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

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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.

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

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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