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Spring-loaded reproduction: effects of body condition and population size on fertility in migratory caribou (*Rangifer tarandus*)

M. Pachkowski, S.D. Côté, and M. Festa-Bianchet

Abstract: In many ungulates, female fecundity is affected by body condition and has important effects on population dynamics. In some species, females adopt a conservative strategy, reducing reproductive effort when population density is high. We investigated what factors affect the probability of gestation in adult female caribou (*Rangifer tarandus* (L., 1758)) from the Rivière-George herd in northern Quebec and Labrador over 5 years that spanned various population sizes and trends. Similar to other populations of migratory caribou, the probability that a female was pregnant in spring increased with body mass and percent body fat. The probability of gestation appeared to be reduced by high infestation of warbles (*Hypoderma tarandi* (L., 1758)). The proportion of females pregnant varied between years and was lower at high population size. Females of similar mass, however, were pregnant regardless of whether the population was increasing at low density, had reached a peak, or was declining. Compared with other ungulates that reduce maternal expenditure at high density, female caribou of the Rivière-George herd may have a risk-prone reproductive strategy.

Key words: migratory caribou, *Rangifer tarandus*, fertility, body condition, population size.

Résumé : Chez de nombreux ongulés, la condition corporelle a une incidence sur la fécondité des femelles qui, elle, a des effets importants sur la dynamique des populations. Les femelles de certaines espèces adoptent notamment une stratégie conservatrice consistant à réduire leur effort de reproduction quand la densité de la population est élevée. Nous avons examiné les facteurs qui influent sur la probabilité de gestation des caribous (*Rangifer tarandus* (L., 1758)) femelles adultes du troupeau de Rivière-George, dans le nord du Québec et au Labrador, sur une période de 5 ans couvrant diverses tailles et tendances de population. À l'instar d'autres populations de caribous migrateurs, plus la masse corporelle et le pourcentage de graisse corporelle étaient élevés, plus la probabilité qu'une femelle soit en gestation au printemps était grande. Un degré élevé d'infestation d'hypodermes (*Hypoderma tarandi* (L., 1758)) semblait se traduire par une probabilité de gestation réduite. La proportion de femelles gestantes variait selon l'année et était plus faible lorsque la taille de la population était grande. Cependant, les femelles de masses semblables étaient gestantes peu importe si la taille de la population augmentait à faible densité, avait atteint un maximum ou était en baisse. Comparativement à d'autres ongulés qui adoptent une stratégie de réduction des dépenses maternelles quand la densité est élevée, les caribous femelles du troupeau de Rivière-George pourraient présenter une stratégie de reproduction risquée. [Traduit par la Rédaction]

Mots-clés : caribou migrateur, *Rangifer tarandus*, fertilité, condition corporelle, taille de la population.

Introduction

Life-history theory assumes that limited resources force trade-offs among fitness components such as growth, reproduction, and survival (Stearns 1992). These trade-offs lead to variation in life-history traits including fecundity, age at primiparity, and reproductive lifespan or aging. Because fecundity affects population productivity (Promislow and Harvey 1990; Macdonald et al. 2009), understanding female reproductive strategy is key to population dynamics and management (Festa-Bianchet and Côté 2008). Indeed, measures of reproductive performance such as fecundity (Cameron and Hoef 1994), female to young ratios, and recruitment rates (Vincent et al. 1995; Couturier et al. 2009b) are regularly suggested as management tools to evaluate population performance.

Reproductive performance can be affected by extrinsic factors including density (Albon et al. 1983; Sand et al. 1996), predation, parasitism (Hughes et al. 2009), and weather (Adams and Dale 1998; Post and Stenseth 1999). It may also vary with individual characteristics such as age (Festa-Bianchet 1988; Sand et al. 1996; Ropstad 2000), previous reproductive experience, and body condition (Sand et al. 1996; Testa and Adams 1998). "Condition" was defined by Harder and Kirkpatrick (1994) as the "state of body components controlled by nutrition". We measured condition through a combination of skeletal measures and measures of energy reserves including mass and fat, all of which have been identified as indicators of caribou (*Rangifer tarandus* (L., 1758)) body condition (Taillon et al. 2011). Most research has focused on how female body size and condition relates to reproductive success through age at primiparity (Jorgenson et al. 1993), lifetime reproductive success, and fecundity (Dauphiné and McClure 1974; Reimers 1983; Crête et al. 1993). Good body condition allows females to reproduce earlier, more often, and produce more or larger offspring with high survival rates (Tveraa et al. 2003). Environmental factors such as climate may affect body condition indirectly by affecting food availability and energy expenditure (Solberg et al. 2001). High population density can limit resource

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availability through increased competition (Clutton-Brock et al. 1982).

