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Conservative maternal care in an iteroparous mammal: a resource allocation experiment

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Abstract When resources are limited, life history theory predicts a trade-off between growth, reproduction and survival. In summer, lactating females of temperate large herbivores such as the white-tailed deer (*Odocoileus virginianus*) normally have access to abundant forage but also face the high energetic needs of lactation and recovery from winter mass loss. At high population density, however, females may face a trade-off between allocating resources for maintenance and for reproduction. To simulate the effects of increased intra-specific competition at high density, we measured for 2 years how an experimental food restriction of approximately 20% affected current reproduction and body mass changes of adult females and their fawns during the fawning and lactation periods. Fawn survival decreased 35%, and fawn growth decreased 26% in the food-restricted treatment. There was no effect of food restriction on female mass. Irrespective of treatment, however, lactating females gained 30 g/day less than non-lactating females, and females that had weaned a fawn the previous year gained 20 g/day less than females that had not. We conclude that when resources were scarce, females adopted a conservative strategy favouring their own survival, mass recovery and future reproductive potential over their current reproduction, probably to maximise their lifetime reproductive success.

Keywords Maternal care · Growth · Reproduction · Body mass · White-tailed deer

Introduction

When resources are limited, the life history theory predicts an allocation trade-off in energy between growth, reproduction and survival, to maximise lifetime reproductive success (Stearns 1992). At high population density, intra-specific competition reduces the amount of resources available per capita, eventually affecting individual life histories and population demography (Fryxell et al. 1999; McCullough 1999). Given the high energetic costs of reproduction, particularly lactation, females of iteroparous mammals face a trade-off between current reproduction and the maintenance of body condition for future reproduction (Festa-Bianchet et al. 1998). Therefore, mothers should adopt a conservative strategy when resources are scarce, favouring their own survival over current maternal care to maximise lifetime reproductive success (Sæther 1993; Festa-Bianchet and Jorgenson 1998; Holand et al. 2006). Greater resource allocation in self than in offspring is expected for iteroparous animals such as ungulates where adults have a much higher survival probability than juveniles (Gaillard et al. 2000).

Growth and survival of offspring can be affected by both paternal and maternal characteristics, but in most ungulates,

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paternal contribution is only genetic. The amount of maternal care provided varies according to individual characteristics such as mass (Hewison and Gaillard 1999; Côté and Festa-Bianchet 2001a), past reproductive history (Rutberg 1986) and genotype. In many vertebrates, maternal mass appears to be a reliable indicator of stored energy that can be invested in reproduction (Doughty and Shine 1997; Côté and Festa-Bianchet 2001b). For example, growth rate and weaning mass in fallow deer (*Dama dama*) fawns are positively correlated with maternal mass (Birgersson and Ekvall 1997).

Growth and survival of young vertebrates could also be affected by birth mass, birth date and litter size. Birth mass is positively correlated with survival in many ungulates (Clutton-Brock et al. 1982; Thorne et al. 1976; Fairbanks 1993). In seasonal environments, early birth could result in higher phenotypic quality at the end of the maternal care period, as was observed in mountain goats (*Oreamnos americanus*; Côté and Festa-Bianchet 2001b) because early-born juveniles benefit from a longer growth period before winter. Litter size is also likely to influence the amount of care a given individual is going to receive because resources are partitioned among the offspring (McMahon and Hindell 2003).

Like many ungulates, white-tailed deer (*Odocoileus virginianus*) occur at high population density in much of their range and have strong negative impacts on forest understory, a situation that is increasingly frequent mainly owing to anthropological factors (Côté et al. 2004). As a consequence, there are fewer resources available per individual at high density (Russell et al. 2001; Côté et al. 2004). For temperate ungulates, resource availability is generally high in summer because of the seasonal vegetation growth, but females also face high energy needs for reproduction, growth and replenishment of body reserves at that time (Cook et al. 2004). Because winter is associated with cold weather and resources scarcity, the winter-carrying capacity of a habitat has long been thought to limit populations of temperate ungulates (Moen 1976; Clutton-Brock et al. 1985). Consequently, few studies (Crête and Huot 1993; Boucher et al. 2004; Cook et al. 2004) have considered whether the carrying capacity of summer habitat may instead limit individual and population productivity. As pointed out by Stewart et al. (2005), more emphasis should be placed on the role of spring and summer nutrition, when lactation and growth occur, on density-dependent processes such as maternal care and population regulation in large, northern herbivores.

