Maternal care in white-tailed deer: trade-off between maintenance and reproduction under food restriction

JEAN-FRANÇOIS THERRIEN*, STEEVE D. CÔTÉ*, MARCO FESTA-BIANCHET† & JEAN-PIERRE OUELLET‡

*Département de Biologie and Centre d'études nordiques, Université Laval
†Département de Biologie, Université de Sherbrooke
‡Département de Biologie and Centre d'études nordiques, Université du Québec à Rimouski

Lactation is the most energetically costly component of maternal investment in mammals. For large temperate herbivores, summer is characterized by relatively abundant forage but also high energetic needs for lactation and recovery from winter mass loss. We experimentally restricted food supply by about 20%, and compared the nursing and foraging behaviours of control and food-restricted adult female white-tailed deer, *Odocoileus virginianus*, and their fawns during lactation. We considered two fawn ages: 0–30 days (after which time spent suckling dropped markedly) and 30–80 days (the end of the nursing period). From 0 to 30 days of age, food-restricted fawns performed 17 more suckling bouts/day and spent twice as much time suckling than control fawns. Compared with controls, food-restricted fawns gained 26% less mass from birth to 80 days. Body growth was inversely related to time spent suckling and to the frequency of nursing bouts, but positively related to survival. Food-restricted fawns had twice as many suckling solicitations and rejected suckling attempts as control fawns. Solicitations for allosuckling and successful allosuckling bouts were also more than twice as high in the food-restricted group as in the control group. Mothers and fawns from the food-restricted group spent more time foraging than control individuals. We conclude that a reduction in food availability during summer, which may occur under high intraspecific competition, should lead to drastic changes in foraging and nursing behaviours as well as reduced growth rate of juveniles of large northern herbivores.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: foraging; growth rates; intraspecific competition; maternal care; nursing; *Odocoileus virginianus*; white-tailed deer

Lactation is the most energetically demanding component of maternal care in mammals and can negatively affect growth, reproduction and survival of mothers (Martin 1984; Oftedal 1985; Stearns 1992). Body condition is affected by the high energy needs of lactation (Rogowitz 1996; Carlini et al. 2004), and fitness costs of lactation, including reduced fecundity after successfully weaning an offspring, have been recorded in many species (Clutton-Brock et al. 1989; Arnbom et al. 1997; Schulman & White 1997; Festa-Bianchet et al. 1998).

For northern temperate herbivores, lactation occurs in summer when resource availability is high. At high population density, however, resource availability per individual decreases sharply because of competition (Côté et al. 2004) and resources may no longer be sufficient to cope with the high energy needs of lactation, growth and replenishment of body reserves. Female ungulates should then adopt a conservative strategy, ensuring their own future reproduction and survival by decreasing the allocation of resources to current reproduction (Festa-Bianchet & Jorgenson 1998), as expected by parental investment theory (Trivers 1974). This trade-off in energy allocation could be expressed through changes in behaviour (Dall & Boyd 2004). For example, females may decrease nursing activities

Correspondence and present address: S. D. Côté, Département de Biologie and Centre d'études nordiques, Université Laval, Québec, QC G1K 7P4, Canada (email: steeve.cote@bio.ulaval.ca). M. F. Bianchet is now at Département de Biologie, Université de Sherbrooke, 2500 boul. de l'Université, Sherbrooke, QC J1K 2R1, Canada. J. P. Ouellet is now at Département de Biologie and Centre d'études nordiques, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

and increase time spent foraging (Clutton-Brock et al. 1982) when resources decrease.

Before weaning, defined as when the rate of milk transfer drops most sharply (Martin 1984), milk is nearly the sole source of nutrients for young mammals and its quantity and quality may have strong impacts on life history traits such as growth, survival and age at first reproduction (Loudon 1985; Sams et al. 1996; Mellish et al. 1999; Hofer & East 2003). As both milk quality and quantity seem to vary according to nutritional plane in cervids (Landete-Castillejos et al. 2003), estimates of milk transfer could provide information on energy allocation to current reproduction. Milking studies can directly assess milk transfer, but involve tremendous disturbance of animals while providing highly variable results (Arman et al. 1974; Garcia et al. 1999; Gjøstein et al. 2004).

Early studies on nursing behaviour proposed that total time spent suckling could be an index of milk transfer (Martin 1984; Gauthier & Barrette 1985; Lavigueur & Barrette 1992), but recent observations suggest that the correlation between time spent suckling and total milk transfer is very weak or nonexistent (Mendl & Paul 1989; Bigersson & Ekvall 1994; Cameron 1998). On the other hand, the rate at which offspring solicit their mothers for suckling and the rate of rejected attempts by the mother could provide information on offspring hunger and motivation, but also on the mother's willingness to nurse (Green et al. 1993). During nursing, young ungulates often use their head to butt at the udder to induce milk release (Lidfors et al. 1994; Haley et al. 1998) and the occurrence of butting could also potentially measure hunger or milk abundance in the udder.

Finally, allosuckling, which occurs when a young obtains milk from a female other than its mother, is frequent in captive ungulates, and allosucklers can obtain extra milk (Packer et al. 1992) that could supplement an inadequate supply of maternal milk (Víchová & Bartoš 2005). The frequency of allosuckling attempts, therefore, should be higher for animals under a low plane of nutrition than for animals with access to abundant resources.

