afterwards (Potvin *et al.* 2003). Balsam fir at browse height has now declined by 70–100%, depending on the stands compared to the mid-1970s (Tremblay *et al.* 2005). Supplemental food from litterfall and windthrown trees may have contributed to maintaining high population density despite chronic browsing. In ungulates, poor winter ranges have often been associated with low body growth (Sæther *et al.* 1996), but summer forage is crucial for the accumulation of body reserves (Sæther *et al.* 1996; Hjeljord & Histøl 1999) that may affect age at primiparity, pregnancy rate and survival (Verme 1969; Albon *et al.* 1986; Cook *et al.* 2004).

BODY MASS

In the absence of predation, density-dependent feedbacks are unlikely to be sufficient to regulate high herbivore density, and forage limitation is therefore expected to affect body growth negatively (Sæther *et al.* 1996). Boucher *et al.* (2004) found that body mass of white-tailed deer in different populations in Quebec was related positively to summer forage availability, and that Anticosti deer were the smallest in the province. Our data on Anticosti suggest that deer have not reached equilibrium with their food resources a century after their introduction. Since 1966–70, body mass has declined simultaneously with forage quality and abundance (Potvin *et al.* 2003; Tremblay *et al.* 2005).

Food shortages in ungulates should affect growth more severely in males than in females (white-tailed deer: McCullough 1999; red deer: Clutton-Brock, Guinness & Albon 1982; roe deer, *Capreolus capreolus*: Toïgo *et al.* 2006). Males have higher nutritional requirements than females (Rose, Clutton-Brock & Guinness 1998), which appear to be more tolerant to low intake of protein and energy (Parker, Barboza & Stephenson 2005). It is therefore not surprising that the decrease in body mass was larger for males than for females. According to life history theory (Eberhardt 2002), forage restrictions should also affect yearlings more severely than prime-aged adults (white-tailed deer: Ashley, McCullough & Robinson 1998; red deer: Coulson *et al.* 2004; bighorn sheep, *Ovis canadensis*: Festa-Bianchet *et al.* 2004). This prediction, however, was not verified in our study as differences in males'
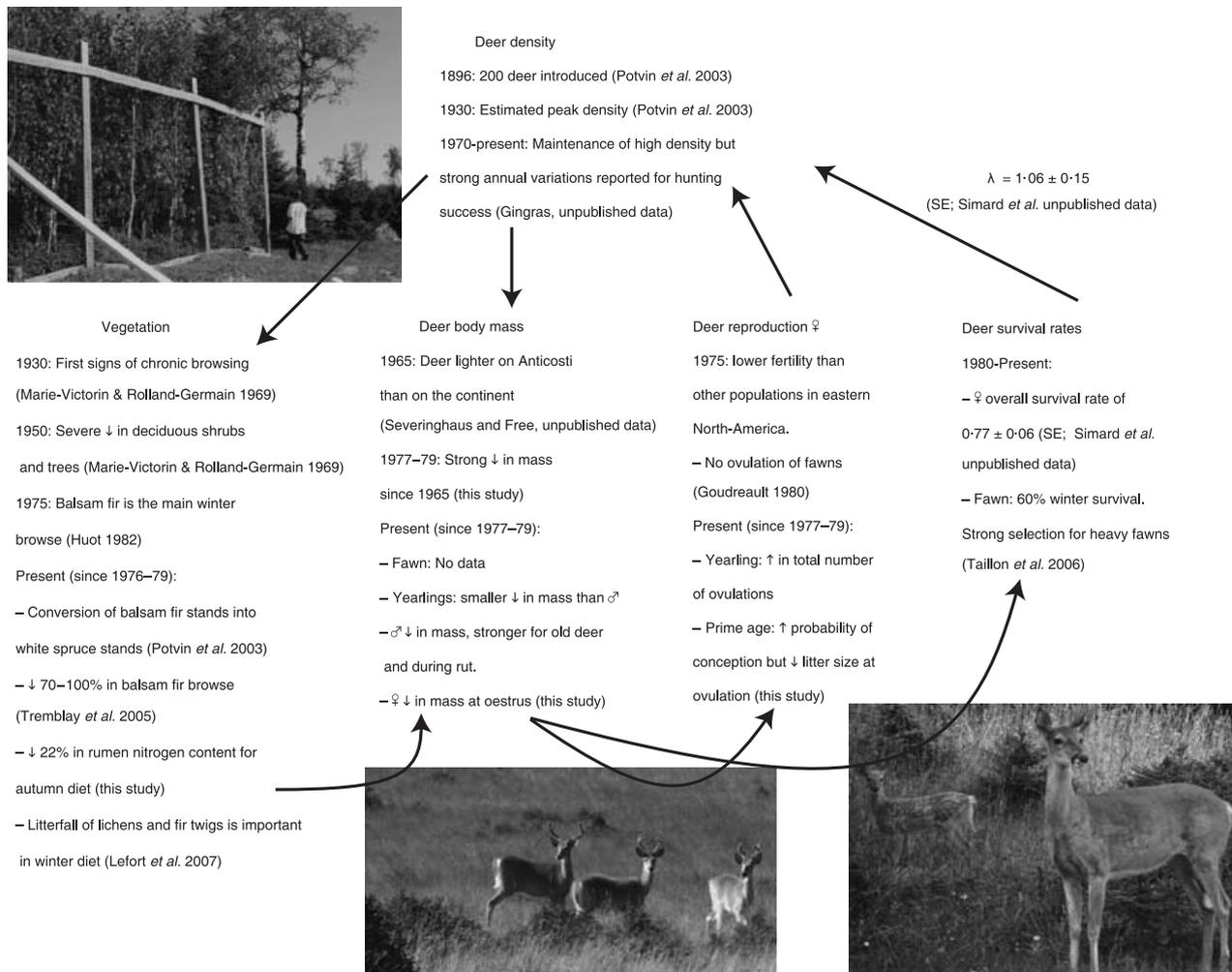
Deer density