Our main objective was to measure the effects of summer nutrition on maternal resource allocation in white-tailed deer. We hypothesised that adult females facing low resource availability in summer would favour their own maintenance by limiting the amount of care devoted to current reproduction, as predicted by Holand et al. (2006). We therefore predicted that food restriction would have a much stronger effect on the mass gain of fawns than of mothers.

Materials and methods

Animals and study site In September 2003, 18 adult female white-tailed deer were introduced in a 3-ha enclosure (3.5-m-high fence) in Saint-Valérien, southeastern Québec, Canada. Females originated from a semicaptive population that included between 40 and 60 animals since 1990 and were marked as fawns. In early May 2004 and 2005, females were separated in 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). Parturition date (food-restricted=3 June±1.1, controls=9 June±3.8) did not differ between groups in either year (2004: F=2.22, p=0.16; 2005: F=0.98, p=0.34) nor did fawn sex ratio (Therrien et al. 2007). Habitats inside the two enclosures were similar and included 60% open areas with grass and forbs and 40% forest. Deer had access to a 15-m² shelter in each enclosure. Three adult females from the control group died in early June 2004 for unknown reasons (not starvation but possibly a disease or postpartum complications) and were replaced in 2005. To isolate the effects of summer nutrition while holding winter conditions constant, we regrouped all deer together in late October and provided ad libitum wheat, oat, barley and hay over winter.

In summer, we fed deer with commercial wheat, oat and barley (1:1:1). Both groups were always provided with ad libitum hay and water and had access to the natural vegetation inside the enclosure. 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 treated group to mimic intra-specific competition generated by high population density. We performed a pilot study in summer 2003 and deprived four females of about 35% of their ration of wheat, oat and barley. These females were in poor condition over the summer but recovered quickly in the fall after returning to ad libitum feeding. All five of their fawns survived. Therefore, we reasoned that an experimental restriction of 25% of the total daily biomass of grains consumed by control deer (which received food ad libitum) should adequately simulate high density while preventing starvation (Landete-Castillejos

et al. 2002). However, because the survival rate of fawns in the experimental group was low in 2004 (Fig. 1), we only restricted food by 20% in 2005 to avoid fawn mortality. Our objective was to measure fawn growth, not survival, which we did not expect to be affected. Food consumption by the control group was measured at noon daily, and the quantity provided to the food-restricted group the following day was adjusted accordingly. Each adult female from the control group ate approximately 1.1 kg/day of wheat, oat and barley. We provided food in six (30×50 cm) feeding troughs per enclosure, to minimise dominance interactions at the troughs. We also placed a trough in each enclosure designed to allow access to fawns only where wheat, oat and barley were always available. This extra feeding trough was provided soon after birth, and fawns started using it at about 30 to 40 days of age.

Fawns were weaned in late August at around 80 days of age but remained with their mothers until the end of October. All deer were individually marked with plastic ear tags. We recorded individual body mass daily (to the nearest 0.1 kg) whenever possible using two electronic platform scales (Weigh-Tronix, Fairmont, MN) linked to remote controls (Bassano et al. 2003) installed in an elevated observation blind. Scales were baited with wheat, oat and barley that were part of the daily measured ration for each group. During the parturition period, two people observed the animals daily to determine the exact birth date of each fawn and to mark and weigh all newborns at about 2 days of age.

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

Fig. 2 Mean summer growth rate (from birth to weaning) of white-tailed deer fawns from control and food-restricted groups. The 2 years of the study (2004, 2005) were pooled, and *numbers in bars* represent sample sizes

to breed with two males: a large adult, 3.5 years old in 2003 and 4.5 years old in 2004, and a different yearling each year. We used two males in case that 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. 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 chosen loci. Thirty-three fawns out of 34 were fathered by the large male. We therefore considered paternal effects to be negligible and pooled all fawns in our analyses. All females reproduced each year, except one that never gave birth and one that had no fawn in 2005. We confirmed all maternities using the parental assignment protocol.