Here we examined behavioural trade-offs in resource allocation to maintenance and maternal care in relation to resource availability in white-tailed deer, *Odocoileus virginianus*. We manipulated food availability to measure how a low plane of summer nutrition, similar to that encountered by deer at high population density, affected maternal and fawn behaviours during lactation, when fawns have high energy needs for growth and survival. We hypothesized that adult females facing low resource availability in summer would diminish maternal care. We predicted that total time spent nursing would be lower for food-restricted mothers than for mothers fed ad libitum and that the numbers of solicitations and rejected suckling attempts would be higher for fawns of food-restricted mothers than for fawns of control females. Finally, we predicted that allosuckling would be more frequent in the food-restricted group and that mothers and fawns would increase foraging activities compared with individuals fed ad libitum to compensate for low food abundance.

METHODS

Animals and Study Site

In September 2003, 18 prime-aged (3–8 years) female white-tailed deer were introduced in a 3-ha enclosure in Saint-Valérien, southeastern Québec, Canada. Females originated from a semicaptive population that had varied between 40 and 60 animals since 1990 and were marked as fawns. In early May 2004 and 2005, females were separated into two groups of nine in two 1-ha enclosures, where they gave birth. Both groups had similar average mass (food restricted = 53.9 ± 3.7 kg, controls = 53.9 ± 7.5 kg; $t_{1,18} = 0.00$, $P = 1.00$) and age (food restricted = 4.8 ± 1.8 years old, controls = 4.6 ± 1.7 years old; $t_{1,18} = 0.27$, $P = 0.79$). Food restriction started on 22 May in 2004 and 26 May in 2005 and the first birth was on 29 May in 2004 and 28 May in 2005. Individual females were assigned to the same treatment group in both summers.

To isolate the effects of summer nutrition from winter conditions, we regrouped all deer together in late October of both years and provided ad libitum wheat, oat, barley and hay overwinter. In summer, we fed deer with commercial wheat, oat and barley (1:1:1) in six feeding troughs in each enclosure. Each trough had a roof to protect the food from rain. We provided hay ad libitum and water in tanks. Because food limitation is the most likely mechanism through which density-dependent effects operate (Sand et al. 1996), we restricted the amount of wheat, oat and barley in the diet to simulate intraspecific competition generated by high population density. The control group received food ad libitum. The food-restricted group received 75% of the quantity consumed by the control group until mid-August and 80% after mid-August the first summer, and 80% during the whole summer the second year (see Ethical note). We weighed daily the food consumed by the control group (quantity given: leftovers 24 h later) taking into account food wastage (only about 30–50 g/day). An additional trough in each enclosure allowed access to fawns only to prevent adults from monopolizing all feeders. For ethical reasons and to isolate the maternal effect of food availability on resource allocation, food was always available for fawns in those feeders.

During the parturition period, two observers conducted behavioural observations daily to determine the exact birth date of each fawn and to mark and weigh all newborns within 3 days of age (most at 2 days). All deer were individually marked with plastic eartags. We attempted to weigh fawns daily (to the nearest 0.1 kg), but we obtained on average one body mass measurement per fawn every 6.1 days to compute individual growth rates. We used two electronic platform scales (Weigh-Tronix, Fairmont, MN, U.S.A.) whose remote controls were installed in an elevated blind from where we also conducted behavioural observations. Fawns started to use the scales at about 1 month of age. Scales were baited with wheat, oat and barley that were part of the daily measured ration for each group. Fawns remained with their mothers until the end of October of each year.

During the rutting seasons of 2003 and 2004 (November through early December), we allowed all females to breed

with only two males: a large adult, 3.5 years old in 2003 and 4.5 years old in 2004, and a different yearling male each year. We used two males in case the large one would be sterile or unable to mate all females. We extracted DNA from ear punches of all deer and conducted parental assignment analyses using the protocols of Anderson et al. (2002) and DeYoung et al. (2003). We used four microsatellite loci (BM4208, BM6438, INRA 011 and OarFCB 193, with four to seven alleles per locus) to perform the analyses and we confirmed all maternities. Thirty-four of 42 fawns could be assigned to a father; the remaining eight fawns could not be assigned because of the low heterozygosity of the loci. Thirty-three of 34 fawns were fathered by the large male. We repeated all analyses using only fawns sired by the large male, and found very similar results to the complete data set. We therefore considered paternal effects to be negligible and pooled all fawns in the analyses.

Behavioural Observations

We observed simultaneously all mothers and their fawns within both enclosures using 8×42 binoculars. Two observers recorded all nursing attempts and nursing bouts for periods of 6–8 h a day, covering all daylight hours. We began observations within a week of birth (late May or early June) and ended them at the approximate age of behavioural weaning (i.e. 80 days; Gauthier & Barrette 1985). Both groups were observed for 272 h during 34 days in 2004 and 258 h during 43 days in 2005. We recorded total time spent suckling with stop watches and the number of butts during each suckling bout, and later computed hourly rates. Suckling bouts were considered effective when nipple contact lasted at least 3 s. Each time a fawn touched a teat with his mouth we counted a suckling attempt and each time a female walked away or prevented a suckle we counted a rejected suckling attempt. Suckling solicitations were computed as the sum of suckling bouts initiated by the fawn and of rejected suckling attempts. We recorded each animal's identity at every nursing activity and since all animals were marked and the mother–fawn relationships were known, we were able to measure allosuckling accurately. All information was recorded continuously on a tape recorder and transcribed later.

