

# Experimental influence of population density and vegetation biomass on the movements and activity budget of a large herbivore

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## Summary

Population density could influence herbivore foraging decisions as it affects the availability of preferred plant species and intraspecific competition. We tested the effect of density on white-tailed deer (*Odocoileus virginianus*) movements and activity budgets at controlled densities of 7.5 and 15 deer/km<sup>2</sup>. We also measured the activity budget of deer and plant biomass in an unfenced area at >20 deer/km<sup>2</sup>. Deer in the unfenced area spent less time active than those at controlled densities, possibly because of the greater time required to process a low quality diet. Biomass of preferred plant species significantly increased through years but did not differ between controlled densities. Adults were less active than yearlings at 7.5 but not at 15 deer/km<sup>2</sup> but, otherwise, movements and activity budgets were similar between densities. Deer at controlled densities responded to the increase of plant biomass by increasing the number of activity bouts and shortening their duration. When vegetation was less abundant, adults at 7.5 deer/km<sup>2</sup> spent more time active. Augmentation of population density and, thus, of intraspecific competition, can have direct effects on deer foraging behavior. Increases in plant biomass, however, revealed that plant biomass appears to have a stronger influence on deer foraging behavior than population density.

*Keywords:* activity budget, controlled-density experiment, density, white-tailed deer, movements, *Odocoileus virginianus*, radiotelemetry.

## Introduction

For herbivores in temperate and boreal regions, summer is a critical season to restore body condition and build up body reserves for over-winter survival

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(Lesage et al., 2001). Increasing energy intake requires that herbivores utilize the most profitable plants in terms of energy content and foraging time necessary to crop them (Bunnell & Gillingham, 1985). Herbivores have access to less forage as population density increases (Healy, 1997; Côté et al., 2004), hence, foraging strategies may become critical at high density. Cervids have become the dominant herbivores in most ecosystems of North America and Europe and they have recently reached historically high densities over large areas (Côté et al., 2004). The impacts of deer on ecosystem functioning are far reaching (Côté et al., 2004) and the influence of population density on deer foraging behavior needs to be assessed.

Deer may alter their foraging behavior in response to changing availability of preferred plant species, abundance of forage biomass or social competition in relation to population density. Many studies have obtained conflicting results regarding the influence of forage quality and availability on the foraging behavior of herbivores (Henriksen et al., 2003). Generally, herbivore density is negatively related to forage availability and quality, and ungulates at high density may be constrained to remain active for longer periods in order to ingest enough forage, especially in low biomass environments (Trudell & White, 1981; Moncorps et al., 1997). Deer also may increase search movements and foraging time with increasing deer density to consume the most rewarding plants and plant parts when the availability of plants has decreased (Wickstrom et al., 1984; Bartmann et al., 1992). As forage is distributed in spatially separated patches, movements and increased foraging time may, however, entail higher time and energy costs (Murray, 1991). Alternatively, deer may respond to forage depletion by foraging less selectively to reduce movement costs (Gates & Hudson, 1983), and their diel active time would then remain unaffected (Kohlmann & Risenhoover, 1994). By feeding on lower quality vegetation, i.e., plants with a high content of structural compounds that reduce plant digestibility (Bryant & Kuropat, 1980; Palo, 1985; Côté, 1998), the rate of passage of forage from the rumen to the lower digestive tract should slow down and rumination time increase (Van Soest, 1982; Spalinger et al., 1986). As vegetation increases in abundance during the growing season, it becomes more lignified and its protein content decreases (Hanley, 1984). Time spent active by herbivores could, thus, differ between periods of plant growth and periods of plant senescence (Gates & Hudson, 1983).