Statistical analyses

We compared fawn survival to weaning between the food-restricted and the control group using χ^2. We also compared fawn survival between the two groups using a mixed model for categorical dependent variables (GLIMMIX), with mother identification fitted as a random factor because 15 out of 18 females were observed in both years, and litter size, birth mass, birth date, fawn's sex and maternal mass as covariates. This procedure is similar to the generalised linear mixed model (GLMM) but fits a binary response (SAS Institute 2005). We compared summer mass of fawns between the two groups using a GLMM with fawn identification fitted as a random factor, day as the independent variable and maternal mass at parturition, birth date,
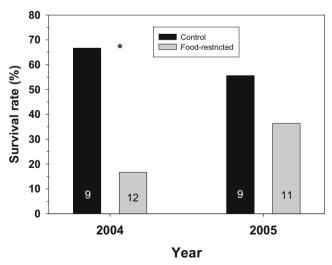

Fig. 1 Survival from birth to weaning of white-tailed deer fawns from control and food-restricted groups in 2004 and 2005. *Numbers in bars* represent sample sizes
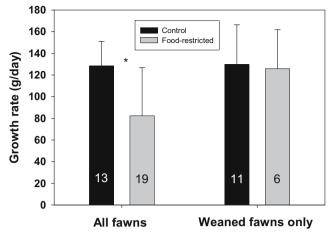
birth mass, litter size and fawn sex as covariates. We tested for differences in growth rate between treatments using the interaction treatment×day. Fawns that died before 3 days of age were excluded from analyses. We compared the summer mass of control and food-restricted adult females using a GLMM with day as the independent variable, female identification and year as random factors, and female reproductive state (lactating or non-lactating) and litter size (number of fawns that survived at least 3 days) as covariates. For all models, we used a stepwise backward procedure, starting with all covariates (and two- and three-way interactions) then removing non-significant terms until only significant terms were left. For the second year of the experiment, we added 'previous year weaning success of the mother' as a covariate and re-ran all the analyses to assess its

effect. All analyses were performed using SAS software (9.1.3). Results are presented as means±SE.

Results

Fawn survival Fawn survival was 35% higher in the control than in the food-restricted group (Fig. 1; 2004: $\chi^2=5.5$, $p=0.02$; 2005: $\chi^2=0.7$, $p=0.4$; years pooled: $\chi^2=5.1$, $p=0.02$). In addition to the treatment effect, we tested a number of covariates (litter size, birth mass, birth date, fawn sex, maternal mass and previous year weaning success of the mother) in a GLIMMIX design, but none affected survival rate (all p values>0.05, data not shown). No female from the food-restricted group weaned more

Table 1 Results from mixed model analyses testing the influence of a food–restriction experiment on mass of fawns and mass of adult females in semi-captive white-tailed deer during summers 2004 and 2005

GLMM		β	SE	df	t	p
(a) Mass of fawns (n=32)						
Intercept		3.55	0.28	1, 30	12.64	<0.001
Day		0.10	0.01	1, 31	10.90	<0.001
Treatment[a]	Control	0.42	0.46	1, 32	0.70	0.49
	Food-restricted	–	–	–	–	–
Treatment×day	Control	0.03	0.01	1, 32	2.02	0.05
	Food-restricted	–	–	–	–	–
Birth mass		1.54	0.33	1, 32	4.72	<0.001
Birth mass×day		0.02	0.01	1, 32	1.07	0.29
Fawn's sex	Male	0.26	0.42	1, 32	0.61	0.54
	Female					
Fawn's sex×day	Male	−0.03	0.02	1, 32	−1.90	0.08
	Female					
Litter size (>3 days)[b]		0.1	0.44	1, 32	0.22	0.83
Litter size (>3 days)×day		−0.01	0.02	1, 32	−0.39	0.70
Birth date		0.00	0.00	1, 32	−1.31	0.20
Birth date×day		0.00	0.00	1, 32	0.53	0.60
Maternal mass		0.07	0.05	1, 32	1.36	0.18
Maternal mass×day		0.00	0.00	1, 32	0.11	0.91
(b) Mass of adult females (n=18)						
Intercept		44.80	1.20	1, 26	37.27	<0.001
Day		0.05	0.01	1, 27	15.56	<0.001
Lactation status	Non-lactating	−2.40	0.42	1, 27	−5.69	<0.001
	Lactating	–	–	–	–	–
Lactation status×day	Non-lactating	0.03	0.01	1, 27	6.84	<0.001
	Lactating	–	–	–	–	–
Treatment[a]	Control	2.10	2.37	1, 17	0.89	0.38
	Food-restricted	–	–	–	–	–
Treatment×day	Control	0.01	0.00	1, 17	1.64	0.11
	Food-restricted	–	–	–	–	–
Litter size (>3 days)[b]		1.35	1.60	1, 27	0.84	0.41
litter size (>3 days)×day		0.00	0.01	1, 27	−0.71	0.48