We measured time spent at the feeders for every fawn with stop watches (± 1 s) during periods of observations of 6–8 h, and computed hourly rates. For mothers, we evaluated time spent foraging (either at the feeders or on hay or plants in the enclosure) using scan sampling (Altmann 1974), recording the instantaneous behaviour of every animal at 10-min intervals. We used a different procedure to estimate the foraging time of adult females compared with fawns because food-restricted adults ate their daily ration completely within a few hours and foraged on natural plants everywhere in the enclosure, while control adults had food in their feeders at all times.

Analyses

Physiological weaning occurs at approximately 30 days of age in white-tailed deer (Gauthier & Barrette 1985) and

we observed a sharp decline in time spent suckling after that age (Fig. 1). Nursing occurred until about 80 days of age but was much less frequent after 30 days. Therefore, we separated lactation into two periods according to fawn age (0–30 and 30–80 days) and computed a mean value for every mother and fawn during each period for total suckling time per hour (in s), suckling bouts per hour, mean duration of suckling bouts, rejected attempts per hour, suckling solicitations per hour and butts per suckling minute. We averaged the 2 years of data for each female to ensure that each female contributed only once to the data set. We compared mean values of suckling behaviour using two-way analyses of variance with groups (control and food restricted) and periods (0–30 and 30–80 days since parturition) as independent variables. We restricted the analyses to 32 fawns that survived at least 3 days (7 of the 10 fawns that died within 3 days were from the control group). Data were tested for normality and homogeneity of variances prior to analyses.

We correlated the mean values of all nursing parameters with the average growth rate of all fawns of a given mother from birth to 80 days of age using Pearson's correlations. We did not detect any bias in the sex ratio of fawns from the two groups during either year (M:F 2004: food restricted = 0.33, control = 3.50; 2005: food
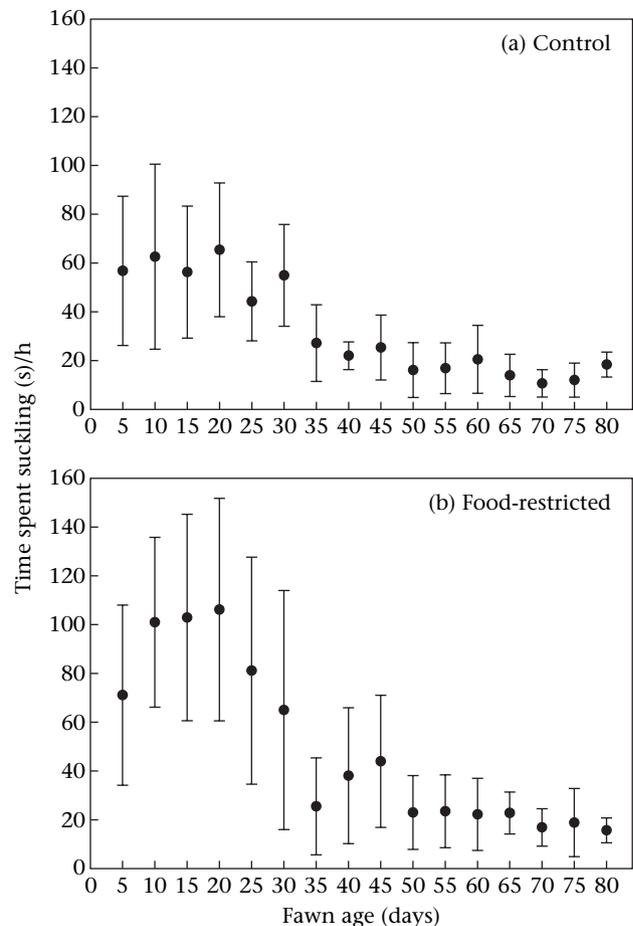

Figure 1. Time spent suckling by white-tailed deer fawns in relation to age. Note the sharp decrease after 30 days of age for both control and food-restricted groups. The 2 years of the study were pooled.

restricted $= 0.57$, control $= 0.29$; all P values > 0.05). Because we did not observe any difference in growth according to sex before 80 days of age (females $= 0.12 \pm 0.03$ kg/day, males $= 0.14 \pm 0.03$ kg/day; Therrien 2006), we pooled all fawns in the analyses. Time spent foraging was compared between groups for adult females and fawns separately using generalized linear mixed models with individual's ID as a random factor and age of the fawn in days as an independent variable. All fawns that survived to 3 days of age were singletons except two pairs (4/32). Because data for twins are not independent, we removed the slowest growing fawn of each of the two twin litters from all analyses since the growth rate of the fastest growing fawn was more similar to that of single fawns. The 2 years of the study were pooled since no significant year effects were detected. All analyses were performed using SAS statistical software (SAS Institute 9.1.3, Cary, NC, U.S.A.) and results are presented as means ± standard error.