When resources are limited, females may increase their survival by limiting investment in reproduction. Indeed, long-lived iteroparous animals typically adopt a conservative reproductive strategy at high population densities by reducing litter size (Sand et al. 1996), maternal care (Bårdsen et al. 2008; Martin and Festa-Bianchet 2010), or fertility (Albon et al. 1983; Sand et al. 1996). Few studies have revealed density-dependent effects on adult female survival (Gaillard et al. 2000), supporting the contention that females favor maintenance and survival over reproduction. That contention is also supported by the sequence with which vital rates usually change as population density increases: first survival of young decreases, then age of primiparity increases, after which reproductive rates decrease, and lastly but rarely, adult survival decreases (Eberhardt 2002).

Potential mechanisms for how density impacts reproductive rates have been identified. Density affected age of primiparity through a reduction in body condition for bighorn sheep (*Ovis canadensis* Shaw, 1804), but also selected for a more conservative reproductive strategy, independent of body condition (Jorgenson et al. 1993). Similarly, density reduced not only adult female mass but also age-specific fecundity in moose (*Alces alces* (L., 1758)) beyond what could be explained by the decrease in body condition (Sand et al. 1996). In hinds of red deer (*Cervus elaphus* L., 1758), the threshold mass required for females to conceive was higher at high than at low population density (Albon et al. 1983).

Understanding reproduction of migratory caribou is of particular interest because populations undergo rapid and extensive fluctuations (Morneau and Payette 2000). Reproduction is one of the first vital rates affected by an increase in population size in migratory populations (Crête et al. 1996). In rapidly increasing populations, yearling females have high pregnancy rates (Parker 1980; Ouellet et al. 1997), but yearlings may stop conceiving at high density (Crête and Huot 1993). Reproduction in caribou is associated with body size (Gerhart et al. 1997) and condition in both autumn (Cameron et al. 1993; Cameron and Hoef 1994; Adams and Dale 1998) and spring (Russell et al. 1998). Female caribou that first reproduce at a young age are typically heavier (Adams and Dale 1998), fatter (Crête et al. 1993), or both heavier and fatter (Thomas 1982) than those that delay primiparity. Among adults, females that conceive are heavier and fatter than those that do not conceive (Allaye Chan-McLeod et al. 1999). Fecundity–body condition relationships for adults have been determined for several populations, including the Denali herd (Adams and Dale 1998), the Porcupine herd (Gerhart et al. 1997), the Central Arctic herd (Cameron et al. 1993), and Peary populations (Thomas 1982).

The relationship between body condition and fecundity in caribou varies with age (Adams and Dale 1998; Cuyler and Østergaard 2005), lactation status (Gerhart et al. 1997), and weather (Adams and Dale 1998). Although the effect of density on reproductive rates has also been examined, its effect on the relationship between condition and fertility has yet to be assessed. Our objectives were to determine if (*i*) the relationship between body condition and fecundity seen in other herds was conserved in the Rivière-George herd and (*ii*) if females adopted a conservative reproductive strategy at high population densities. We hypothesized that once age and body size were controlled for, females in better body condition (higher mass and percent body fat) and health (lower parasitic infection) would have a higher gestation rate in spring compared with females in poorer condition and (or) health. As well, because caribou are long-lived and iteroparous, we expected females to adopt a conservative reproductive strategy so that the threshold body condition required to reproduce would increase with population density.

Materials and methods

Study area and population estimates
The Rivière-George herd is a migratory caribou herd in northern Quebec and Labrador. The annual range estimate was 174 000 km² between 2008 and 2012 (J. Taillon, personal communication), although range size varies with population size (Couturier et al. 2010). The Rivière-George increased from approximately 5000 in the 1950s to an apparent peak approximating 1 000 000 individuals in 1989 (Crête et al. 1996). It then declined to 776 000 in 2001 (Couturier et al. 2009*b*) and to less than 75 000 individuals in 2010 (Quebec Government aerial count).

Data collection
Scientific culls from the Rivière-George have been conducted for decades, but sampling methods and purposes differed between researchers and years. We restricted analyses to collections where the selection of females was not biased towards particular reproductive classes. Age of females was assessed by counting the cementum annuli of an incisor (Miller 1974). Data we used were collected from late February to April and limited to known-age individuals, where the presence or absence of a foetus was recorded. Data meeting these requirements were collected in April 1980 by G. Parker; in April 1984 by J. Huot; and in March 1986–1987, February and April 1987, and March 2002 by S. Couturier.