Fawn sex, birth date, birth mass, litter size, maternal lactation status and maternal mass were considered as covariates.
[a] Refers to the difference between control and food-restricted groups
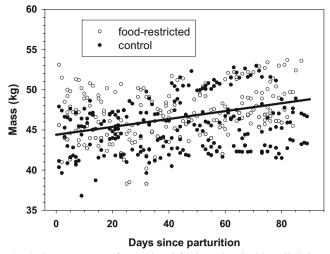[b] Refers to litter size for fawns that survived at least 3 days

than one fawn over the 2 years of study, whereas a female from the control group weaned twins in both years, and three others weaned at least one fawn in both years.

Fawn growth Fawn growth was 26% lower in the food-restricted than in the control group (Fig. 2) as the slope of mass with day varied significantly with treatment (Table 1a, interaction treatment×day, $p=0.05$). This difference, however, disappeared when only fawns that survived to weaning were considered ($n=17$; $t=0.06$, $p=0.95$; Fig. 2). Curvilinear or asymptotic curves did not provide a better fit to mass gain of fawns over summer. Birth mass, birth date, litter size, sex and maternal mass did not affect the growth rate of fawns, but fawns that were born relatively heavy remained heavy throughout summer (Table 1a). In the second year of the experiment, previous year weaning success of the mother did not affect fawn growth rate ($t=0.68$, $p=0.50$).

Female summer mass Control and food-restricted females gained mass at similar rates during summer (Fig 3; Table 1b). Females that were not lactating, however, gained an average of 30 g/day more than lactating ones in both groups (Table 1b). Litter size did not affect summer mass in females (Table 1b). In the second year of the experiment, females that had weaned a fawn the previous summer gained 20 g/day less than females that did not wean a fawn (interaction previous weaning success and day; $n=17$, $t=-2.68$, $p=0.02$).

Discussion

White-tailed deer fawn growth and survival decreased substantially in the food-restricted group. Food-restricted females, however, had similar summer mass gain as control females, suggesting no direct short-term negative effects of high intra-specific competition on body mass. Lactation entails high energy expenditures (Oftedal 1985), and lactating females gained mass at a slower rate than non-lactating ones during summer. This pattern has also been observed in elk (*Cervus elaphus*; Cook et al. 2004) and suggests that lactating females were not able to fully compensate for the high energetic costs of lactation during summer. Moreover, the observation that females that had weaned a fawn the previous year experienced lower mass gain compared to females that did not wean a fawn highlights possible long-term costs of previous reproduction. Our results suggest that as resource availability declined and intra-specific competition increased, maternal care decreased while maternal mass gain did not vary. White-tailed deer females seemed to value their own mass

Fig. 3 Summer mass of control and food-restricted white-tailed deer females in relation to days since parturition. The 2 years of the study (2004, 2005) were pooled

gain over that of their offspring, possibly to avoid compromising their future reproductive success, as documented for bighorn ewes (*Ovis canadensis*) facing high intra-specific competition (Festa-Bianchet and Jorgenson 1998). This strategy is likely to be selected in species where adult survival is high and stable, while juvenile survival is low and variable, so that mothers have a greater residual reproductive value than offspring. Because reproductive success increases when environmental conditions improve, at low resource availability, a conservative strategy may offer greater fitness returns than one of increasing maternal care, possibly to the detriment of maternal survival or future reproduction (Stearns 1992).

