

Linking conception and weaning success with environmental variation and female body condition in a northern ungulate

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Success or failure of any stage of reproduction is generally related to maternal characteristics and environmental influences. In addition, postreproductive body condition of females should be a function of effort allocated to reproduction. Using data on > 800 female white-tailed deer (*Odocoileus virginianus*) harvested during 4 years on Anticosti Island (Quebec, Canada), we investigated factors affecting reproductive status, from ovulation to weaning, and measured the resulting effect on female body condition. The probability of ovulation (single or double) increased with female age, but weaning success was unrelated to age. Female reproduction was determined by climatic conditions in each season and the availability of preferred habitat, but high density only affected young primiparous females. More specifically, snowy autumns decreased ovulation rate, dry springs disfavored the production of twins, and cold and snowy winters decreased weaning success. Habitat with high summer plant biomass favored both 1st ovulation and weaning success. We suggest that restricted forage conditions encountered during their 1st year of life selected for higher-quality females, that is, females with fewer reproductive pauses and higher weaning success. Reproductive effort generally decreased female body condition, which was lower in lactating than nonlactating females. We suggest that twin production occurred in higher-quality females because, although females conceiving twins had reduced fat reserves, they maintained larger body size and higher muscular mass than mothers of singletons. Our results demonstrate that females adjusted reproductive effort according to seasonal environmental conditions, probably to minimize the consequences of reproduction on body condition, a proxy of reproductive cost.

Key words: fertility, habitat, litter size, population density, reproductive pause

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During reproduction, female mammals face the challenge of producing offspring while maintaining a positive energy balance with other requirements, such as growth and body maintenance (Bronson 1985). Ovulation itself has a relatively low energetic cost (Bronson and Manning 1991), but late gestation and particularly lactation increase energetic demand, especially for large litters (Moen 1978; Oftedal 1985; Mauget et al. 1999). Reproductive potential depends on initial condition of a female (Garel et al. 2009) and her ability to regulate energetic balance by increasing food intake, catabolizing fat reserves and proteins, or reducing energy allocated to other activities (Chan-McLeod et al. 1994; Parker et al. 2009; Monteith et al. 2013). In capital breeders such as large ungulates, conception (Adamczewski et al. 1997), litter size (Wilson et al. 2009), and age at primiparity (Jorgenson et al. 1993) are often determined by female body condition.

Failure to maintain energy balance during reproduction can affect female condition (Chan-McLeod et al. 1999; Cook et al. 2004; Monteith et al. 2013) and may induce reproductive costs (Morano et al. 2013). Reproductive costs are observed by a decline in survival, lower probability of future reproduction, and reduced offspring quality (e.g., Pyle et al. 1997; Hamel et al. 2010). The risk associated with reproductive costs depends both on individual characteristics and environmental factors (Tavecchia et al. 2005). High reproductive costs are generally experienced by young and old females and during years of high population density or severe weather conditions (Festa-Bianchet et al. 1998; Tavecchia et al. 2005). Principles of



TABLE 1.—Model selection procedure used to select the best model (based on delta Akaike information criterion [Δ AIC] values) explaining A) the probability of 1st conception (primiparity), B) reproductive pause (having conceived before), and C) litter size at conception of female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Quebec, Canada; 2002–2005). Model selection was based on the procedure from Hosmer and Lemeshow (2000), which starts from an initial model that is biologically possible (H1 based on Simard et al. [2010]) and improves it through successive steps. I) We first built model H1 (same for A, B, and C), which was compared to the null model. We then modified H1 by removing (H2–H5), interchanging (H6–H7), or adding (H8–H16) variables. Models that had a lower Δ AIC compared to H1 and fewer variables (among equivalent models) were integrated into improved models (IM1–IM3, specific to A, B, and C). II) We used the best improved model (IM1) to test interactions (H17–H38). III) When interactions had Δ AIC < 2 they were integrated to build the final best model (BM). Variables are expressed using the following acronyms: A = age, Db = density at birth, Nb = North Atlantic Oscillation index (NAO) in spring of birth, D = density at conception, S = snow, au = autumn at conception, sp = spring before conception, H = habitat (f = balsam fir, p = peatland, s = spruce, o = open), N = spring normalized difference vegetation index (NDVI), G = spring green-up before conception.

		n variables	Δ AIC		
			A) 1st conception	B) Reproductive pause	C) Litter size at conception
I) Selection of single-effect variables					
(ΔAIC compared to H1 = 0)					
Initial (H1) and null model (H0)					
H0	Intercept	0	13.2	15.0	27.7
H1	A + D + Sau	3	0	0	0
Removing variables to H1					
H2	A + Sau	2	1.1	-1.6	4.2
H3	A + D	2	9.3	8.0	-0.4
H4	D + Sau	2	2.2	8.1	21.7
H5	A	1	10.6	6.0	3.7
Interchanging variables in H1					
H6	A + D + NAOau	3	8.1	8.2	-0.9
H7	A + D + NAOsp	3	10.3	9.9	-2.2
Adding variables to H1					
H8	A + A ² + D + Sau	4	-0.1	1.8	-3.6
H9	A + D + Sau + Ho	4	0.3	1.9	0.9
H10	A + D + Sau + Hf	4	1.9	0	0.7
H11	A + D + Sau + Hs	4	1.7	1.9	2.0
H12	A + D + Sau + Hp	4	-2.3	2.0	1.2
H13	A + D + Sau + Db	4	1.9	-2.9	-2.3
H14	A + D + Sau + Nb	4	1.9	1.0	-1.6
H15	A + D + Sau + Nsp	4	1.9	2.0	0.4
H16	A + D + Sau + G	4	1.1	1.3	0.2
Improved model H1 (IM) using H2–H16					
IM1	A + D + Sau + Hp	4	-2.4		
IM2	A + A ² + D + Sau + Hp	5	-2.3		
IM1	A + Sau + Db	3		-5.6	
IM2	A + Sau + Db + Hf	4		-4.9	
IM1	A + A ² + NAOsp	3			-6.8
IM2	A + A ² + NAOsp + Db	4			-6.8
IM3	A + A ² + NAOsp + D	4			-5.5
II) Selection of interactions					
(ΔAIC compared to IM1 = 0)					
Adding interactions to improved model ^a					
IM1	Specific to A, B and C	3	0	0	0
H17	+ A × D	4	-2.1	1.2	1.8
H18	+ A × Sau	4	0.8	2.9	9.1
H19	+ A × NAO ^{bc}	4	7.9	11.6	0.1
H20	+ A × H ^c	4	Hp: 2.6	Hf: -0.2	Hf: 2.0
H21	+ A × G	4	0.8	-1.0	3.1
H22	+ A × Db	4	3.6	2.0	0.9
H23	+ A × Nb	4	2.9	-0.7	3.3
H24	+ D × Sau	4	1.9	2.4	3.6
H25	+ D × NAO	4	8.6	10.4	3.1
H26	+ D × H	4	2.9	-1.6	2.8
H27	+ D × G	4	3.2	5.0	4.1
H30	+ D × Db	4	1.5	3.9	2.8
H31	+ D × Nb	4	3.4	4.9	3.3
H32	+ Sau × H	4	2.0	-0.9	3.1

TABLE 1.—Continued.

			ΔAIC		
			A)	B)	C)
			1st conception	Reproductive pause	Litter size at conception
		<i>n</i> variables			
H33	+ Sau × G	4	−0.4	2.7	0.4
H34	+ Sau × Db	4	3.3	1.2	1.4
H35	+ Sau × Nb	4	0.6	3.3	3.4
H36	+ H × G	4	3.0	2.6	2.4
H37	+ G × Db	4	5.7	3.0	2.8
H38	+ G × Nb	4	3.0	3.4	4.1
III) Best model (BM)			(ΔAIC compared to the lowest model AIC among all)		
BM-A	A + D + Sau + Hp + A × D		0		
BM-B	A + Sau + Db			1.6	
BM-C	A + A ² + NAOsp				0

^a All single effects were included with interactions.

^b Snow data and NAO were never included in the same model because of low number of years.

^c Among all variables of NAO, Habitat, and NDVI tested as single effect, we only tested the one that had the lowest AIC in section I in interactions.

energy allocation suggest that long-lived females should be risk sensitive and adjust reproductive effort to minimize reproductive costs, ensuring their own survival (Cresswell et al. 1992; Bårdsen et al. 2008, 2010).