Caribou body condition
Body condition indices typically measured included whole mass and (or) eviscerated body mass, hind-foot length and (or) metatarsal length, kidney fat mass and kidney mass, percent femur marrow fat, and parasite load denoted by the absolute number of warbles (*Hypoderma tarandi* (L., 1758)) counted. Protocols for animal culls and body condition measurements are described elsewhere (Parker 1980; Huot 1989; Couturier et al. 2009*a*). Percent body fat was calculated as 0.091 × KFFI − 1.382 based on Crête et al. (1993), where KFFI is the kidney fat femur index (KFI + % femur marrow fat) (Huot and Picard 1988). KFI is the kidney fat index based on the Riney fat index (Riney 1955). The mean of the right and left kidney masses and kidney fat masses were used to calculate the KFI, except for 15 of 172 cases where only one kidney or kidney fat was weighed.

Because body condition varies seasonally, we used ANCOVAs to test for an effect of collection date on mass and percent body fat and for a possible interaction between these variables and pregnancy status. Because mean mass differed between years (Table 1), we used data outside the scope of this study, eviscerated masses collected from February to May in 1987, to test for an effect of collection date on body mass. Collection date neither affected eviscerated body mass ($F_{[1,38]} = 0.94$, $p = 0.34$) nor affected pregnant and barren females differently (interaction: $p = 0.63$).

Pooling all years, percent body fat decreased from late February to April ($F_{[3,161]} = 5.80$, $p < 0.01$) and in interaction with pregnancy status ($p = 0.02$) such that there was a decrease in body fat for gestating but not for barren females. We therefore adjusted body fat of pregnant females to 23 March, the middle of the sampling period for all years. Pregnant females lost, on average, 0.05% body fat per day. The maximum number of days corrected for was 24 with a maximum correction of 1.08% body fat loss.

To compare metatarsal lengths measured in 1980 with hind-foot lengths measured in 1984–2002, we transformed metatarsal lengths using a correlation based on 131 adult females from the Rivière-George from 8 years (1986–1988, 2001–2003, and 2007), including collections outside of this study ($F_{[1,129]} = 275.80$, $r^2 = 0.68$, $p < 0.01$; hind-foot length = 1.31 ± 0.08 × metatarsal length + 4.69 ± 3.14).

Because not all age classes were sampled equally in all years and to avoid possible complications associated with early primiparity, we defined adult females as ≥3 years old. The limited number of

Table 1. Mean mass (kg), body fat (%), transformed hind-foot length (hflT) (cm), number of warbles (*Hypoderma tarandi*), and age with standard error (SE) and sample size (*n*) grouped by reproductive status (pregnant or barren) and demographic trend (low and increasing, high and increasing, or low and decreasing) of known-age female caribou (*Rangifer tarandus*) aged 3–16 years from the Rivière-George herd collected in 1980, 1984, 1986, 1987, and 2002.

	Mass (kg)			Body fat (%)			HflT (cm)			Warbles			Age		
	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*N*	Mean	SE	*n*
Reproductive status															
Pregnant	92.5a	0.8	117	11.1a	0.2	111	56.7a	0.1	122	35.3a	4.2	82	6.7a	0.2	137
Barren	79.0b	2.6	16	8.9b	0.6	14	56.6a	0.4	18	146.8b	67.3	4	5.6b	0.4	23
Demographic trend															
Low	94.0a	0.9	81	11.2a	0.2	76	57.0a	0.1	80	36.4a	4.5	76	7.2a	0.3	81
High	86.2b	1.9	39	10.2b	0.3	40	56.2b	0.2	47	71.9b	31.7	10	5.7b	0.2	66
Decreasing	85.5b	2.6	13	11.4ab	1.3	9	56.8ab	0.5	13				7.1b	0.6	13

Note: Presence or absence of a foetus was recorded during March and April, except for five individuals collected in late February in 1987. Values that differ significantly based on Tukey's post hoc tests for mass, body fat, and hind-foot length and based on Kruskal–Wallis tests for differences in age distribution and number of warbles are denoted by different letters. Bonferroni correction was applied to determine significance between demographic trends for age ($p = 0.02$).

old individuals sampled precluded the analysis of senescence effects. We therefore excluded the oldest female collected, a barren 17-year-old, from analyses. Our data set included 160 females, of which 23 were barren and 137 were pregnant.