Ethical Note

There is no quantitative information in the literature on tolerance of food deprivation in wild deer in summer. In 2003, we ran a pilot project and deprived four females of about 35% of their ration. These females were in poor condition over the summer but recovered quickly in the autumn after returning to ad libitum feeding. All five of their fawns (which we did not weigh) survived. We therefore did not foresee that a reduction of 25% in high-quality forage for females would affect fawn survival. Fawns had unlimited access to high-quality forage (which they began consuming at about 3 weeks of age) and all deer had unlimited access to hay. Fawn mortalities occurred in both control and food-restricted groups ($N = 9$ and $N = 17$, respectively). Over the 2 years, 10 fawns died within 3 days of birth (seven in the control group and three in the food-restricted group). An additional 14 fawns from the food-restricted group and two from the control group died over the summer at >16 days of age. Carcasses were examined, but we were unable to effectively discriminate if these deaths were caused by disease, starvation, or both. We altered the treatment in mid-August the first year (20% restriction) to reduce fawn mortalities. We weighed fawns as often as possible through the remote-control scales to avoid imposing additional stress on the deer with recapture. All procedures were in accordance with the Animal Care and Use Committee of Université du Québec à Rimouski, Canada (CPA16-03-08).

Table 1. Nursing behaviour of control and food-restricted white-tailed deer fawns during the first month of lactation (0−30 days) and the next 50 days (30−80 days) when fawns nursed from their mother and from other adult females (allosuckling)

	Control	Food restricted			
	$\overline{X} \pm$ SE	$\overline{X} \pm$ SE	df	F	P
Own mother					
0−30 days					
Time spent suckling (s)/hour	42±7	87±6	1,14	22.73	<0.001
Suckling bouts/hour	0.5±0.1	1.2±0.1	1,14	33.61	<0.001
Solicitations*/hour	1.1±0.2	2.4±0.2	1,14	21.78	<0.001
Rejected suckling attempts/hour	0.7±0.1	1.5±0.1	1,14	18.68	<0.001
Mean duration of suckling bouts (s)	96±9	85±7	1,14	0.88	0.37
Number of butts in the udder/suckling minute	0.6±0.4	1.6±0.4	1,14	2.61	0.13
30−80 days					
Time spent suckling (s)/hour	15±5	31±3	1,11	7.21	0.02
Suckling bouts/hour	0.4±0.1	0.7±0.1	1,11	8.95	0.01
Solicitations*/hour	1.0±0.4	2.5±0.3	1,11	11.91	0.01
Rejected suckling attempts/hour	0.6±0.3	1.8±0.2	1,11	11.19	0.01
Mean duration of suckling bouts (s)	44±3	44±2	1,11	0.00	0.98
Number of butts in the udder/suckling minute	3.4±1.1	1.4±1.2	1,11	1.47	0.26
Allosuckling					
0−30 days					
Time spent suckling (s)/hour	7±7	39±5	1,30	13.08	0.001
Suckling bouts/hour	0.1±0.1	0.6±0.7	1,30	13.53	<0.001
Solicitations*/hour	0.5±0.3	1.5±0.2	1,30	7.41	0.01
Rejected suckling attempts/hour	0.4±0.2	1.1±0.7	1,30	5.26	0.03
Mean duration of suckling bouts (s)	27±5	40±10	1,30	1.81	0.33
Number of butts in the udder/suckling minute	0.8±1.1	1.8±0.6	1,30	0.65	0.43
30−80 days					
Time spent suckling (s)/hour	6±2	15±2	1,23	8.42	0.01
Suckling bouts/hour	0.1±0.1	0.4±0.2	1,23	11.70	<0.01
Solicitations*/hour	0.4±0.3	1.5±0.2	1,23	11.87	<0.01
Rejected suckling attempts/hour	0.2±0.2	1.1±0.2	1,23	11.34	<0.01
Mean duration of suckling bouts (s)	31±6	30±4	1,23	0.06	0.82
Number of butts in the udder/suckling minute	2.4±0.8	2.7±0.5	1,23	0.12	0.74

*The number of effective suckling bouts initiated by the fawn plus the number of rejected attempts.

Table 2. Correlations between growth rate of white-tailed deer fawns from 0 to 80 days of age and their suckling behaviour during their first month of life (0−30 days) and the next 50 days (30−80 days)

	Fawn age			
	0−30 days		30−80 days	
	Pearson	P	Pearson	P
Time spent suckling (s)/h	−0.54	0.03	−0.26	0.36
Suckling bouts/h	−0.44	0.09	−0.33	0.25
Solicitations*/h	−0.40	0.12	−0.33	0.25
Rejected suckling attempts/h	−0.38	0.14	−0.032	0.26
Mean duration of suckling bouts (s)	−0.13	0.50	0.01	0.96
Number of butts in the udder/suckling minute	0.01	0.96	0.23	0.30

Correlations shown are for pooled fawns from control and food-restricted groups.
*The number of effective suckling bouts initiated by the fawn plus the number of rejected attempts.

RESULTS

Nursing Behaviour

Total suckling time was twice as high in the food-restricted group as in the control group during both the 0- to 30-day and the 30- to 80-day periods (Table 1). Similarly, suckling frequency was twice as high in the food-restricted group as in the control group during both periods (Table 1). As expected, the number of rejected suckling attempts and the number of solicitations were twice as high in the food-restricted group as in the control group for both periods (Table 1). The mean duration of suckling bouts and the number of butts per suckling bout did not differ between treatments (Table 1).