In northern latitudes, where duration of the plant growing season is short, ungulate conception rates and reproductive success are closely linked to plant green-up, forage quality (Langvatn et al. 1996; Therrien et al. 2008), and population density (Sæther 1997; Stewart et al. 2005). The relative strength of environmental influences on reproduction is likely to be associated with the timing of important reproductive moments (Bårdsen et al. 2010; Monteith et al. 2013). In cervids, for example, unfavorable forage conditions during late winter or spring may induce early fawn mortality (Verme 1965; Hewison and Gaillard 2001; Bishop et al. 2008), because of increased energetic demand associated with late gestation and early lactation (Moen 1978). Because environmental conditions during reproduction are unpredictable, it may be advantageous for females to conceive, especially because ovulation is not energetically demanding, while later facing the possibility of losing offspring following unfavorable stochastic events (Cresswell et al. 1992; Hewison and Gaillard 2001).

Here, we assessed seasonal environmental influences on the reproduction of female white-tailed deer (*Odocoileus virginianus*) and postreproductive consequences on body condition. We expected strong annual and spatial variability in reproductive output, because the study population subsists under harsh environmental conditions in absence of predation. Because of high deer density, long and snowy winters, and low food quality and abundance on Anticosti Island (Quebec, Canada—Simard et al. 2008), fertility rate is among the lowest measured for white-tailed deer in the wild (Simard et al. 2010). We supposed that low availability of resources limited female reproduction, with annual variations in seasonal climate or density having strong consequences on reproductive status and postreproductive condition.

We first determined how females of various ages adjusted reproductive effort in response to environmental conditions, by

assessing variation in different reproductive events: 1st-time conception, reproductive pause, conceiving twins, and weaning success. Because high density and low forage availability in autumn negatively influenced body condition of females on Anticosti Island (Simard et al. 2008), we predicted a similar effect on the probability of conception and the probability of conceiving twins, but we expected primiparous females to be more affected than multiparous females (Tavecchia et al. 2005; Simard et al. 2010; H1 in Table 1). We also predicted that weaning success would depend on early spring conditions that influence plant quality during late gestation and lactation (Simard et al. 2010; Morano et al. 2013; H1 in Table 2). Secondly, we assessed the influence of reproductive status on condition by measuring autumn body condition of harvested female deer. We assessed conception status (number of recent reproductive structures on ovaries: C₀, C₁, and C₂) and lactation status the following autumn (lactating or not: L and NL, respectively). We predicted that greater reproductive effort (C₀-NL < C₁-NL < C₂-NL < C₁-L < C₂-L) would have negative consequences on body mass, fat reserves, muscle mass, and body size, taking age into account (Chan-McLeod et al. 1999; Barboza and Parker 2008; H1 in Table 3). We used several parameters of body condition because allocation to reproductive effort may have different effects on fat, muscle, or growth (Monteith et al. 2013), and each factor may predict future reproduction and survival differently (Sand 1998; Parker et al. 2009).

MATERIALS AND METHODS

Study area.—White-tailed deer were introduced on Anticosti Island in the Gulf of St. Lawrence (49°N, 62°W; 7,943 km²; Quebec, Canada), at the northern limit of the species' range in eastern Canada. Despite cool, rainy summers and long, snowy winters (rain 630 mm/year and snow 406 cm/year—Environment Canada 2006), deer introduction was highly successful because of the absence of predators. From the 220 deer introduced in 1896, the herd increased to > 20 deer/km²

TABLE 2.—Model selection procedure used to select the best model (based on delta Akaike information criterion [Δ AIC] values) explaining the probability of weaning success for female white-tailed deer (*Odocoileus virginianus*) that conceived in autumn on Anticosti Island (Quebec, Canada; 2002–2005). Model selection was based on the procedure from Hosmer and Lemeshow (2000), which starts from an initial model that is biologically possible (H1 based on Simard et al. [2010]) and improves it through successive steps. I) We first built model H1, which was compared to the null model. We then modified it by removing (H2–H5), interchanging (H6–H7), or adding (H8–H16) variables. Models that had a lower Δ AIC compared to H1 and fewer variables (among equivalent models) were integrated into improved models (IM1–IM2, specific to A, B, and C). II) We used the best improved model (IM1) to test interactions (H17–H38). III) When interactions had Δ AIC < 2 they were integrated to build the final best model (BM). Variables are expressed using the following acronyms: A = age, Db = density at birth, Nb = North Atlantic Oscillation index (NAO) in spring of birth, D = density at conception, S = snow, win = winter before parturition, sp = spring of parturition, H = habitat (f = balsam fir, p = peatland, s = spruce, o = open), N = spring normalized difference vegetation index (NDVI), and G = spring green-up at parturition.

		<i>n</i> variables	Δ AIC Weaning success
			(Δ AIC compared to H1 = 0)
D) Selection of single-effect variables			
Initial (H1) and null model (H0)			
H0	Intercept	0	-1.6
H1	A + Ssp	2	0
Removing variables to H1			
H2	A	1	-1.3
H3	Ssp	1	-0.7
Interchanging variables in H1			
H4	A + NAOwin	2	-7.4
H5	A + NAOsp	2	-4.5
H6	A + Swin	2	7.9
H7	A + D	2	12.9
Adding variables to H1			
H8	A + A ² + Ssp	3	0.3
H9	A + Ssp + Ho	3	-4.0
H10	A + Ssp + Hf	3	1.6
H11	A + Ssp + Hs	3	-0.9
H12	A + Ssp + Hp	3	1.9
H13	A + Ssp + Db	3	2.2
H14	A + Ssp + Nb	3	-1.9
H15	A + Ssp + NDVIsp	3	1.9
H16	A + Ssp + G	3	1.9
Improved model H1 (IM) using H2–H16			
IM1	NAOwin + Ho + Nb	3	-13.2
IM2	NAOwin + Ho	2	-11.1
II) Selection of interactions			
Adding interaction to improved model ^a			
IM1	NAOwin + Ho + Nb	3	0
H17	+ A × D	4	4.4
H18	+ A × Ssp	4	13.5
H19	+ A × NAOwin	4	2.2
H20	+ A × Ho	4	2.7
H21	+ A × Nsp	4	2.2
H22	+ A × Db	4	0.7
H23	+ A × Nb	4	-1.4
H24	+ D × Ssp	4	11.0
H25	+ D × NAOwin	4	0
H26	+ D × Ho	4	3.4
H27	+ D × G	4	2.3
H30	+ D + Db	4	2.6
H31	+ D + Nb	4	3.6
H32	+ Ssp × Ho	4	1.3
H33	+ Ssp × Nsp	4	2.8
H34	+ Ssp + Db	4	3.7
H35	+ Ssp + Nb	4	2.0
H36	+ Ho × Nsp	4	3.7
H37	+ Nsp + Db	4	3.1
H38	+ Nsp + Nb	4	2.5

TABLE 2.—Continued.

		<i>n</i> variables	ΔAIC Weaning success
III) Best model (BM)			(ΔAIC compared to lowest model AIC among all)
BM	NAOwin + Ho + Nb		1.4

^a All single effects were included with interactions.

^b Snow data and NAO were never included in the same model because of low number of years.

^c Among all variables of NAO, Habitat, and NDVI tested as single effect, we only tested the one that had the lowest AIC in section I in interactions.

(Potvin and Breton 2005). The island is located in the balsam fir (*Abies balsamea*)–white birch (*Betula papyrifera*) vegetation domain, but severe deer browsing has modified species composition by suppressing regeneration of dominant deciduous trees and balsam fir and nearly extirpating the shrub layer and most palatable plant species (Tremblay et al. 2005). Other than old balsam fir stands, white spruce (*Picea glauca*)

and black spruce (*P. mariana*) are dominant forest stands. The study area is divided into 5 hunting zones: Western end (476 km²), West (585 km²), Central-South (580 km²), North-East (1,005 km²), and South-East (491 km²). The proportion of different habitats varied among zones, with relatively more balsam fir stands in the Western end, West and Central-South zones and more peatlands in the North-East and South-East

TABLE 3.—Model selection based on delta Akaike information criterion (ΔAIC) values used to select groupings among categories of reproductive status in autumn that were best differentiated for each body condition index, that is, dressed mass, rump fat, peroneus muscle mass, and body size index (principal component analysis [PCA] axis 1) of female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Quebec, Canada; 2002–2005). Reproductive status (R) depended on litter size at conception (0, 1, or 2 = C₀, C₁, C₂) and lactation status (lactating [L] versus nonlactating [NL]): 1, C₀-NL; 2, C₁-NL; 3, C₂-NL; 4, C₁-L; 5, C₂-L. Initial model included covariables of age (A) and date (Da) selected from previous model selection (see Supporting Information S1 for selection of covariables), which included the 5 categories of R. Model H1 tested the hypothesis that body condition should decrease linearly with categories of reproductive status, whereas model H0 tested the null hypothesis that R had no effects. Successive models grouped R in 4 (H2–H4), 3 (H5–H8), or 2 categories (H9–H12) based on similarities in parameter estimates of R in the initial model (underlying that the grouping of R is specific to each parameter of body condition). The best model associated with groupings of R for each parameter of body condition (lowest ΔAIC with the lowest number of parameters) is presented in the last row. Equivalent models with the same number of parameters also are considered in the “Discussion.” Transformations applied to each variable of body condition are shown in column headings.