Population estimates

Population counts were available for 2 years when body condition data were collected (1980 and 1984). Population size for 1986, 1987, and 2002 was estimated by fitting a loess smoothing spline on available population counts. Aerial counts were made in 1988, 1993, and 2001, so all population estimates were within 1 or 2 years of actual counts. We accounted for population size and trend in three ways: (1) as a continuous vector using actual counts and inferred estimates; (2) grouped into two categories (above and below 500 000 individuals) following Couturier et al. (2009*a*); and (3) grouped into three phases that accounted for both population density and trend (low and increasing (1980), high and approaching the peak (1984–1987), and declining (2002)).

Statistical analyses

We used R software version 2.12.1 (R Development Core Team 2010) for all statistical analyses. General linear models (GLM) with a binomial distribution were used to model the probability of gestation as a function of female age, mass, hind-foot length, percent body fat, warble infection, and population size and trend. Year of collection was tested as a random effect in mixed models but was not significant so analyses were performed using GLMs. Our data were nonorthogonal. Unequal sample sizes were due to missing data on several individuals. We first used maximum sample sizes (ranging from 86 to 160) to model the probability of gestation based on each variable separately. We then excluded warble counts from further multivariate analyses, as counts were only available for 2 of the 5 years, to test all other body condition variables with population size and trend. These analyses were performed using a data set with 115 individuals. Subsequent analyses excluded body fat and therefore only included variables that can be measured or estimated on live animals. Body fat was not available for 16 females. Therefore, when body fat was excluded for analyses, the sample increased to 131 individuals.

We checked all explanatory variables for collinearity before combining them in the same model. We used the vif function in the "car" package to test the variance inflation factor (vif) of variables in all full models. Variables were not combined in models if vif exceeded 2. The highest correlation for both sample sets was between mass and body fat ($r = 0.47$) in the set containing all variables ($n = 115$) (Table 2). All other variables were only weakly correlated ($r < 0.32$) (Table 2). Older females tended to be larger, heavier, and fatter than younger females because age, hind-foot length, mass, and body fat were all positively correlated. Warble count and population size were negatively correlated to all other

Table 2. Correlation matrix between mass, transformed hind-foot length (hflT), percent body fat corrected to 23 March (bodyfatC), population estimate (popest), and age of female caribou (*Rangifer tarandus*) from the Rivière-George herd aged 3–16 years collected in late February, March, and April in 1980, 1984–1987, and 2002.

	hflT	bodyfatC	popest	age
mass	0.32	0.47	−0.25	0.15
hflT		0.10	−0.16	0.03
bodyfatC			−0.15	−0.10
popest				−0.29

Note: The data set was restricted to 115 individuals with all variables measured.

variables such that older, larger, heavier, and fatter females had fewer warbles and were mostly sampled at low population size.

We considered all results significant at $\alpha < 0.05$ for univariate GLMs. Because of the small sample size, model selection was performed using second-order Akaike's information criterion (AIC_c). The model with the lowest AIC_c was retained (Burnham and Anderson 2002). Differences in AIC_c values of at least 2 were used to determine if one model was better than another. Because several models were indistinguishable based on AIC_c values, we used the modavg function from the "AICmodavg" package in R to calculate weighted (w_i) parameter estimates for explanatory variables along with their standard errors (SE) and 95% confidence intervals (95% CI). Variables were considered significant if the confidence interval of their estimate did not overlap zero. Stepwise model selection following McCullagh and Nelder (1989) led to similar models being selected.

Results

Adult female body condition

Pregnant females were, on average, 13.5 kg heavier, 2.2% fatter, were older, and had fewer warbles than barren females, but they did not differ in hind-foot length (Table 1). Females were in good condition when the population was low and increasing (1980), as they were heavier and larger (based on hind-foot length) than when the population was high (1984–1987) or decreasing (2002) (Table 1). The different age distribution in 1980 compared with all other periods (Table 1) was likely due to a wider age range in 1980 caused by a larger sample size and different sampling method. Based on percent body fat, females were in good condition with over 10% body fat for all periods of demographic trend (Table 1). However, females had 1.1% less body fat when the population was nearing a peak than when the population size was low (Table 1). Mean number of warbles nearly doubled as the population increased (Table 1).