Compared to fawns of unrestricted mothers, fawns of food-restricted mothers spent more time suckling and solicited more suckles but were rejected more often and showed a reduced growth rate (Therrien et al. 2007). Food-restricted mothers and their fawns increased their time spent foraging compared to mothers and fawns from the control group, probably to compensate for the food restriction (Therrien et al. 2007). Those behavioural adjustments of mothers and fawns under food restriction support the results presented here on reduced fawn growth and survival.

Differences in phenotypic quality among offspring at the end of maternal care persist to adulthood in many ungulates including white-tailed deer (Schultz and Johnson 1995), fallow deer (Birgersson and Ekvall 1997), bighorn sheep (Festa-Bianchet et al. 1996) and moose (*Alces alces*; Keech et al. 1999). Fawns born in years with low food availability might therefore become poor reproducers as adults because of their lower phenotypic quality compared to fawns raised under good nutritional conditions. Adult females in our study may thus have reduced care in offspring when resources were insufficient to produce offspring of high phenotypic quality, as suggested by a higher frequency of

rejected suckling attempts in the treatment group (Therrien et al. 2007). Increased maternal investment might have jeopardized female's survival and subsequent reproductive potential, while possibly leading to low fitness returns.

Fawns that survived to weaning showed a similar growth rate regardless of the food available. From birth to physiological weaning at about 30 days of age (Gauthier and Barrette 1985; Lavigueur and Barrette 1992), fawns rely almost entirely on milk. Older fawns begin to forage and become independent of maternal milk. Therefore, if food-restricted fawns can forage efficiently and compensate for a slow start, as observed because they spent more time foraging than control fawns (Therrien et al. 2007), they could reach an autumn mass similar to that of control fawns. Pre-weaning maternal care, however, has to be sufficient to ensure fawn survival. In our experiment, some fawns died before weaning, possibly leaving only the best-quality individuals in the sample. Selective fawn mortality may explain why there was no difference in growth rate between surviving food-restricted and control fawns. The feeding trough that was only accessible to fawns probably enhanced the possibility of compensation. Fawns at high population density in the wild may suffer higher mortality from density-dependent food restriction than those in our experiment because they do not have access to supplemental food (Cook et al. 1971; Steigers and Flinders 1980; Ricca et al. 2002).

The food-restriction treatment was less severe in 2005 (20% restriction) than in 2004 (25%). That small difference apparently had a positive impact on fawn survival, but we did not observe any other differences between the 2 years. Previous year reproductive success of mothers and maternal mass did not affect fawn growth or survival. For growing fawns, differences in care according to maternal characteristics may be subtle compared to the effects of food availability, where a small difference could result in large consequences for fawn growth. Because many predator-free ungulate populations are increasing worldwide (Côté et al. 2004), the effects of low food availability generated by high intra-specific competition are also increasing and may become the main limiting factor for population growth (Boucher et al. 2004). Our research suggests that summer food restriction has a profound negative impact on white-tailed deer recruitment. Although browse availability in winter is important for survival (Mautz 1978; Clutton-Brock et al. 1985), we suggest that forage availability during summer may play a much more important role as a limiting factor in population dynamics of temperate herbivores than has been generally assumed (Cook et al. 2004). A key role for spring–summer forage is to be expected given the high energetic needs of lactation, the importance of food abundance for maternal care and recruitment and the strong effects of summer nutrition on growth and subsequent ability to reproduce.

Our experimental set-up allowed us to manipulate food availability, to follow precisely all individuals for daily mass changes and to control for possible paternal effects on the life history of fawns. Because we did not observe any significant decrease in maternal mass under food restriction and growth rates were similar for all weaned fawns, food restriction seems ultimately to affect the survival of offspring. We showed that females in a temperate and long-lived iteroparous mammal employ a conservative strategy, favouring their own mass recovery at the expense of survival of their offspring. This is an experimental demonstration of selfish maternal care in a polygynous ungulate.

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