Studies on ungulates have shown that yearlings spend more time active than adults because of their smaller mass and relatively smaller digestive system, and higher metabolic rate and energetic demands of growth (Bunnell & Gillingham, 1985; Côté et al., 1997; Shi et al., 2003). As metabolic requirements are allometrically related to body mass, larger individuals need less energy per unit of mass than smaller individuals (Kleiber, 1932). In addition, because gut size increases linearly with body size while turnover time declines, larger individuals can extract more energy from forage than smaller individuals (Demment & Van Soest, 1985). Active time, thus, tends to decrease with increasing age (Moncorps et al., 1997; Mysterud, 1998; Ruckstuhl, 1998; Pérez-Barbería & Gordon, 1999; Jeschke & Tollrian, 2005) and body mass (Pelletier & Festa-Bianchet, 2004). Given their different use of resources, an increase in population density should affect juveniles and adults differently. For example, juvenile survival is more affected by density than adult survival (Jorgenson et al., 1997).

Controlled-density experiments have been used as a research tool for many years to study the foraging behavior of domestic animals and its use is now strongly encouraged for wild ungulates (Hester et al., 2000). Most studies have investigated the effects of herbivore densities on vegetation abundance and diversity (Tilghman, 1989; Hester et al., 2000); however, controlled-density experiments may also be useful to understand how herbivores modify their behavior at different population densities. Using a controlled-density experiment established in recently cut balsam fir stands, our objective was to assess how the daily and summer activity patterns of yearling and adult white-tailed deer (*Odocoileus virginianus*) vary in relation to population density and plant biomass. Because the experiment was conducted in recent clear-cuts, we expected a net increase in plant biomass with the number of years after the onset of the controlled-density experiment. We predicted that deer at high density would be more active and have higher movement rates than those at lower densities because of the increased time necessary to gather forage at high density. An alternative hypothesis is that deer should increase time spent inactive at high density because processing vegetation of lower quality (i.e., more fibrous) due to repeated browsing is longer than processing higher quality vegetation, leading to an increase in the length of inactive bouts. We also predicted that differences in deer behavior between densities would increase with time after the onset of the controlled-density experiment (because plant biomass should increase annually) and as plant biomass increases throughout the summer.

## Material and methods

### *Study area*

Anticosti Island (49°28'N, 63°00'W) is located in the Gulf of St. Lawrence, Québec, Canada and covers 7943 km<sup>2</sup>. The climate on Anticosti is typically maritime and characterized by longer and milder winters than on the continent. Mean temperatures are -15°C in January and 12°C in July and the annual average precipitation is 917 mm (Environment Canada, 2006). On average, a third of the total precipitation falls as snow. Balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and black spruce (*P. mariana*) naturally dominate the forests of Anticosti Island. White birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) are irregularly found. About 200 deer were introduced on the island at the turn of the 19<sup>th</sup> century. The population spread and grew rapidly because of the absence of predators. Today, deer densities of >20 deer/km<sup>2</sup> are found in most areas on the island (Potvin & Breton, 2005). Forest composition has been strongly modified by selective browsing, deciduous browse species have almost disappeared (Tremblay et al., 2005) and balsam fir stands are now being replaced by white spruce stands (Potvin et al., 2003).

### *Experimental design*

The experimental design consisted of 3 blocks (A, B, C) which comprised 2 enclosures of different sizes (20 and 40 ha) into which we introduced deer. Our setup is part of a larger study aimed at determining which deer densities are compatible with balsam fir regeneration (Tremblay et al., 2006). There was also an unfenced area (F.R. = free-ranging deer) where density was estimated at >20 deer/km<sup>2</sup> (Tremblay et al., 2006). We located all blocks and the unfenced area in similar balsam fir-dominated forests partially cut in the summer of 2001. Two of the blocks (B, C) were located in the center of the island; the other one (A) and the unfenced area were located 130 km away in the western part of the island. In the enclosures, 30 to 40% of residual forest patches of different sizes (0.19–21.6 ha) were left. The proportion of forest was similar in all enclosures. Water was easily accessible to deer in streams or artificial water holes. To assess the effects of population density on activity and movements of deer, 2 controlled densities were established in blocks A, B and C. Controlled densities were 7.5 (L.D. = low density; 40 ha enclosures

with 3 deer) and 15 deer/km<sup>2</sup> (H.D. = high density; 20 ha enclosures with 3 deer). We chose these densities to include white-tailed deer density proposed for sustainable tree regeneration (7 deer/km<sup>2</sup>; Tilghman, 1989; deCalesta & Stout, 1997) and the estimated density on Anticosti Island at the beginning of the experiment (15.6 deer/km<sup>2</sup>; Rochette et al., 2003). The dimensions of the enclosures are slightly smaller than summer home ranges of white-tailed deer at high density on Anticosti (about 60 ha; data not shown). We considered the enclosure as the experimental unit to take into account the potential problem of autocorrelation between deer in a same enclosure.