Fig. 1. Logistic regressions of the probability of gestation according to body condition indices and population size for Rivière-George female caribou (*Rangifer tarandus*) aged 3–16 years collected in spring of 1980, 1984, 1986, 1987, and 2002. Regressions predicting presence (1) or absence (0) of foetus for (A) mass, (B) percent body fat, and (F) population size were significant. Regressions for (C) hind-foot length and (D) age were not significant. Logistic regression of (E) the number of warbles (*Hypoderma tarandi*) was significant (solid line) but became marginally insignificant after removing the female with the highest warble count (broken line). Raw data (points) are shown, except for (F), where grey bars show the proportion of pregnant females at given population sizes.
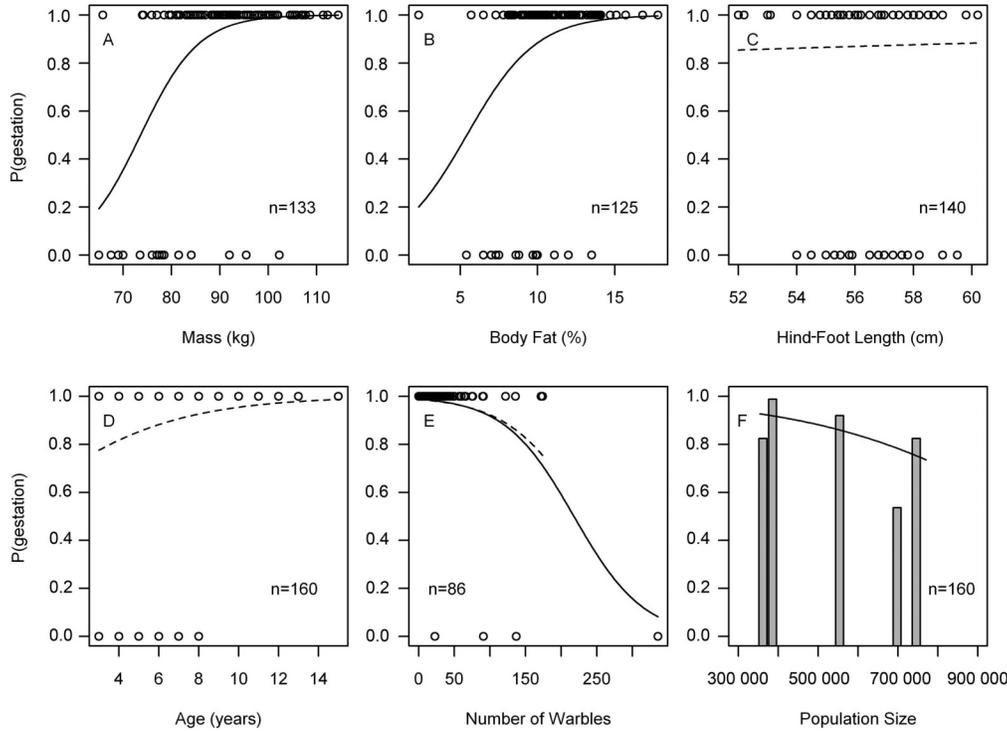
Table 3. Model selection based on second-order Akaike's information criterion corrected for small sample size (AIC$_c$) for the determinants of gestation in adult female migratory caribou (*Rangifer tarandus*) of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987, and 2002.

Model	k	AIC$_c$	ΔAIC$_c$	AIC$_c$ Wt.	Cum. Wt.	LL
mass + hflT	**3**	**60.64**	**0**	**0.19**	**0.19**	**−27.21**
mass	**2**	**61.14**	**0.5**	**0.15**	**0.34**	**−28.52**
age + mass + hflT + bodyfatC	**5**	**61.4**	**0.76**	**0.13**	**0.48**	**−25.42**
mass + bodyfatC	**3**	**61.59**	**0.95**	**0.12**	**0.6**	**−27.69**
mass + hflT + bodyfatC	**4**	**61.74**	**1.1**	**0.11**	**0.71**	**−26.69**
popest + mass	**3**	**62.49**	**1.85**	**0.08**	**0.79**	**−28.14**
mass + age	**3**	**62.51**	**1.87**	**0.08**	**0.86**	**−28.15**
age + mass + hflT + bodyfatC + popest	6	62.67	2.03	0.07	0.93	−24.95
popest × mass	4	63.64	3	0.04	0.97	−27.64
bodyfatC + age	3	65.43	4.8	0.02	0.99	−29.61
popest + bodyfatC	3	68.13	7.49	0	1	−30.96
popest × bodyfatC	4	70.17	9.54	0	1	−30.9
bodyfatC	2	70.92	10.28	0	1	−33.41
hflT + bodyfatC	3	72.97	12.34	0	1	−33.38
popest	2	74.86	14.22	0	1	−35.37
popest × age	4	75.91	15.27	0	1	−33.77
age	2	76.82	16.18	0	1	−36.36
popest + hflT	3	76.87	16.24	0	1	−35.33
popest × hflT	4	77.52	16.89	0	1	−34.58
null	1	78.98	18.34	0	1	−38.47
hflT	2	81.05	20.41	0	1	−38.47

Note: Models include 115 known-age individuals with all morphological measurements including mass (mass), percent body fat adjusted to 23 March (bodyfatC), and transformed hind-foot length (hflT). Population size (popest) and interactions denoted by a time (×) symbol were also included in models along with a model containing no explanatory variables (null model). Models are listed in rank order with the six best models, with AIC$_c$ values that do not differ by more than 2, in boldface type. Number of estimated parameters (*k*), change in AIC$_c$ from lowest AIC$_c$ value (ΔAIC$_c$), and cumulative weight of model (Cum. Wt.) based on the log-likelihood (LL) that that model is the best model are presented.