1896: 200 deer introduced (Potvin *et al.* 2003)

1930: Estimated peak density (Potvin *et al.* 2003)

1970-present: Maintenance of high density but strong annual variations reported for hunting success (Gingras, unpublished data)

$\lambda = 1.06 \pm 0.15$ (SE; Simard *et al.* unpublished data)

Vegetation

1930: First signs of chronic browsing (Marie-Victorin & Rolland-Germain 1969)

1950: Severe ↓ in deciduous shrubs and trees (Marie-Victorin & Rolland-Germain 1969)

1975: Balsam fir is the main winter browse (Huot 1982)

Present (since 1976–79):

– Conversion of balsam fir stands into white spruce stands (Potvin *et al.* 2003)

– ↓ 70–100% in balsam fir browse (Tremblay *et al.* 2005)

– ↓ 22% in rumen nitrogen content for autumn diet (this study)

– Litterfall of lichens and fir twigs is important in winter diet (Lefort *et al.* 2007)

Deer body mass

1965: Deer lighter on Anticosti than on the continent (Severinghaus and Free, unpublished data)

1977–79: Strong ↓ in mass since 1965 (this study)

Present (since 1977–79):

– Fawn: No data

– Yearlings: smaller ↓ in mass than ♂

– ♂ ↓ in mass, stronger for old deer and during rut.

– ♀ ↓ in mass at oestrus (this study)

Deer reproduction ♀

1975: lower fertility than other populations in eastern North-America.

– No ovulation of fawns (Goudreault 1980)

Present (since 1977–79):

– Yearling: ↑ in total number of ovulations

– Prime age: ↑ probability of conception but ↓ litter size at ovulation (this study)

Deer survival rates

1980-Present:

– ♀ overall survival rate of 0·77 ± 0·06 (SE; Simard *et al.* unpublished data)

– Fawn: 60% winter survival. Strong selection for heavy fawns (Taillon *et al.* 2006)

Fig. 2. Deer–forest dynamics on Anticosti Island since the introduction of white-tailed deer in 1896. The main documented changes on vegetation, density and deer life-history traits are indicated. Large arrows represent the direct influence(s) of each variable, while ↓ and ↑ indicate decline and increase. Adult males and females are represented by ♂ and ♀ and exponential population growth rate by λ. Pictures represent a 20-year deer exclosure illustrating the dramatic effect of deer on vegetation, and males and females in early September on Anticosti.

body mass between 1977–79 and 2002–04 were only 4·3% for yearling males but, surprisingly, averaged 18% for old males (≥ 8·5 years old). To our knowledge, similar data have not been reported previously. A possible explanation is a strong selection for size in the survival of fawns, so that only large fawns survived, resulting in little variation in yearling size. This hypothesis is supported by the results of Taillon *et al.* (2006), who reported that fawns surviving winter on Anticosti were 25% heavier in late autumn than fawns that did not. An alternative explanation is that an increase in deer tooth wear under low diet quality, especially in winter, may occur so that older individuals may have more difficulty in processing food and accumulating mass than young individuals (Skogland 1988; Loe *et al.* 2003).