Model identification	R levels	ΔAIC for different categories of reproductive status (R)			
		Dressed mass ^{0.6}	(Rump fat + 0.1) ^{0.5}	Muscle mass ^{0.5}	Body size (PCA axis 1)
Initial model:		A + A ² + Da + Da ² + R	A + A ² + Da + Da ² + R + Da × R	A + A ² + R ^a	A + A ² + Da + R + A × Da
R = 5 categories					
IM	5	3.5	3.3	4.6	5.9
R = linear					
H0	0	35.7	87.5	4.2	7.9
H1	1	5.6	7.9	3.2	7.6
R = 4 categories					
H2	4	1–2, 3, 4, 5 = 2.3	1–2, 3, 4, 5 = 1.5	1, 3, 2–4, 5 = 3.0	1–2, 3, 4, 5 = 3.9
H3	4	1–3, 2, 4, 5 = 2.5	1–3, 2, 4, 5 = 0.9	1–3, 2, 4, 5 = 2.7	1, 2–3, 4, 5 = 4.0
H4	4	1, 2, 3, 4–5 = 1.6		1, 3, 4, 2–5 = 2.8	1–5, 2, 3, 4 = 3.9
R = 3 categories					
H5	3	1–2, 3, 4–5 = 0.4	1–2, 3, 4–5 = 6.0	1–3, 2–4, 5 = 1.0	1–2–5, 3, 4 = 2.0
H6	3	1–2–3, 4, 5 = 1.9	1–2–3, 4, 5 = 0	1–3, 4, 2–5 = 0.8	1–2–3, 4, 5 = 1.9
H7	3	1–3, 2, 4–5 = 0.6		1–3–5, 2, 4 = 1.7	
H8	3			1, 2–3–5, 4 = 1.4	
R = 2 categories					
H9	2	1–2–3, 4–5 = 0	1–2–3, 4–5 = 5.1	1–2–3, 4–5 = 2.0	1–2–3, 4–5 = 4.5
H10	2			1–3–5, 2–4 = 0	1–2–5, 3–4 = 1.4
H11	2			1–2–3–5, 4 = 0.8	1–2–3–5, 4 = 0
H12	2			1–3, 2–4–5 = 0.2	
Best R grouping					
BM	2 or 3	C _{0, 1} or 2-NL versus C ₁ or 2-L	C _{0, 1} or 2-NL versus C ₁ -L versus C ₂ -L	C _{0, 2} -NL, C ₂ -L versus C ₁ NL, C ₁ L	C _{0, 1} or 2-NL, C ₂ L versus C ₁ L

^a R was not selected in the best model (Supporting Information S1) but was added in H1 to compare its AIC with different groupings of R, and without R in model H0.

zones (details in Simard et al. 2014). Deer generally select peatlands and open patches resulting from forest perturbations (e.g., logging, fire, windthrow, or insect outbreaks; hereafter “open habitat”) in their summer home range (average size = $0.4 \pm 0.06 \text{ km}^2$; *SE* values are presented unless otherwise stated) and balsam fir stands in their winter home range (average size = $0.3 \pm 0.05 \text{ km}^2$ —Massé and Côté 2012). Availability of winter browse (Tremblay et al. 2005) and quality of autumn diet (Simard et al. 2008) have declined over the last 25 years, but the deer population continued to increase slightly (Simard et al. 2010).

Assessment of reproductive status.—We measured reproductive effort by collecting ovaries and monitoring lactation status of females harvested by sport hunters during autumns of 2002–2005. We only considered adult females (≥ 2.5 years old at harvest; $n = 811$) because yearlings do not reproduce on Anticosti. Although hunters may have avoided harvesting females accompanied by fawns (Nilsen and Solberg 2006), we assumed no bias in reproductive status of adult females based on harvest selectivity. Written questionnaires with hunting guides suggested that $< 20\%$ of hunters may have adopted such a selection on Anticosti Island, most of which were foreign hunters (M. A. Simard, pers. obs.). Lactation rate did not differ among harvested deer of local versus foreign hunters ($56\% \pm 4\%$ and $58\% \pm 4\%$, respectively; $t_{1,4} = 1.1$, $P = 0.5$). Furthermore, the opportunity to avoid shooting females with fawns is not necessarily common, because selectivity is more difficult in forested than in open environments (Mysterud et al. 2006).

We used tooth replacement to identify adults (2.5 years and older) and cementum layers in incisor teeth to age them (same observer throughout the study—Hamlin et al. 2000). Females were aged in autumn at time of harvest and during the weaning period; hence age at conception during the previous autumn was 1 year lower than age at harvest.

We assessed conception (1 year prior to harvest) based on luteal scars of the immediately preceding pregnancy found on ovaries at harvest (Langvatn et al. 1994). We collected ovaries and prepared histological slides using the method described in Simard et al. (2008). We examined (same observer at magnification $10\times$) mounted ovaries and identified corpora rubra and corpora albicantia (Langvatn et al. 1994). The corpus rubrum is the regressive stage of the corpus luteum developing after ovulation and remaining 6–10 months after birth, and further regressing into corpus albicans (i.e., smaller size and fewer luteal cells—Langvatn et al. 1994). The number of corpora rubra reliably indicates the number of fetuses conceived the preceding year (fertility rate—Langvatn et al. 1994). Twins were associated with ≥ 2 scars (2 cases of triplets counted as twins). We differentiated primiparous females from multiparous females based on the presence of corpora albicantia; absence of corpora albicantia indicated that females had never reproduced before (Langvatn et al. 1994). Number of corpora albicantia may not provide a correct estimate of the number of past reproductive events, but the presence of corpora albicantia provides a safe assessment that the female

reproduced in the past (Langvatn et al. 1994). We did not consider corpora lutea because ovulation occurs after the harvest period.

We assessed weaning success based on the presence of milk in the udder of females during field dressing. On Anticosti Island, milk is still present in the udder 4–6 months after birth, and we assumed that fawns of lactating females were still alive in autumn. Because predators are absent, most mortality of fawns likely occurs in spring and early summer. Although milk detection may have been easier in early than late autumn, we found no differences in lactation rate throughout autumn ($65\% \pm 6\%$ before 15 October versus $69\% \pm 7\%$ after 15 October; $t_{1,4} = -1.55$, $P = 0.2$). The proportion of females identified as nonlactating but having conceived (with corpora rubra) was similar throughout autumn ($13\% \pm 2\%$ before 15 October versus $12\% \pm 3\%$ after 15 October; $t_{1,4} = 0.37$, $P = 0.7$); therefore we assumed neonatal mortality (or less likely failure during gestation) rather than incorrect identification of lactation rate. Still, misidentification of reproductive status occurred, because 5% of females had no sign of conception but were identified as lactating. We corrected female reproductive status for such error, but we could not verify if nonlactating conceiving females were misidentified as lactating. Such misidentification may have underestimated the effect of climatic conditions on weaning success and the impact of lactation on body condition indexes.

Assessment of postreproductive body condition.—We evaluated autumn body condition of females at harvest (weaning period) using several indexes. We used dressed mass (i.e., total mass minus viscera and bleedable blood measured with a spring scale $\pm 0.25 \text{ kg}$) as an integrative index of all parameters of condition (Taillon et al. 2011). Rump fat thickness served as an index of fat reserves because it was linearly related to total fat reserves in large ungulates, and it predicted body fat better than other indexes in summer and autumn (Cook et al. 2001; Stephenson et al. 2002). Rump fat thickness was measured with a ruler ($\pm 0.25 \text{ cm}$) inserted in the rump fat at 5 and 10 cm (average of both) from the base of the tail, and at a 45° angle with the backbone. We obtained an index of muscle mass using the fresh mass of the peroneus muscle ($\pm 0.5 \text{ g}$; measured with a Pesola scale; Pesola AG, Baar, Switzerland), which is a group of 3 muscles (peroneus longus, brevis, and tertius) originating from the fibula and extending into the metatarsals. Peroneus mass reliably estimates protein mass in ungulates (Crête et al. 1993; Taillon et al. 2011). Although indexes of protein stores are less commonly used than those of fat stores, they are important to consider when assessing the effect of reproductive effort (Monteith et al. 2013).