A very similar pattern occurred for allosuckling, as total time spent suckling, suckling frequency, number of rejected attempts and number of solicitations were all higher in the food-restricted group than in the control group, especially during the first month of life (Table 1). Mean duration of allosuckling bouts and the number of butts did not differ between treatments (Table 1).

Growth of Fawns

Total time spent suckling between 0 and 30 days of age was inversely correlated with growth rate of fawns (Table 2, Fig. 2). Moreover, we observed nearly significant negative correlations between suckling frequency, number of solicitations and rejected attempts, and fawn growth rate (Table 2, Fig. 2). When analysing the groups separately, however, we found no correlation between the growth rate of fawns and any nursing behaviours, indicating a clear effect of treatment on growth rate (Therrien 2006). Moreover, surviving fawns had higher growth rates than fawns that died (0.13 ± 0.01 versus 0.07 ± 0.01 kg/day, $t_{1,32} = -4.96$, $P < 0.001$).

Time Spent Foraging

Food-restricted mothers spent 21% more time foraging than control mothers (9:34 and 7:56 h/day, respectively; Table 3, Fig. 3a). Time spent foraging remained constant throughout summer (Table 3, Fig. 3a). Time spent at the feeders by fawns was independent of sex, increased with age in both groups, and was on average 24 min/day longer for fawns in the food-restricted group than for those in the control group (Table 3, Fig. 3b).

DISCUSSION

Fawns from the food-restricted group spent more time suckling and soliciting suckling from their mothers than control fawns, suggesting that they tried harder to obtain milk. Despite these efforts, fawns of food-restricted mothers grew at a slower rate than control fawns (Therrien 2006). Many earlier studies of lactation have assumed that time spent suckling is proportional to milk consumption and could be a measure of maternal resource allocation (Gauthier & Barrette 1985; Lavigueur & Barrette 1992), but other studies since have shown that time spent suckling is not a reliable measure of milk intake (Birgersson & Ekvall 1994; Cameron 1998; Cameron et al. 1999).

Our study confirms that mean duration of suckling is not a good indicator of milk transfer or hunger as it did not vary according to nutritional plane and was not correlated with growth rates. Moreover, the number of butts while suckling did not seem to reflect the level of hunger of fawns nor milk flow, as it did not differ between treatments and was not correlated with growth rate, contrary to previous studies (Haley et al. 1998; but see Cameron et al. 1999). Our study agrees, however, with Mendl & Paul (1989), who showed that time spent suckling and suckling frequency are not good indicators of milk transfer, but represent a behavioural indication that milk transfer is insufficient. Even though fawns tried harder to obtain milk in the food-restricted group, they did not receive enough, and suffered higher mortality and reduced growth compared with control fawns (Therrien 2006).

The number of solicitations and rejected suckling attempts were also good predictors of hunger in early lactation because fawns from the food-restricted group, which had lower growth rates, had much higher values than control fawns for both parameters. The correlations between growth rate and nursing behaviours were generated by the treatment, that is, there was no correlation between growth rate and nursing behaviour within groups. The relationships were due to the lower growth rate of food-restricted fawns compared with control fawns (Therrien 2006).

Allosuckling was very frequent in our experiment, probably because of captive conditions (Packer et al. 1992). Nevertheless, it was much higher in the food-restricted group than in the control group. Our results support the hypothesis of Víchová & Bartoš (2005) that fawns suckle alien mothers to compensate for milk
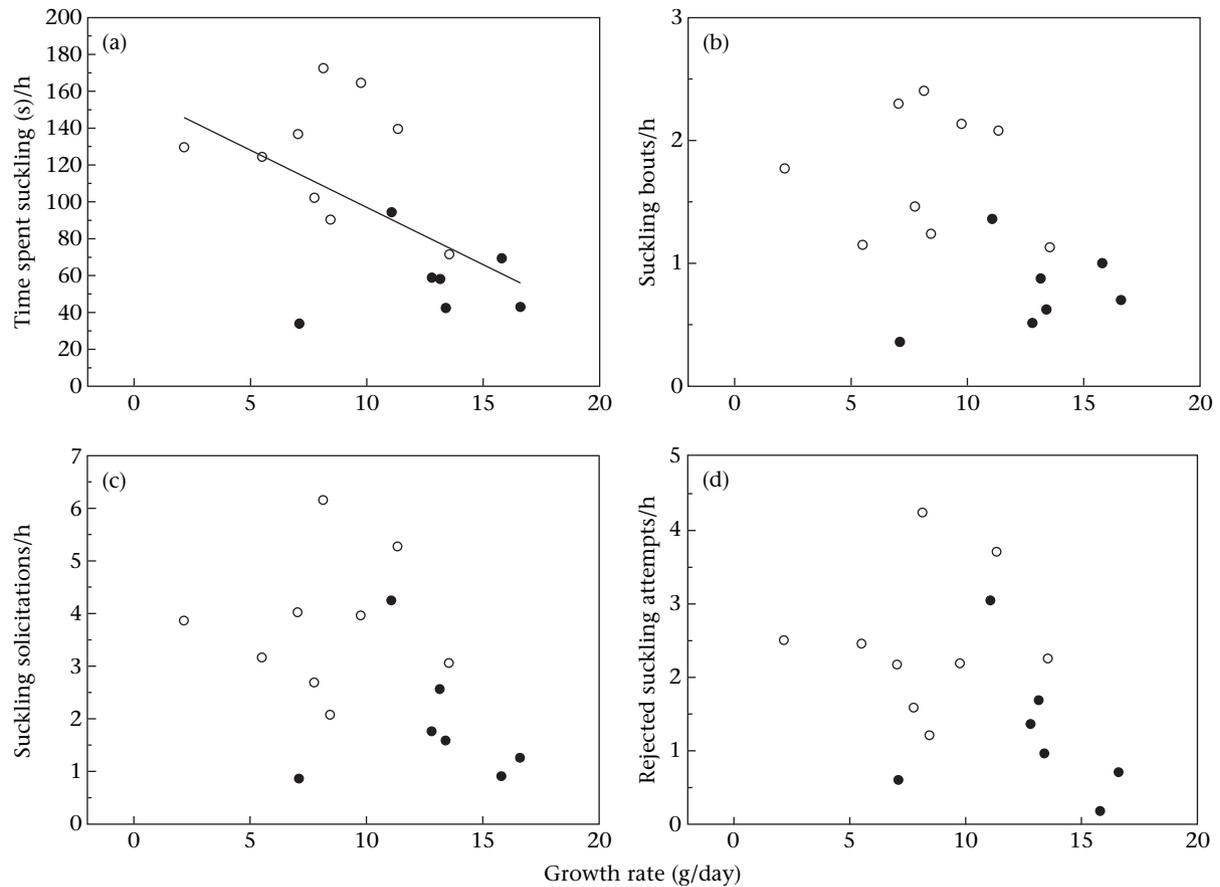
Figure 2. Correlations between growth rate of control (●) and food-restricted (○) white-tailed deer fawns from 0 to 80 days of age and their suckling behaviour during their first month of life (0–30 days); (a) time spent suckling per hour, (b) suckling bouts per hour, (c) suckling solicitations per hour and (d) rejected suckling attempts per hour.