Table 4. Model averaged parameter estimates, standard error (SE), and 95% confidence intervals (CI) for variables from the six competing models from Table 3 for the determinants of gestation in adult female migratory caribou (*Rangifer tarandus*) of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987, and 2002.

Variable	Estimate	SE	CI Low	CI High	Significant
mass	0.15	0.07	0.01	0.3	Yes
hflT	−0.42	0.28	−0.97	0.13	No
bodyfatC	0.25	0.19	−0.3	0.62	No
age	0.31	0.25	−0.18	0.81	No
popest	0	0	0	0	No

Note: Models included 115 known-age individuals with all morphological measurements including mass, percent body fat adjusted to 23 March (bodyfatC), transformed hind-foot length (hflT), and population size (popest).

Gestation predictors

Warble infestation reduced the probability of gestation (estimate = −0.02 ± 0.01, $n = 84$, $p = 0.01$; Fig. 1E). When the female with the highest infestation (336 warbles) was removed, however, the regression was not significant (estimate = −0.02 ± 0.01, $n = 83$, $p = 0.06$; Fig. 1E). If we excluded this potential outlier but included 2-year-olds as in Gerhart et al. (1997) and Hughes et al. (2009), the negative effect remained significant. For females aged 3 or older, hind-foot length (estimate = 0.03 ± 0.17, $n = 140$, $p = 0.90$) and age (estimate = 0.26 ± 0.13, $n = 160$, $p = 0.08$) did not affect fecundity in simple logistic models (Figs. 1C and 1D, respectively). Fecundity increased with both mass (estimate = 0.17 ± 0.04, $n = 133$, $p < 0.01$) and percent body fat (estimate = 0.44 ± 0.04, $n = 132$, $p < 0.01$) (Figs. 1A, 1B). Fewer females were pregnant at high population size than at lower population size (estimate = −0.0004 ± 0.0001, $n = 160$, $p < 0.01$; Fig. 1F).

In simple logistic models, body mass was the best predictor of pregnancy rate and explained 22.5% of the variation in fertility. Percent body fat was significant but explained only 12.1% of the variation. At mean mass (91.2 kg), females had a 91% probability of being pregnant. All but three nonpregnant females were lighter than this threshold. At mean percent body fat (10.9%), females had a 95% chance of being pregnant.

Population size as a predictor of pregnancy

Population size as a continuous variable had the lowest AIC_c value (62.8) compared with population size grouped into two groups ($AIC_c = 64.3$) or population trend (three groups) ($AIC_c = 63.1$). Therefore, we used population size as a continuous variable in AIC_c model selection. There were 115 females with all variables measured, including body fat. Both AIC_c and stepwise model selection with nested models suggested that mass was the most important factor affecting the probability of gestation (Tables 4, 5). The inclusion of a quadratic effect of age did not affect model selection based on AIC_c and did not alter parameter estimates. Although hind-foot length was included among the best models using AIC_c, its parameter estimate did not significantly differ from zero (Table 4) and it bordered on significance ($p = 0.07$) in models obtained by a stepwise selection. Based on AIC_c model selection, the relationship between mass and fertility did not vary according to population size because no interaction between population size and body condition variables were retained (Table 3). Although population size did appear in one of the best models, its parameter estimate was not significantly different than zero (Table 4).

When body fat was not considered, the best model explaining gestation in adult females included hind-foot length and mass (Table 5). The relationship between mass and probability of gestation remained positive for mass (0.22 ± 0.07, 95% CI: 0.09 to 0.34; Fig. 2) but the effect of hind-foot length became negative once mass was controlled (−0.58 ± 0.26, 95% CI: −1.1 to −0.07; Fig. 2). The model containing both hind-foot length and mass explained 31%

Table 5. Model selection based on second-order Akaike's information criterion corrected for small sample size (AIC_c) for the determinants of gestation in adult female migratory caribou (*Rangifer tarandus*) of the Rivière-George herd in spring (March and April) 1980, 1984, 1986, 1987, and 2002.