We assessed female overall body size with a principal component analysis (PCA) including hind-foot length (from the calcaneum to the edge of the hoof, $\pm 0.5 \text{ cm}$), chest girth (circumference behind the front legs, $\pm 0.5 \text{ cm}$, by applying a 2-kg pulling force), and body length (from the nose to the base of the tail, $\pm 1 \text{ cm}$). We used the 1st axis of the PCA (explaining 74.5% of the variation) that differentiated long and

massive from short and slender deer (loadings of 0.11, 0.47, and 0.87 for hind foot, chest, and body length, respectively). Differences in morphometric measurements among observers ($n = 12$) averaged 1%, 0.1%, and 1% for hind foot, chest, and body length, respectively (based on differences with 1 control observer—Simard et al. 2014). We adjusted data for 3 observers with an error rate $> 2\%$ based on their average differences with the reference observer.

Assessment of environmental influences on reproductive status.—We determined annual and spatial variation in population density from hunting statistics. We used the number of deer seen per day per hunter because it was not influenced by hunter selectivity (Solberg et al. 2004), and it appeared to be a reliable index to assess deer density on Anticosti Island (Pettorelli et al. 2007; Simard et al. 2012) and elsewhere (Myserud et al. 2007). We verified the influence of density during autumn prior to conception using the deer-seen statistics (hereafter “density”) available for 5 zones during 4 years. Although density during lactation could negatively influence weaning success (Therrien et al. 2008), it was not verified because of circularity issues, that is, fawn production positively influenced the number of deer seen. We assessed the potential effect of forage competition early in life on reproduction using a density index during the autumn of birth.

We estimated habitat composition based on deer location at harvest as identified by hunters on maps of their hunting zone (precision averaged $1.45 \text{ km}^2/\text{cm}$). We created a 1-km^2 buffer zone around each location and superimposed a 1:20,000 forest map (created from photo-interpretation of 1:15,000 aerial photographs taken in 1997, but adding recent cuts [Quebec Ministry of Natural Resources, Quebec, Quebec, Canada]) on it to extract the proportion of each habitat available to each deer. We identified 4 main types of habitat that could be discriminated in terms of vegetation abundance. Peatlands had the highest forb abundance, followed by open habitats that had the highest grass biomass (Massé and Côté 2009). Forbs were more abundant in spruce than in fir forests, but only in openings (Massé and Côté 2009). The proportion of different habitats surrounding deer locations did not reflect habitat selection and included imprecision, but it should represent a good estimate of habitat availability prior to conception and during lactation.

Because temperature and precipitation data were only available for the western end of the island, we verified the influence of weather conditions during spring, summer, and autumn on conception and the influence of the following winter and spring on weaning success using North Atlantic Oscillation index (NAO), a global indicator recognized to represent large-scale climatic patterns (Forchhammer and Post 2004; Osborn 2006). We used spring, autumn, and winter NAO, but not summer NAO because its use has been criticized (Forchhammer and Post 2004) and because it was not correlated to local weather variables (Simard et al. 2010). On Anticosti Island, low values of NAO in autumn and spring were associated with abundant rain, whereas high NAO in winter corresponded to low temperatures and abundant snow (Simard et al. 2010). We

verified the effect of NAO during the spring of birth because it influences lifetime reproductive performance (Tavecchia et al. 2005; Hamel et al. 2009b).

Snow abundance was measured at 15-day intervals from October to May at 3 stations in balsam fir stands (2 in Western end and 1 in West), each having 10 graduated 3-m rulers. We measured snow and sinking depth (cm) using a penetrometer that approximated the foot pressure exerted by deer during locomotion (Verme 1968). We estimated compacted snow thickness by subtracting sinking depth from total snow depth. The index of snow conditions encountered by deer corresponds to the addition of all 15-day estimates of snow depth (expressed in $\text{cm}\cdot\text{day}$, but $\text{m}\cdot\text{day}$ in models—Dumont et al. 2000). We used data on cumulative compact snow in autumn of conception (November–December) to estimate the hard layer that impeded digging for access to vegetation. This measure was more closely related to reproductive rate than was cumulative snow (Simard et al. 2010). In winter (November–May) and spring (March–May), we used cumulative sinking depth to take into account energy expenditure due to locomotion in snow prior to giving birth (Dumont et al. 2000).

We assessed the effect of vegetation productivity on conception and weaning success using the normalized difference vegetation index (NDVI) during the spring prior to conception and during the spring of birth. We computed NDVI data from satellite imagery (Pettorelli et al. 2005) collected from the Terra MODIS sensor (Moderate Resolution Imaging Spectroradiometer—MODIS Science Team 2007) at a resolution of $250 \times 250 \text{ m}$, in a composite of 16 days of images eliminating most cloud cover. We superimposed a map of land cover on MODIS imageries to exclude pixels of water. We extracted average NDVI for each of the 5 hunting zones from 2001 to 2005 to estimate vegetation productivity in spring (average NDVI in May) and the rate of change in plant productivity during spring green-up (average slope between NDVI in May and late June). High NDVI values in spring are associated with high vegetation productivity (Pettorelli et al. 2005) and are inversely related to the speed of spring green-up (detailed in Simard et al. 2014). Late spring onset involves delayed but more rapid plant growth, which translates generally into higher plant quality (Van der Wal et al. 2000).

Although we had only 4 years of data to assess environmental variations, the data covered a large range of conditions, because both climate and density varied strongly between years (e.g., snow conditions in autumn varied from 0 to $230 \text{ cm}\cdot\text{day}$). Nevertheless, any relationships with snow or NAO should be considered within the limits of the studied time period.

Statistical analyses: environmental influences on reproductive status.—We performed generalized linear mixed models of the binomial family (package lme4 of R 2.10.1 software—R Development Core Team 2009) to estimate the influence of female age and environmental conditions on different reproductive events. Mixed models accounted for the experimental design with the random term expressed as the interaction of 4 years and 5 zones (20 group levels). All models

TABLE 4.—Parameter estimates \pm SE (with Z- and P-values) for selected models (see Table 1 for model selection) explaining reproductive status of female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Quebec, Canada; 2002–2005). Reproductive status includes 1st conception ($n = 219$), reproductive pause having conceived before ($n = 530$), litter size at conception ($n = 614$), and weaning success having conceived ($n = 597$). A = age, S = snow, Db = density at birth (log), Nb = North Atlantic Oscillation index (NAO) at birth, D = density (log), au = autumn, sp = spring, win = winter, Ho = open habitat, Hp = peatland habitat.

	1st conception			Reproductive pause			Litter size at conception			Weaning success						
	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P				
Intercept	7.0	3.0	2.2	0.03	1.0	1.0	0.9	0.4	-4.0	1.0	-4.4	< 0.001	1.9	0.2	8.8	< 0.001
Age	-1.2	0.8	-1.6	0.1	-0.4	0.1	-3.6	< 0.001	0.9	0.3	2.9	< 0.001				
Age ²									-0.05	0.02	-2.3	0.02				
Snow																
or NAO	Sau: -0.007	0.002	-3.8	< 0.001	Sau: 0.006	0.002	3.6	< 0.001	NAOsp: -0.9	0.3	-3.3	< 0.001	NAOwin: -1.2	0.4	-3.4	< 0.001
Others	D: -3.0	1.0	2.5	0.02	Db: -0.9	0.4	-2.3	0.02					Ho: 1.1	0.5	2.2	0.03
	Hp: 1.9	0.8	2.3	0.02									Nb: 0.3	0.2	2.0	0.04
Interactions	A × D: 0.6	0.3	2.0	0.05												

included age as a covariable. We selected seasonal environmental effects to be tested based on their potential to affect each reproductive stage. Overall we considered that conception could be influenced by conditions encountered during the preceding spring, summer, and autumn, whereas the following winter, spring, and summer after conception should affect weaning success (density had to be assessed during autumn of conception). Snow and NAO variables were never included in the same model because they applied to the same year group, with only 4 replicates.