Table 3. Factors affecting time spent foraging by mothers (from parturition to 80 days after fawn birth) and by fawns (from 30 to 80 days of age) in control and food-restricted groups of white-tailed deer

|	GLMM	β	SE	df	t	P
Mothers						
Intercept		20.60	1.19	1,15	17.28	<0.0001
Day		−0.02	0.02	1,15	−0.98	0.34
Group	Food restricted	4.13	1.23	1,15	3.37	<0.01
	Control					
Group*day	Food restricted	−0.01	0.04	1,15	−0.33	0.74
	Control					
Fawns						
Intercept		−0.88	0.63	1,12	−1.40	0.21
Day		0.04	0.01	1,12	3.78	<0.01
Group	Food restricted	1.06	0.40	1,12	2.67	0.02
	Control					
Group*day	Food restricted	0.00	0.00	1,12	−1.23	0.22
	Control					
Sex	Female	3.14	2.23	1,12	1.41	0.18
	Male					
Sex*day	Female	−0.04	0.04	1,12	−0.95	0.36
	Male					

GLMM, Generalized Linear Mixed Model.
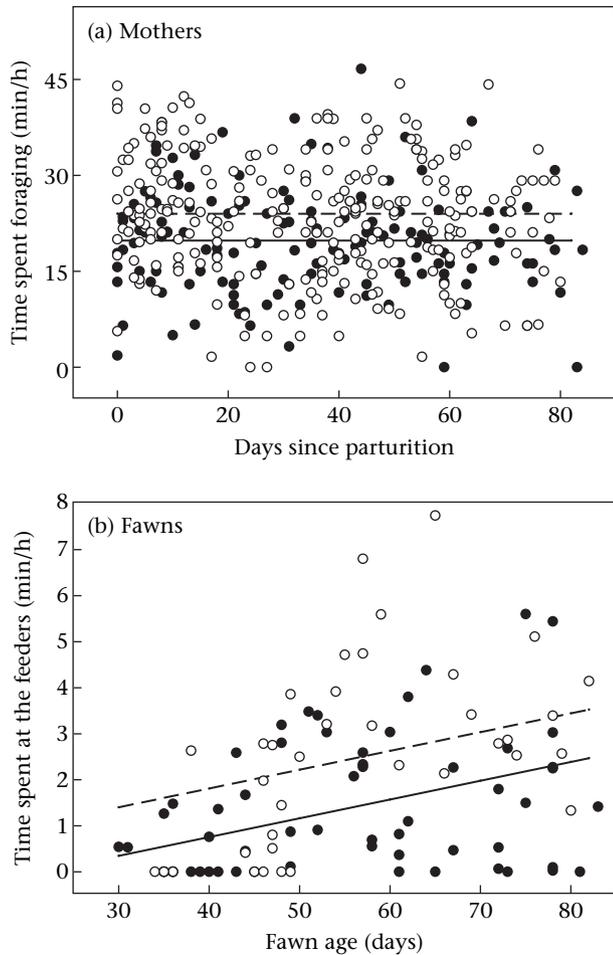
Figure 3. Time spent foraging by control (●, —) and food-restricted (○, − −) white-tailed deer (a) mothers from parturition to 80 days after fawn birth and (b) fawns from 30 to 80 days of age.

deficiency, and therefore that maternal allocation in the food-restricted group was insufficient.