Model	k	AIC_c	ΔAIC_c	AIC_c Wt.	Cum. Wt.	LL
mass + hflT	**3**	**67.26**	**0**	**0.72**	**0.72**	**−30.53**
mass	2	70.96	3.7	0.11	0.83	−33.43
mass + age	3	71.68	4.43	0.08	0.91	−32.75
popest + mass	3	72.11	4.85	0.06	0.97	−32.96
popest × mass	4	73.84	6.58	0.03	1	−32.76
popest + age	3	93.38	26.12	0	1	−43.59
age	2	94.64	27.39	0	1	−45.27
popest	2	94.96	27.7	0	1	−45.43
popest × age	4	95.09	27.84	0	1	−43.39
hflT + age	3	96.55	29.29	0	1	−45.18
popest + hflT	3	96.71	29.45	0	1	−45.26
popest × hflT	4	98.65	31.39	0	1	−45.17
null	1	99.28	32.02	0	1	−48.62
hflT	2	101.26	34	0	1	−48.58

Note: Models include 131 known-age individuals with measured mass and transformed hind-foot length (hflT). Population size (popest) and interactions denoted by a time (×) symbol were also included in models. Models are listed in ranked order with the best model in boldface type. Number of estimated parameters (k), change in AIC_c from lowest AIC_c value (ΔAIC_c), and cumulative weight of model (Cum. Wt.) based on the log-likelihood (LL) that that model is the best model are presented.

Fig. 2. Model predictions, from best model with 131 individuals selected using second-order Akaike's information criterion corrected for small sample size (AIC_c) in Table 5, of gestation in relation to mass in April and May at mean hind-foot length (left panel) and in relation to hind-foot length at mean mass (right panel) for adult female caribou (*Rangifer tarandus*) of the Rivière-George herd in 1980, 1984, 1986, 1987, and 2002.
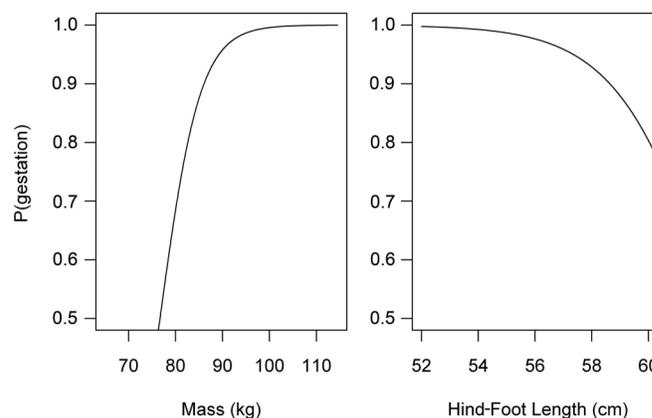
of the variation, 8.5% more than mass alone. To have a 50% chance of pregnancy, females had to be ~76 kg in spring. However, females of a given mass were ~5% less likely to be pregnant if their hind-foot length was ~4 cm larger.

Discussion

Fecundity–condition relationships seen in other caribou herds were mainly confirmed in the Rivière-George herd. High warble infection was associated with a reduced probability of pregnancy in spring. Mass and percent body fat positively affected gestation rates and there was no effect of age. Hind-foot length itself was not a good indicator of whether a female would reproduce, but reduced the probability of gestation after body mass was controlled.

Population size negatively affected the proportion of females that were pregnant, but contrary to our prediction, threshold mass and body fat necessary for gestation did not vary with pop-

ulation size, suggesting that females did not adopt a conservative reproductive strategy when resources were scarce. Productivity of this herd remained high but was reduced by lower mean mass at high population size.

Condition–fecundity relationships

When we included 2-year-olds to compare with analyses of the Dolphin–Union herd (Hughes et al. 2009), our results corroborated the finding that the probability of gestation in spring decreases with warble abundance. Because parasite load is correlated with body condition, it is difficult to ascertain whether individuals are in poor condition because of high parasite load or poor condition allows high intensity infections. Both parasite load and condition are correlated with fecundity (Stien et al. 2002). For caribou from the Dolphin–Union herd, high warble infection was correlated to minimal back fat levels (Hughes et al. 2009); for the Rivière-George herd in this study, both mass ($r = -0.22$, $n = 82$) and percent body fat ($r = -0.26$, $n = 82$) were negatively correlated to infection intensity. Although condition may be more closely associated to fecundity, parasite abundance may affect population growth in the genus *Rangifer* (Albon et al. 2002). Since intensity of infection typically increases with host density (Arneberg et al. 1998), as observed in this population, it is important to monitor parasite loads, especially if parasite abundance is influenced by climate change (Brotton and Wall 1997).