We used the Akaike information criterion (AIC) to select best models (Burnham and Anderson 2002 [each parameter included in models lowered the AIC > 2—Arnold 2010]) and adaptive Gauss–Hermite quadrature, with 5 points per axis for greater accuracy in the evaluation of the log-likelihood (Crawley 2007). We based the model selection process on Hosmer and Lemeshow (2000), which is advised when dealing with numerous explanatory variables (details in Simard et al. 2014). The 1st step was to build a reference model (H1) that had biological realism. Based on results of Simard et al. (2010), we initially tested the hypothesis that age, density, and snow in autumn influenced conception (H1 in Table 1; 3 variables) and that age and snow conditions in spring influenced weaning success (H1 in Table 2; 2 variables). We first compared H1 to the null hypothesis H0, a model that only included the intercept. Secondly, we created a set of successive models from which we removed variables (H2–H5 in Table 1; H2–H3 in Table 2), interchanged variables (H6–H7 in Table 1; H4–H7 in Table 2), or added variables (H8–H17 in Table 1; H8–H16 in Table 2). When modified models (H2–H16) had a lower AIC than H1 (i.e., AIC < 2 with the same number of parameters or fewer—Arnold 2010) they were used to modify the initial model H1 into a set of improved models (IM1–3 specific to each analysis [Tables 1 and 2]). Improved models were built by adding, removing, or interchanging variables originally included in H1 with those that lowered the AIC in H2–H16. We used the best improved model (IM1 best model without interaction) to test the pertinence of adding interaction terms (H17–H38 in Tables 1 and 2). We allowed previously removed variables to reenter the model through interactive effects (single effects were automatically included with interactive terms—Hosmer and Lemeshow 2000). We selected the model with interactions only if it lowered AIC > 2, but otherwise presented IM1 as the best model (BM in Tables 1 and 2). For selected best models, we estimated P-values using Monte Carlo resampling procedures (5,000 iterations—Table 4; Bates 2010) to validate selection procedure by AIC (based on concerns of Raffalovich et al. 2008). Variables selected through AIC were all significant using P-values, which added confidence to our modeling approach. We also present Z-values and SE of parameter estimates to compare the effect size of selected variables (Nakagawa and Cuthill 2007).

Statistical analyses: body condition associated with reproductive status.—We performed additional generalized linear mixed models to determine how body condition (dressed mass, rump fat, peroneus muscle mass, and body size index

TABLE 5.—Parameter estimates \pm SE (with Z- and P-values) for selected models (Supporting Information S1; Table 2) explaining variation in body condition (i.e., dressed mass, rump fat, peroneus muscle mass, and body size index principal component analysis [PCA] axis 1) of female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Quebec, Canada; 2002–2005). Models included effects of reproductive status (R), as well as covariables age, date, and their interactions. Reproductive status depended on litter size at conception (0, 1, or 2 = C₀, C₁, C₂) and lactation status (lactating [L] versus nonlactating [NL]): 1, C₀-NL; 2, C₁-NL; 3, C₂-NL; 4, C₁-L; 5, C₂-L; but categories were grouped to improve model fit (details in Table 2). We present only parameters of selected groups. Transformations applied to each variable of body condition are shown in column titles with sample sizes.

	Variables (d.f.)															
	Dressed mass ^{0.6} (750)				(Rump fat + 0.1) ^{0.5} (748)				Muscle mass ^{0.5} (760)				Body size (PCA axis 1) (730)			
	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
Intercept	7.6	0.2	48.9	< 0.001	0.83	0.09	9.5	< 0.001	9.3	0.1	73.6	< 0.001	-16.7	1.8	-9.4	< 0.001
Age (A)	0.23	0.03	7.7	< 0.001	0.07	0.02	4.3	< 0.001	0.11	0.03	3.5	< 0.001	3.4	0.4	8.4	< 0.001
Age ²	-0.012	0.002	-6.2	< 0.001	-4 × 10 ⁻³	1 × 10 ⁻³	-3.9	< 0.001	-0.005	0.002	-2.6	0.006	0.18	0.03	5.4	< 0.001
Date (Da)	0.026	0.005	5.6	< 0.001	0.015	0.003	5.4	< 0.001					-0.13	0.02	-5.5	< 0.001
Date ²	-19 × 10 ⁻⁵	6 × 10 ⁻⁵	-3.4	< 0.001	-10.6 × 10 ⁻⁵	3.1 × 10 ⁻⁵	-3.4	< 0.001								
R 2 nd ^a	4-5: -0.32	0.05	-6.2	< 0.001	4: -0.420	0.059	-7.1	< 0.001	2-4: -0.12	0.05	-2.5	0.008	4: -1.8	0.6	-3.1	0.002
R 3 rd ^a					5: -0.47	0.08	-5.7	< 0.001								
Interactions					Da × 4: 0.005	0.001	3.6	< 0.001					A × Da 0: -0.013	0.005	-2.7	0.006
					Da × 5: 0.003	0.002	1.8	0.06								

^a Model is fixed at the 1st group of reproductive status, and we present parameters for the 2nd and 3rd groupings (when present).

PCA axis 1) was related to reproductive status in autumn and thus reproductive effort. Five categories of reproductive status in autumn were based on the presence of 0, 1, or 2 corpora rubra at conception (C₀, C₁, and C₂) and lactation status (L or NL): 1 = no conception and no lactation (C₀-NL; n = 169), 2 = conceiving singleton but no lactation (C₁-NL; n = 85), 3 = conceiving twins but no lactation (C₂-NL; n = 24), 4 = conceiving singleton and lactation (C₁-L; n = 400), and 5 = conceiving twins and lactation (C₂-L; n = 133). Dependent variables were transformed to best satisfy the normality of residuals, using a Box–Cox transformation (Crawley 2007). Again, the interaction between 4 years and 5 zones (20 levels) was defined as a random effect, and model selection was achieved using the same procedure as described above (Hosmer and Lemeshow 2000). We first selected variables affecting body condition, including reproductive status in autumn, age, and date in autumn (including quadratic effects and interactions [models 0–27 in Supporting Information S1, DOI: 10.1644/13-MAMM-A-036.S1]). Finally, we used the best improved model (IM; Table 3) that included the 5 categories of reproductive status, and verified if certain categories produced similar effects and could be grouped. We grouped categories of reproductive status if they had similar parameter estimates, which implies that groupings are specific to each body condition index (Table 3). We first tested the prediction that body condition indexes should decrease linearly with reproductive effort and the null model of no distinction among categories of reproductive effort (models H1 and H0, respectively [Table 3]). We selected the model with the lowest ΔAIC with the same number of parameters or less to obtain the most-parsimonious grouping. Again, results obtained with AIC agreed with those obtained using P-values (Table 5). Unless otherwise stated, we present estimates \pm SE predicted from models with covariates centered on their means.

RESULTS

Environmental influences on reproductive status.—The probability of conception averaged 84% for all females. Comparatively, the probability of 1st conception for nulliparous females having never conceived before varied from 45% \pm 5% for 1.5-year-olds to 69% \pm 9% for 4.5-year-olds (at average density [Table 4]). Density reduced the probability of 1st conception in younger nulliparous females, but not in older ones (Table 4; Fig. 1a). The probability of 1st conception was 70% \pm 6% in absence of compact snow cover in autumn but 32% \pm 6% with abundant cumulative compact snow in the same season (230 cm*day [Table 4; Fig. 1b]). The probability of 1st conception increased from 43% \pm 6% to 83% \pm 10% as the proportion of available peatland habitat rose from 0% to 96% (Table 4).