The most striking differences in lactation behaviours between the two groups appeared in the first month of life, that is, before physiological weaning (Gauthier & Barrette 1985). This period is the most critical for lactation as fawns then rely almost entirely on maternal milk for resource acquisition (Martin 1984). After the first month, differences between the treatments in suckling frequency and total suckling time decreased, probably because all mothers reduced their energy allocation to milk production and continued the weaning process (Lavigueur & Barrette 1992). Even though milk is no longer the sole nutritive source after 30 days of age, food-restricted fawns still solicited their mothers and were rejected more often than control fawns, suggesting that they still needed maternal resources to meet their growth and maintenance requirements and to compensate for the low availability of milk early in life.

Mothers adjusted their foraging behaviour to cope with the reduced abundance of resources and increased daily time spent foraging in the food-restricted group.

Fawns in the food-restricted group also tried to compensate for food shortage by increasing time spent feeding, as observed in red deer (Clutton-Brock et al. 1982) and white-tailed deer in winter (Taillon et al. 2006). The energy needed to extract a similar amount of resources from a given habitat increases when resources are scarce and, under natural conditions, these changes in foraging behaviour may negatively affect survival and growth. For example, the energy expenses of foraging cannot be invested in growth or other development functions (Thompson et al. 1973). Moreover, mothers in natural conditions that spend more time foraging and less time in close proximity to their fawns are less vigilant and may be less likely to detect potential predators of their offspring (Fitzgibbon 1990; Lima & Dill 1990). Finally, active fawns also increase their detectability and vulnerability to predation (Fitzgibbon 1990; Lingle et al. 2005).

Winter is thought to be critical for temperate northern herbivores because of possible climatic stress or malnutrition (Moen 1976; Clutton-Brock et al. 1985), but our experimental data provide evidence that summer may also act as a limiting factor for individuals. Intraspecific competition for limited resources, generated by high population density or by density-independent processes such as drought, can be high during summer, and the substantial energy needs of lactation and recovery from winter mass loss can force individuals to adjust their behaviour to cope with reduced food availability. A shortage of resources in summer appeared to lead to parent–offspring conflicts (Trivers 1974): fawn behaviour suggested that they were lacking resources, while the behaviour of mothers suggested a trade-off between caring for the current offspring and ensuring future survival and reproduction. Increased intraspecific competition in summer could limit survival and reproduction in populations that are no longer limited by predation.

Our results suggest that behavioural measurements of nursing and foraging are useful to assess the amount of maternal care in current offspring. Fawns that suckled, solicited or were rejected the most often were also those that had lower growth rates, as observed in mice and cats (Mendl & Paul 1989). Fawns with low growth rates also experienced reduced survival. Worldwide, densities of many species of ungulates are increasing (Côté et al. 2004). We showed that when resources were scarce, mothers and fawns adjusted their foraging and lactating behaviours. A decrease of only 20% in resource availability during summer can lead to drastic changes in behaviour and life history traits, such as growth rate of juveniles of large northern herbivores.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.

Anderson, J. D., Honeycutt, R. L., Gonzales, R. A., Gee, K. L., Skow, L. C., Gallagher, R. L., Honeycutt, D. A. & DeYoung, R. W. 2002. Development of microsatellite DNA markers for the automated genetic characterization of white-tailed deer populations. *Journal of Wildlife Management*, **66**, 67–74.

Arman, P., Kay, R. N. B., Goodall, E. D. & Sharman, G. A. M. 1974. Composition and yield of milk from captive red deer (*Cervus elaphus*). *Journal of Reproduction and Fertility*, **37**, 67–84.

Arnbom, T., Fedak, M. A. & Boyd, I. L. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology*, **78**, 471–483.

Birgersson, B. & Ekvall, K. 1994. Suckling time and fawn growth in fallow deer (*Dama dama*). *Journal of Zoology*, **232**, 641–650.

Cameron, E. Z. 1998. Is suckling behaviour a useful predictor of milk intake? A review. *Animal Behaviour*, **56**, 521–532.

Cameron, E. Z., Stafford, K. J., Linklater, W. L. & Veltman, C. J. 1999. Suckling behaviour does not measure milk intake in horses, *Equus caballus*. *Animal Behaviour*, **57**, 673–678.

Carlini, A., Marquez, M., Panarello, H., Ramdohr, S., Daneri, G., Bornemann, H. & Plotz, J. 2004. Lactation costs in southern elephant seals at King George Island, South Shetland Islands. *Polar Biology*, **27**, 266–276.

Clutton-Brock, T. H., Iason, G. R., Albon, S. D. & Guinness, F. E. 1982. Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. *Journal of Zoology*, **198**, 227–236.

Clutton-Brock, T. H., Major, M. & Guinness, F. E. 1985. Population regulation in male and female red deer. *Journal Animal Ecology*, **54**, 831–846.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature*, **337**, 260–262.

Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C. & Waller, D. M. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution and Systematics*, **35**, 113–147.

Dall, S. R. X. & Boyd, I. L. 2004. Evolution of mammals: lactation helps mothers to cope with unreliable food supplies. *Proceedings of the Royal Society of London, Series B*, **271**, 2049–2057.

DeYoung, R. W., Demarais, S., Honeycutt, R. L., Gonzales, R. A., Gee, K. L. & Anderson, J. D. 2003. Evaluation of a DNA microsatellite panel useful for genetic exclusion studies in white-tailed deer. *Wildlife Society Bulletin*, **31**, 220–232.