White-tailed deer on a better summer diet should accumulate mass faster than deer on a lower-quality diet (Asleson, Hellgren & Varner 1997). Accordingly, deer on Anticosti accumulated less mass during autumn in 2002–04 than 25 years ago, which might be a consequence of the decline in diet quality. In mid-November, at the peak of oestrus on Anticosti, males are currently about 12% lighter than in 1977–79, and about 50% smaller than deer from the source population (Boucher *et al.* 2004), while females are about 6% lighter. A decline in mass at the rut may reduce reproductive effort in mature males (Mysterud, Langvatn & Stenseth 2004) and the fecundity of females (Verme 1969). Because of reduced forage abundance, female reindeer delayed the birth of calves and could not replenish their body reserves totally once freed from lactation, resulting in a decline in overall female mass (Skogland 1983).

HIND FOOT LENGTH

Changes in leg length or skeletal growth are a slow process that may result from long-term local adaptations and are therefore not as sensitive to resource reduction as body mass (Klein *et al.* 1987; Krafft *et al.* 2006; Toïgo *et al.* 2006). Deer on Anticosti have a smaller body length : hind foot length

ratio than deer at high density in other regions, but under milder winter conditions (Lesage *et al.* 2001). Deer skeletal size on Anticosti did not seem to have changed greatly in the last 25 years. The small difference in male hind foot length between 1977–79 and 2002–04 in early autumn appears to be a consequence of hunter selectivity for larger males earlier in the season in 1977–79. We observed no change in female hind foot length. Our results indicate that deer on Anticosti are now thinner than 25 years ago, i.e. that they have a similar skeletal size, but a smaller mass.

REPRODUCTION

Under habitat degradation, female deer are expected to conceive at progressively higher body mass (Albon *et al.* 1983). In the 1970s, female fecundity rate on Anticosti was already lower than elsewhere in eastern North America (Goudreault 1980). Between 1975–79 and 2002–04, however, the total number of ovulations has remained statistically unchanged, despite reduced diet quality and body mass at oestrus. Nevertheless, we observed changes in reproductive strategies as the probability of conception increased 15% and litter size at ovulation declined 15% for females $\geq$ 3·5-year-olds, the age-class most likely to produce twins. We suggest that by reducing litter size at ovulation, females conserved energy and could possibly increase the probability of reproducing during most years, trading off litter size and annual reproduction. Such a trade-off was detected only in prime-aged females. Surprisingly, yearling females were the only age-class for which we observed an increase in the total number of ovulations, although it was marginally significant (36%; $P = 0·05$). This was unexpected, as age at first reproduction should be the first parameter to increase under resource limitation (Coulson *et al.* 2004; but see Sæther *et al.* 1996). Another possibility is that a decrease in the probability of survival could increase reproductive effort at a young age (Festa-Bianchet 2003; Proaktor, Coulson & Milner-Gulland 2007). In addition, a strong natural selective pressure on fawns (Taillon *et al.* 2006) may be favouring high-quality yearlings that experience greater reproduction.

Skogland (1990) reported that 30 years of resource limitation for reindeer and an associated 23% decline in body mass did not lead to a decline in reproduction, but to a 15% increase in fecundity. He suggested that under long-term resource limitation, selective pressure may favour increased reproductive effort per unit body mass. Similarly, in greater snow geese (*Anser caerulescens atlanticus*), 20 years of overbrowsing under high density have induced a decline in female and male body condition, but no change in reproductive outputs was detected (Reed & Plante 1997). The decline in body mass at oestrus did not seem to affect the reproductive performance of females at conception, but we have no information on the production of weaned fawns. Females may now give birth later to smaller offspring, or invest less into lactation than in 1975–79, so that fawns may have reduced survival rates (e.g. caribou *R. tarandus*, Adams 2005; elk *C. elaphus*, Cook *et al.* 2004; white-tailed deer, Therrien *et al.* 2007). Finally, the

probability of conception might have increased because of high neonatal fawn mortality lowering the costs of current reproduction and increasing the probability of reproduction the following year.

Conclusions

Following introduction or rapid increase of ungulate populations, stochastic environmental variations (Bayliss & Choquenot 2002) and alternative sources of food uncoupled with density-dependent feedbacks (Tremblay *et al.* 2005) can restrain ungulate populations to reach equilibrium with their food supply. Our study brings new insight into irruptive population behaviour, suggesting that the long-term tolerance of herbivores to limiting resources may be another factor explaining why ungulates could maintain a high density, but without reaching equilibrium with their forage. White-tailed deer introduced into the boreal forest of Anticosti Island illustrate the high plasticity of deer in response to decreasing diet quality, as despite reduced asymptotic body mass females maintained reproduction. Our results support Sæther *et al.* (1996), suggesting that in absence of predation, equilibrium with food resources is unlikely for large herbivores.

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