The probability that females took a reproductive pause (no conception), while having conceived in previous years, was 6% \pm 1% on average, but was higher in 2.5-year-olds (19% \pm 6%) than for \geq 9.5-year-olds (3% \pm 1% [Table 4]). Reproductive pauses were 9% \pm 3% more frequent when

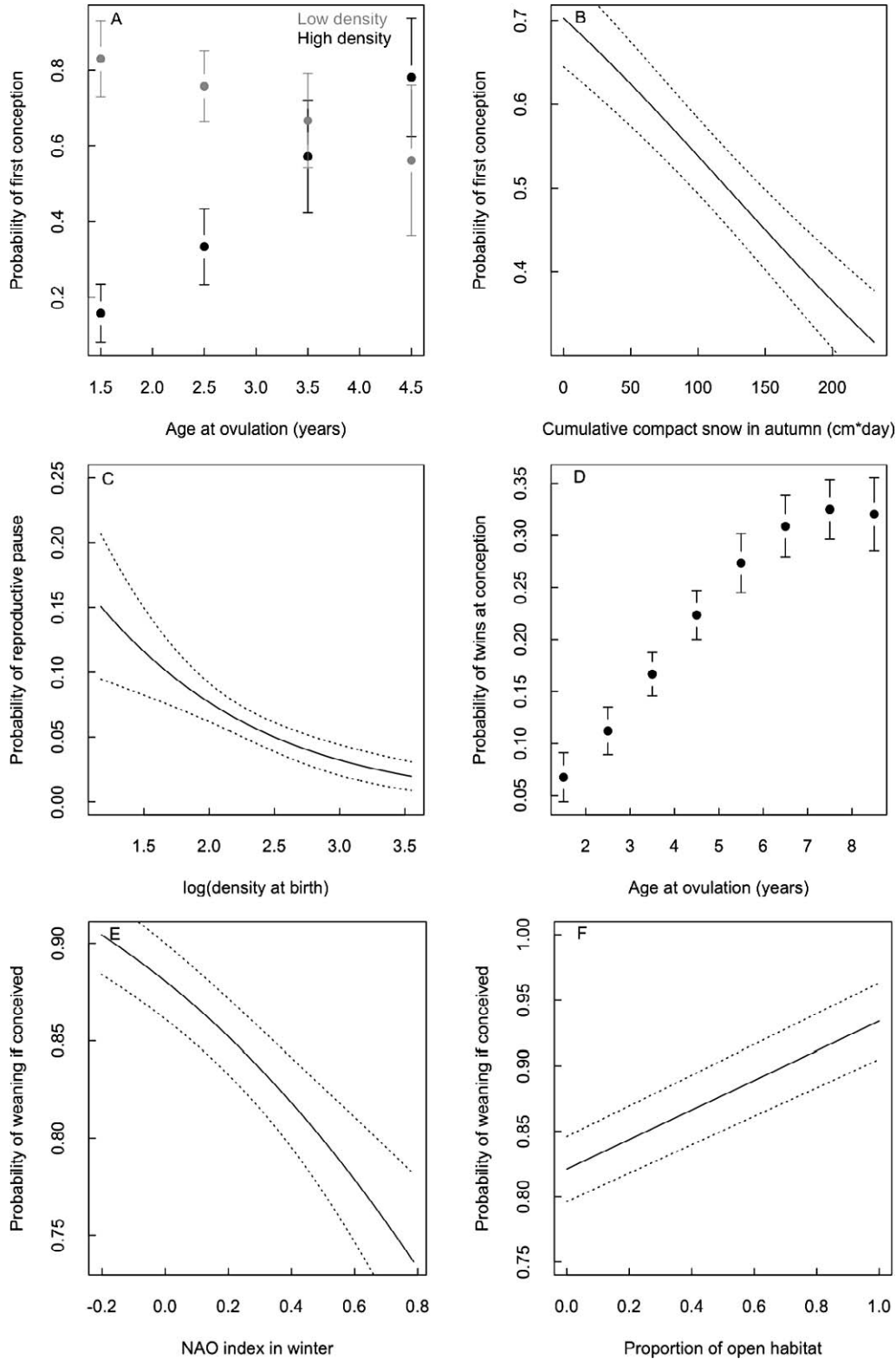


FIG. 1.—a) Influence of age, index of population density (deer seen per hunter per day), and b) cumulative compact snow in autumn on the probability of 1st conception in nulliparous female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Quebec, Canada; 2002–2005). Also shown, c) the influence of population density at birth on reproductive pause (having conceived before), and d) the influence of age on litter size at conception. Finally, e) the influence of winter North Atlantic Oscillation index (NAO), and f) the proportion of available open habitat on weaning success for females that have conceived. Data and *SE* are extracted from models presented in Table 4 and corrected for covariables.

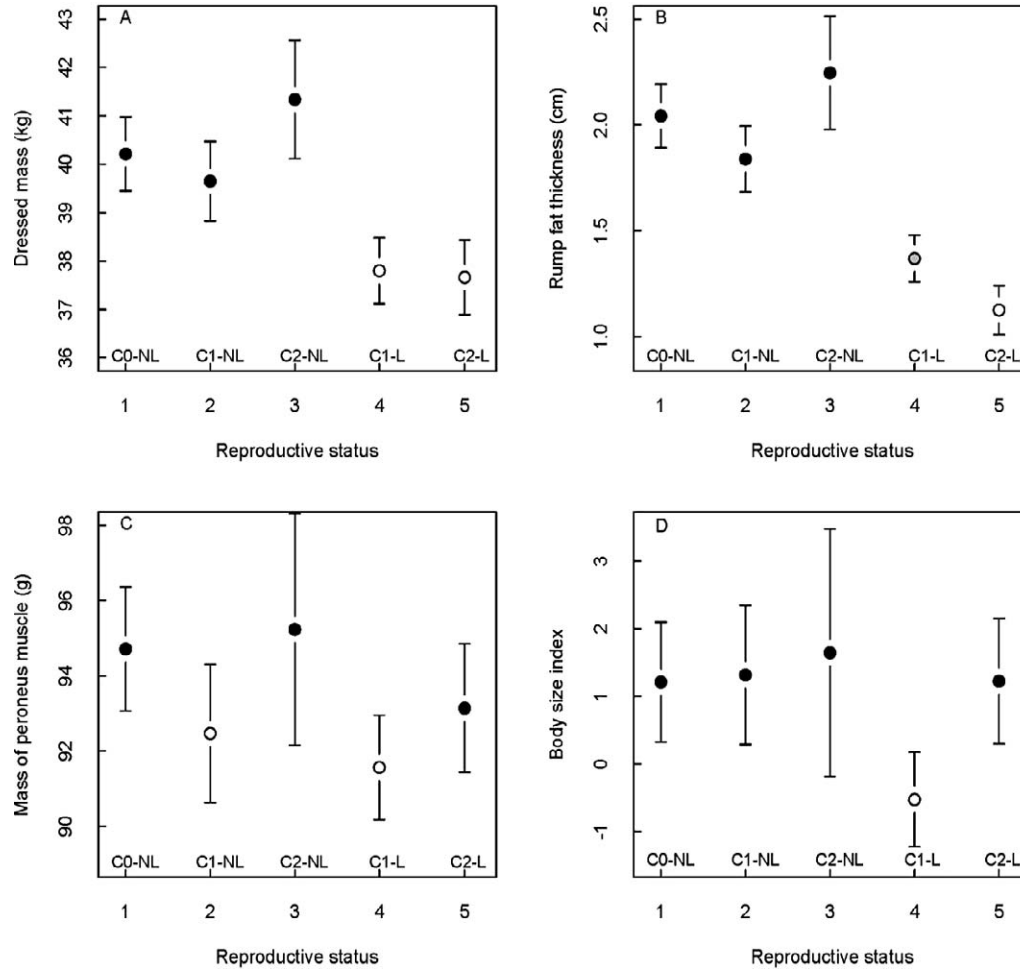


FIG. 2.—Variation in body condition: a) dressed mass, b) rump fat thickness, c) muscle mass, and d) body size index, principal component analysis (PCA) axis 1 ± SE relative to reproductive status in autumn for female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Quebec, Canada; 2002–2005). Reproductive status was based on litter size at conception (reproductive scars on ovaries; C₀, C₁, and C₂) and lactation status (lactating [L] versus nonlactating [NL]): 1, C₀-NL; 2, C₁-NL; 3, C₂-NL; 4, C₁-L; 5, C₂-L. Color of symbols (black, gray, or white) corresponds to group categories of reproductive status based on similarity extracted from the best model and correcting for covariables (Table 5).

compact snow cover was high (Table 4). Surprisingly, high population density in the 1st year of life decreased the probability of reproductive pauses: females born at low density had a 14% ± 5% chance of taking a reproductive pause compared to 2% ± 1% if born at high density (Table 4; Fig. 1c).

Among females that conceived, 22% ± 2% on average conceived twins, but this varied curvilinearly with age (Table 4; Fig. 1d). Conceiving twins was more frequent under low values of NAO in the previous spring (rainy spring; 31% ± 4%) compared to high values (dry spring; 17% ± 2%).

Among females that conceived, apparent weaning success was 85% ± 2% (Table 4), without an effect of age. Low winter temperature and abundant snow (i.e., high NAO in winter) negatively influenced weaning success (Table 4; Fig. 1e). Weaning success was 79% ± 4% for females born under rainy springs (low NAO) compared to 90% ± 3% when born under dry springs (high NAO; opposite effect than for conception of twins). Increasing the proportion of available open habitat from

0% to 100% increased weaning success from 82% ± 3% to 93% ± 3% (Table 4; Fig. 1f).