Festa-Bianchet, M. & Jorgenson, J. T. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology*, **9**, 144–150.

Festa-Bianchet, M., Gaillard, J. M. & Jorgenson, J. T. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist*, **152**, 367–379.

Fitzgibbon, C. D. 1990. Anti-predator strategies of immature Thomson's gazelles: hiding and the prone response. *Animal Behaviour*, **40**, 846–855.

Garcia, A., Landete-Castillejos, T., Molina, A., Albinana, B., Fernandez, C., Garde, J. & Gallego, L. 1999. Lactation curves in captive Iberian red deer (*Cervus elaphus hispanicus*). *Journal of Animal Science*, **77**, 3150–3155.

Gauthier, D. & Barrette, C. 1985. Suckling and weaning in captive white-tailed and fallow deer. *Behaviour*, **94**, 128–149.

Gjøstein, H., Holand, Ø. & Weladji, R. B. 2004. Milk production and composition in reindeer (*Rangifer tarandus*): effect of lactational stage. *Comparative Biochemistry and Physiology A*, **137**, 649–656.

Green, W. C. H., Rothstein, A. & Griswold, J. G. 1993. Weaning and parent–offspring conflict: variation relative to interbirth interval in bison. *Ethology*, **95**, 105–125.

Haley, D. B., Rushen, J., Duncan, I. J. H., Widowski, T. M. & De Passillé, A. M. 1998. Butting by calves, *Bos taurus*, and rate of milk flow. *Animal Behaviour*, **56**, 1545–1551.

Hofer, H. & East, M. L. 2003. Behavioral processes and costs of coexistence in female spotted hyenas: a life history perspective. *Evolutionary Ecology*, **17**, 315–331.

Landete-Castillejos, T., Garcia, A., Gomez, J. A. & Gallego, L. 2003. Lactation under food constraints in Iberian red deer *Cervus elaphus hispanicus*. *Wildlife Biology*, **9**, 131–139.

Lavigueur, L. & Barrette, C. 1992. Suckling, weaning, and growth in captive woodland caribou. *Canadian Journal of Zoology*, **70**, 1753–1766.

Lidfors, L. M., Jensen, P. & Algers, B. 1994. Suckling in free-ranging beef-cattle: temporal patterning of suckling bouts and effects of age and sex. *Ethology*, **98**, 321–332.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Lingle, S., Pellis, S. M. & Wilson, W. F. 2005. Interspecific variation in antipredator behaviour leads to differential vulnerability of mule deer and white-tailed deer fawns early in life. *Journal of Animal Ecology*, **74**, 1140–1149.

Loudon, A. S. I. 1985. Lactation and neonatal survival of mammals. *Symposia of the Zoological Society of London*, **54**, 183–207.

Martin, P. 1984. The meaning of weaning. *Animal Behaviour*, **32**, 1257–1259.

Mellish, J. E., Iverson, S. J. & Bowen, W. D. 1999. Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology*, **72**, 677–690.

Mendl, M. & Paul, E. S. 1989. Observation of nursing and sucking behavior as an indicator of milk transfer and parental investment. *Animal Behaviour*, **37**, 513–515.

Moen, A. N. 1976. Energy conservation by white-tailed deer in the winter. *Ecology*, **57**, 192–198.

Oftedal, O. T. 1985. Pregnancy and lactation. In: *Bioenergetics of Wild Herbivores* (Ed. by R. J. Hudson & R. G. White), pp. 215–238. Boca Raton, Florida: CRC Press.

Packer, C., Lewis, S. & Pusey, A. 1992. A comparative analysis of non-offspring nursing. *Animal Behaviour*, **43**, 265–281.

Rogowitz, G. L. 1996. Trade-offs in energy allocation during lactation. *American Zoologist*, **36**, 197–204.

Sams, M. G., Lochmiller, R. L., Qualls, J. C. W., Leslie, D. M. & Payton, M. E. 1996. Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer. *Journal of Mammalogy*, **77**, 179–190.

Sand, H., Bergström, R., Cederlund, G., Östergen, M. & Stalfelt, F. 1996. Density-dependent variation in reproduction and body mass in female moose *Alces alces*. *Wildlife Biology*, **2**, 233–245.

Schulman, A. B. & White, R. G. 1997. Nursing behaviour as a predictor of alternate-year reproduction in muskoxen. *Rangifer*, **17**, 31–35.

Stearns, S. C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.

Taillon, J., Sauvé, D. G. & Côté, S. D. 2006. The effects of decreasing winter diet quality on foraging behavior and life-history traits of white-tailed deer fawns. *Journal of Wildlife Management*, **70**, 1445–1454.

Therrien, J.-F. 2006. Allocation des ressources maternelles en fonction de la compétition intraspécifique chez le cerf de Virginie. M.Sc. thesis, Université Laval.

Thompson, C. B., Holter, J. B., Hayes, H. H., Silver, H. & Urban, W. E., Jr. 1973. Nutrition of white-tailed deer. 1. Energy requirements of fawns. *Journal of Wildlife Management*, **37**, 301–311.

Trivers, R. L. 1974. Parent–offspring conflict. *American Zoologist*, **14**, 249–264.

Víchová, J. & Bartoš, L. 2005. Allosuckling in cattle: gain or compensation? *Applied Animal Behaviour Science*, **94**, 223–235.