As seen in other caribou herds, both mass and fat were important determinants of fecundity (Dauphiné and McClure 1974; Thomas 1982; Cameron et al. 1993; Adams and Dale 1998; Russell et al. 1998). Although it has been proposed that a critical level of mass and fat are needed for caribou to conceive (Crête et al. 1993), we did not observe a sharp threshold. A threshold may have existed during autumn when ovulation occurred but did not persist until spring. We did not detect an effect of age on the probability of gestation. Congruent with results from the Porcupine caribou herd (Gerhart et al. 1997), hind-foot length in simple logistic regressions did not affect the probability of gestation.

Mass was clearly the best predictor of gestation in the study herd. Our results contradicted those of the Porcupine herd in autumn, where body fat (Gerhart et al. 1997) was the best predictor of pregnancy. This could be due to several factors. Firstly, in our study, body fat was measured compared with body condition scores that were used for the Porcupine herd. Secondly, seasonal differences between the two herds could account for the different results. For example, body condition for females of different reproductive classes in the Porcupine herd converged over winter (Allaye Chan-McLeod et al. 1999). Similarly, percent body fat of pregnant females decreased over the collection period in the Rivière-George herd. Lastly, pregnancy–condition relationships may vary among herds.

Although percent body fat affected whether or not a female would be pregnant in spring, it did not improve on mass as a predictor of gestation. When body fat was excluded from models, our results corroborated those from the Porcupine herd; mass and hind-foot length together affect the probability of pregnancy (Gerhart et al. 1997). The negative effect of hind-foot length after accounting for body mass suggests that caribou with relatively less body reserves were less likely to be pregnant. However, given the small effect size of hind-foot length and its exclusion from models with a smaller sample size, the importance of hind-foot length appears to be minor.

Effect of population size

Female fecundity was lower when population size was high. Contrary to our expectation, the threshold condition necessary for gestation did not vary with population size, despite an estimated difference of 400 000 individuals, suggesting a near-doubling of population size. Therefore, based on gestation rates, caribou did not adopt the conservative reproductive strategy re-

ported in other ungulates (Festa-Bianchet et al. 1998; Therrien et al. 2007).

Calf mass is affected by female condition (Adams 2005; Taillon et al. 2012), suggesting that females modulate resources to their foetus according to their own condition. Lactation is the most energetically costly component of reproduction (Gerhart et al. 1997), and when resources are scarce, females may allocate more to maintenance than to offspring growth postpartum (Bårdsen et al. 2009). Females from the Rivière-George herd, however, appeared to prioritize gestation over their own condition, as suggested by the decrease in mass and not in gestation rate. We therefore hypothesize that for caribou, the fitness cost of foregoing reproduction is high relative to the investment of carrying a calf to term. Despite this apparently fixed reproductive strategy, we still observed a reduction in herd productivity during the population increase.

Similar to the Denali population (Adams and Dale 1998), we suggest that the mechanism affecting gestation rates in Rivière-George females was a reduction in mass. However, our results contrast with those from the Porcupine herd where variation in body condition of females was not reflected in pregnancy rates (Gerhart et al. 1997). Despite a drastic increase in population size, pregnancy rates in the Rivière-George herd remained high compared with other populations. For example, in Peary caribou, pregnancy rates fell as low as 4% at high density (Thomas 1982). One explanation for the high pregnancy rates could be that female condition, based on percent body fat, remained high throughout the period of increase and was maintained even during the beginning of the subsequent decline. During our study, percent body fat averaged 11.0% ± 0.2% ($n = 115$), consistent with high pregnancy rates if indeed the threshold of 7.3% body fat needed for females to conceive (Crête et al. 1993) holds true. Although we suggest that a decline in mass reduced reproductive rates, other demographic parameters including age at primiparity and survival may have also affected productivity.

Determining both intrinsic and extrinsic factors that affect the probability of gestation in caribou is important to understand population dynamics. Although there is no known causal relationship between body condition and fertility, the relationship between body condition and gestation remains uncontested. For management purposes, adult female mass and hind-foot length measurements in spring predict pregnancy rates in the Rivière-George herd. Both measures can be obtained through live captures. We showed that caribou prioritize reproduction even at high population densities, as we were unable to detect a conservative reproductive strategy for gestation. High gestation rates, however, did not seem to affect changes in population size in this herd. That result highlights the importance of monitoring post-gestational demographic parameters such as calf mass, recruitment, and adult survival.

Acknowledgements

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