Body condition associated with reproductive status.—The main difference in dressed body mass at harvest, after accounting for curvilinear effects of both age and date of harvest, was between nonlactating (40.1 ± 0.7 kg) and lactating females (37.7 ± 0.7 kg) independent of litter size at conception (Tables 3 and 4; Fig. 2a; Supporting Information S1).

Large differences in rump fat (corrected for age and date) occurred among different categories of reproductive status in autumn (Table 5; Fig. 2b). Nonlactating females (either having conceived or not) had significantly more fat (2.0 ± 0.1 cm in mid-October) than females conceiving singletons and lactating (1.4 ± 0.1 cm), whereas females conceiving twins and lactating had the lowest fat (1.1 ± 0.1 cm [Table 5; Fig. 2b]). Rump fat increased at a slower rate during autumn for females with twins and lactating than for those with a singleton and lactating, or for nonlactating (“twin” or “singleton” refer

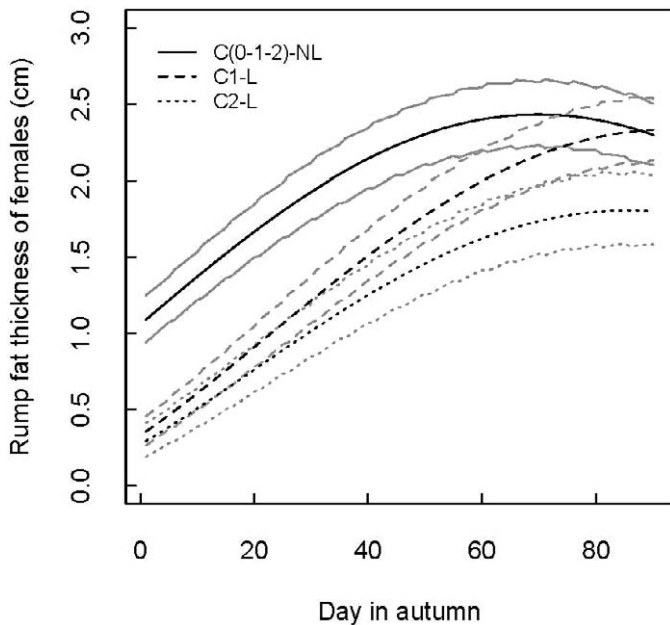


FIG. 3.—Variation in rump fat accumulation (cm) during autumn as a function of reproductive status in autumn of female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Quebec, Canada; 2002–2005). Categories of reproductive status were grouped based on model selection (corrected for covariables; Table 3) and corresponded to nonlactating with conception of 0, 1, or 2 offspring (C_{0-1-2} -NL: solid line); lactating with conception of singleton (C_1 -L: dashed line); and lactating with conception of twins (C_2 -L: dotted line). *SE* is shown in gray.

to 1 or 2 corpora rubra at conception). Females with twins and lactating never accumulated as much fat reserves at the end of autumn as other females (Table 5; Fig. 3). Rump fat of lactating females that had singletons increased similarly to nonlactating females during autumn, but the latter reached a plateau earlier, such that both groups had similar fat levels in late November (Fig. 3).

Prior to pooling categories of reproductive status in autumn, peroneus muscle mass did not seem affected by reproductive status, because the best model only suggested a curvilinear effect of age (Table 5; Supporting Information S1). However, when we grouped different categories of reproductive status we observed a relationship between muscle mass and litter size at conception: females conceiving a singleton, lactating or not, had a lower peroneus mass (91.8 ± 1.4 g) than females conceiving twins, lactating or not, or than females not conceiving (94.1 ± 1.4 g [Table 5; Fig. 2c]). Although other groupings using the same number of parameters were equivalent, they all suggested that lactating females with a singleton had a lower muscle mass than nonlactating females without conception or nonlactating females conceiving twins (Table 3).

Reproductive status in autumn also affected body size index (PCA axis 1), and we documented a strong curvilinear effect of age and an interaction of age with date indicating that body size increased during autumn but only in young females (Table 5;

Supporting Information S1). The best model distinguished females conceiving a singleton and lactating, which were short and skinny (smaller total length and chest girth; index = -0.52 ± 0.70), compared to nonlactating females (disregarding conception) or females conceiving twins and lactating that had a longer total length and were rounder (index = 1.26 ± 0.70 [Fig. 2d; Table 5]). An equivalent model suggested that females that were not lactating but having conceived twins could be considered similar to lactating mothers of singletons (Table 3).

DISCUSSION

To minimize reproductive costs, females should adjust reproductive effort as a function of experience and environmental conditions (Tavecchia et al. 2005; Bårdsen et al. 2010; Monteith et al. 2013). Accordingly, the probability of conception for primiparous and multiparous females increased with age, although age did not influence weaning success. We observed a seasonal effect in environmental variables: rainy springs prior to conception favored the production of twins, and autumn snow cover decreased the probability of conception, whereas deer density in autumn negatively affected conception but only for young primiparous females. Cold and snowy winters during gestation decreased weaning success. Habitats with abundant forbs during summer favored the probability of 1st conception and weaning success. Overall, reproductive status influenced body condition in autumn, which was better in nonlactating than in lactating females. Twins appeared costly for fat reserves, but females conceiving twins had high muscle mass and large body size. Although our study only lasted 4 years, which is somewhat limited when testing for environmental effects on life-history parameters, the documented effects of density and of spring and autumn climate on reproductive status corroborated the general patterns observed on average reproductive rates during a 23-year period for the same population (Simard et al. 2010), but it allowed a much better investigation of underlying mechanisms.

Environmental influences on reproductive status.—Fertility generally increases with age in ungulates, until reproductive senescence (Mysterud et al. 2002). Although we confirmed that conception rate increased with age, we observed an apparent absence of senescence in older females, similarly to DeGiudice et al. (2007), who found no indication of senescence in white-tailed deer females up to 15.5 years old. This is possible because female ungulates with high longevity are generally of higher quality and experience lower reproductive costs than shorter-lived females (Weladji et al. 2006; Hamel et al. 2009a). Age did not affect weaning success in our study, similarly to white-tailed deer in Illinois (Nixon and Etter 1995), but unlike European roe deer (*Capreolus capreolus*—Hewison and Gaillard 2001). Our results suggest that once conception occurs, reproductive success appears largely determined by environmental conditions (see also Hamel et al. 2010; Milner et al. 2013).

Environmental conditions in autumn, more specifically the abundance of compact snow in November and December, determined the probability of conception for all females. A negative effect of autumn snow cover also was reported on average reproductive and survival rates (23-year study—Simard et al. 2010). Autumn snow likely reduces access to vegetation and compromises fat gain, which normally increases steeply before winter (Tollefson et al. 2010; Simard et al. 2014). In female arctic hares (*Lepus arcticus*) and muskoxen (*Ovibos moschatus*), for which mass gain principally occurs in autumn (Parker et al. 1990), earlier adverse winter conditions translated into lower recruitment rates, likely through an effect of nutrition (Mech 2000). Because minimal fat reserves are often required to initiate ovulation (Thomas 1982), adverse autumn nutrition decreasing female condition could delay estrus (Verme 1965; Garel et al. 2009) or reduce fertility (Testa and Adams 1998). In northern latitudes, where estrus is already late, reduced fertility is more likely (Langvatn et al. 2004).

Because they may not have completed growth, young primiparous females are likely more vulnerable to environmental conditions in autumn than are other females (Clutton-Brock et al. 1983; Jorgenson et al. 1993). Accordingly, high density in autumn reduced the probability of 1st conception only for young females (≤ 3.5 years), although it had a negative effect on autumn fat reserves and muscle mass for all females (Simard et al. 2014). High population density may compromise breeding at an early age because reproductive costs of early breeders are normally higher in periods of resource shortage, reducing offspring survival (bighorn sheep [*Ovis canadensis*—Festa-Bianchet et al. 1995]) or female survival (northern elephant seals [*Mirounga angustirostris*—Reiter and Le Boeuf 1991]). Alternatively, habitats with abundant resources in summer (e.g., peatlands) favored reproduction of primiparous females (see also McLoughlin et al. 2008), possibly because these habitats improved the accumulation of fat reserves (Tollefson et al. 2010; Simard et al. 2014).

Despite higher resilience of multiparous females to changes in environmental conditions (Strickland et al. 2008), previous reproduction may prevent the replenishment of body reserves in time for estrus (Cameron 1994). Reproductive pauses are more frequent under restricted forage conditions (white-tailed deer—Verme 1965), high density (mountain goats [*Oreamnos americanus*—Hamel et al. 2010]), or during short periods of access to vegetation in summer or autumn (this study and red deer [*Cervus elaphus*—Langvatn et al. 2004]). On average, only 6% of adult females took reproductive pauses on Anticosti Island, but this rose to 20% when considering only younger females (2.5-year-olds having reproduced as yearlings), which confirmed that reproductive pauses are more frequent the year following 1st reproduction (Adams and Dale 1998; Tavecchia et al. 2005).

Surprisingly, the probability of reproductive pause was lower for females born at high density than at low density. This result seems counterintuitive because unfavorable environmental conditions in the year of birth are expected to lead to cohorts

of low-quality individuals (e.g., roe deer—Pettorelli et al. 2002; Hamel et al. 2009b). However, other studies documented that severe conditions in early life could favor high-quality cohorts, because mild environmental conditions favoring 1st year survival should allow more low-quality individuals to remain in the cohort than under harsh conditions where only high-quality individuals survive (e.g., red deer [Nussey et al. 2005], Soay sheep [*O. aries*—Tavecchia et al. 2005], and bighorn sheep [Hamel et al. 2009b]). A similar scenario is possible on Anticosti Island because fawns exhibiting a mass below a determined threshold die during their 1st winter (Taillon et al. 2006) and because females born at high density and having survived are more resilient to high density, storing more fat reserves than the average female born and surviving at low density (Simard et al. 2014). The positive effect of dry climate (high NAO) during the spring of birth on weaning success also supported this hypothesis, because it is opposite to the positive effect of rainy springs (low NAO) on twinning and reproductive rates (this study; Simard et al. 2010). Therefore, we concluded that unfavorable environmental conditions had a divergent effect on demography whether we considered short- or long-term consequences: unfavorable environment impairs individuals in the short term, but in the long term, it favors selection for good-quality individuals that are less vulnerable to adverse annual environmental conditions, resulting in more stable body condition (Simard et al. 2014) and reproduction.

Rainy conditions during spring (low NAO) favored female reproduction prior to conception, increased production of twins, and positively affected overall lactation rate, likely through reduced neonatal mortality (Simard et al. 2010). In a similar manner, white-tailed deer density was explained by high precipitation in previous years (Teer et al. 1965) and the probability of pregnancy in elk (*C. elaphus*) was increased by higher precipitation (Morano et al. 2013). We hypothesized that rainy springs enhanced early vegetation quality or growth during a period of high energy requirements (Toigo et al. 2006; Morano et al. 2013), possibly allowing reproductive females to reach better autumn body condition (Herfindal et al. 2006; Simard et al. 2014). Conceiving twins may be risky for females under unfavorable forage conditions because litter size is often inversely related to body size, and consequently offspring survival (Doughty and Shine 1997; Huber et al. 1999). An apparent trade-off in the conception of twins to increase the probability of conception has already been documented on Anticosti Island following the long-term deterioration of forage conditions (Simard et al. 2008).

Unfavorable winter and spring conditions preceding birth may generate a prolonged energy deficit, so that reproductive females are forced to compromise their reproduction as opposed to their own survival (Parker et al. 2009; Morano et al. 2013). Similar to other ungulates (Bårdsen et al. 2010; Hamel et al. 2010; Hegel et al. 2010), white-tailed deer on Anticosti Island had a low weaning success under cold and snowy winters (low NAO). This suggests that females cannot bear the energetic demand of reproduction under adverse weather conditions, such that females give birth to smaller

fawns with higher mortality risk or are constrained to restrain their investment into lactation (Moen 1978; Therrien et al. 2008). Weaning success of white-tailed deer was enhanced under high availability of open habitats, possibly because those areas allowed earlier access to highly digestible new forage, which is critical during the last trimester of gestation through its influence on birth mass and neonatal survival (Verme 1965, 1969; Moen 1978). Observed patterns of energy allocation by reproductive females in relation to environmental constraints correspond to a risk-sensitive allocation strategy, as suggested by other studies (Bårdsen et al. 2008, 2010; Monteith et al. 2013).

Body condition associated with reproductive status.—We did not observe a linear gradient between categories of reproductive status in autumn (based on litter size at conception and lactation) and body condition (predicted as $C_0\text{-NL} > C_1\text{-NL} > C_2\text{-NL} > C_1\text{-L} > C_2\text{-L}$) because different categories sometimes translated into the same observed effects on body condition. For example, nonlactating females had similar body condition whether they had conceived or not, possibly because energy costs of gestation were small (Ofstedal 1985; Clutton-Brock et al. 1983; Sand 1996). The observed relationship between reproductive status and body condition in autumn varied depending on which parameter was investigated. We first found that body mass was lower for lactating than nonlactating females, independent of litter size at conception. An experimental study on white-tailed deer reported that nonlactating females could gain 30 g/day more than lactating females during summer, but again, litter size did not affect mass gain (Therrien et al. 2007). In roe deer, females raising twins had a higher body mass than those with a singleton (Mauget et al. 1999), although the opposite pattern was found in moose (*Alces alces*—Sand 1996).

Similar to what was observed for body mass in moose (Sand 1996), we found that rump fat was not only lower for lactating than nonlactating female deer, but also even lower for those lactating and having conceived twins. Other studies on *Odocoileus* spp. documented a greater fat depletion for females raising twins rather than singletons (Sadleir 1982; Cothran et al. 1987; Monteith et al. 2013). Females with twins were found to have a slower rate of fat accumulation in autumn than females with singletons, the latter having similar fat levels to nonlactating females in late autumn (see also Cook et al. 2004). Because fat reserves in autumn are related to conception and survival (Thomas 1982; Parker et al. 2009), females with twins possibly face greater reproductive costs than others (Sand 1996).

Nevertheless, lactating females that conceived twins, although their fat reserves were lower, tended to have higher peroneus muscle mass and body size than those that conceived singletons, similar to what was reported for roe deer mass (Mauget et al. 1999). The ability to conserve or to rapidly build up lean mass could favor fawn survival and female fertility, because protein reserves may strongly influence reproductive potential in ungulates (Chan-McLeod et al. 1994; Parker et al. 2009). In subantarctic fur seals (*Arctocephalus tropicalis*),

large body size translated into higher lifetime reproductive success and a better ability to provision pups with greater and more regular energy supply (Beauplet and Guinet 2007).

Several studies suggested that the capacity to produce large litter sizes is an inherent phenotypic trait, visible when looking at female condition (Gunn and Doney 1975; Gerhart et al. 1997; Testa and Adams 1998). Our study offered a rare opportunity to explore this hypothesis because we distinguished both litter size at conception and lactation status. Unfortunately, we are limited by a low sample size for nonlactating females with 2 ovulations ($n = 20$), no information regarding the date of reproductive interruption, and the assumption that lactating females conceiving twins truly raised twins. Still, our observations suggested that females that conceived twins were of higher phenotypic quality, although they had depressed fat reserves. Results of Bårdsen et al. (2010) and Monteith et al. (2013) documented that females with high reproductive investment are often better at conserving energy during winter than other females, compensating for low initial fat reserves. In mule deer (*Odocoileus hemionus*), depletion of lean mass and fat reserves in winter was inversely related to age and number of fetuses (Monteith et al. 2013). We found that females having conceived twins but that terminated reproduction (nonlactating) tended to reach higher body condition than those that had not conceived or that conceived singletons. Because indexes of muscle mass and fat reserves better expressed subtle differences in autumn reproductive status than did body mass, their use should be encouraged whenever possible, especially as they also better predicted future reproduction and survival (Parker et al. 2009).

Our study allowed us to disentangle effects of conception and lactation to estimate reproductive effort. In long-lived species, females should not compromise their survival during reproduction and should respond to a changing environment (Clutton-Brock 1988; Hamel et al. 2010). Accordingly, using a large sample size from a northern population of white-tailed deer at high density, we demonstrated that females adjusted reproductive effort according to local environmental conditions at different times of the year. Such plasticity in reproduction minimized loss in body condition and possibly reproductive costs (see also Bårdsen et al. 2008, 2010; Monteith et al. 2013).

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Model selection procedure based on delta Akaike information criterion (Δ AIC) values to identify the effects of age, date, and reproductive status (R) on body condition indexes, that is, dressed mass, rump fat, peroneus muscle mass, and body size index (principal component analysis [PCA] axis 1) of female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Quebec, Canada; 2002–2005).

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