#### *Forage abundance*

To assess plant biomass available, we randomly placed 20 sampling points in cuts and 20 sampling points under forest cover in each experimental unit. At each sampling point, we estimated percent of plant cover in September of each year in two 1-m<sup>2</sup> plots randomly located in a 10×10 m quadrat centered on the sampling point. We obtained estimates for the most important species consumed by deer on Anticosti island: *A. balsamea*, *P. glauca*, *B. papyrifera*, small forbs (*Cornus canadensis*, *Maianthemum canadense*, *Trientalis borealis*), large forbs (*Epilobium angustifolium*, *Rubus idaeus*, *Rubus pubescens*), *Cirsium* spp. and *grass* spp. Plant biomass was assessed using regressions between percent plant cover, height and mass of dried plants (Bonham, 1989). Number of samples needed for regressions was estimated by plotting regression coefficients with number of samples until an asymptote was reached (Tremblay et al., 2006).

#### *Deer captures and radiotelemetry*

We used different methods to capture deer: dart guns, netguns shot from a helicopter, Stephenson box traps and cannon nets. In June or early July of the 1st, 2nd and 3rd year after the onset of the controlled-density experiment, we released deer in the enclosures. On the 2nd year, we also monitored 4 adult females in the unfenced cutblock. The Animal Care and Use Committee of Université Laval, Québec, Canada (Reference number 2005-008) approved all capture methods.

All deer were fitted with VHF collars equipped with sto-2a variable-pulse activity sensors (LMRT series, Lotek Engineering, Newmarket, Ontario, Canada). We used yearling ( $N = 21$ ) and adult deer ( $N = 19$ ) of

both sexes (17 males, 23 females). We verified reproductive status of adult females by direct observation at capture and at the end of summer. As we preferentially captured does that did not appear to bear a young with the objective of maintaining set densities, only 2 reproductive females were monitored. We did not include reproductive status as a variable in the analyses, but we verified if results changed when excluding females with fawns.

### *Movements*

Deer were located with receivers (SRX-400 version W9, Lotek Engineering, Newmarket, Ontario, Canada and TR-2 scanner/receiver, Telonics, Meza, AZ, USA), a unidirectional yagi antenna and a compass. Telemetry stations were positioned with a GPS Garmin (Garmin International, Olathe, KS, USA; precision of <5 m) on forest roads adjacent to the enclosures. To limit human disturbance, stations were generally located more than 100 m away from the enclosures. At least 3 azimuths differing by a minimum of 30° were obtained by moving between stations with a vehicle (White & Garrott, 1990). To reduce location error, positioning was completed within 15 min (White & Garrott, 1990). Periods of the day were evenly sampled by separating them into three periods of 8 h (0800–1600 h, 1600–0000 h and 0000–0800 h). These 8-h periods were rotated between two observers and between groups of enclosures every 3 days to evenly sample the complete 24 h of a day and all enclosures. We recorded deer locations in blocks A, B, and C for the first 2 years of the experiment.

LOAS software (Location of a Signal; Version 2.07, Ecological Software Solutions, Schwägalpstrasse, Urnäsch, Switzerland) was used to estimate positions and error polygons (using 'Andrews' estimator). The average error from plotted to actual locations was determined by placing VHF collars at known locations throughout the enclosures and was estimated at 107 m (SE = 88 m;  $N = 88$  trials). We deleted telemetry locations with error polygons greater than 0.1 ha. After processing, 2916 locations were obtained. The minimum movement rate was estimated as the linear distance between two successive deer locations separated by less than 3 h ( $\bar{X} \pm SE = 98 \pm 27$  min separating successive locations,  $N = 2219$  movements) and divided by the time elapsed between these two locations. A deer also was fitted with a GPS collar to verify the influence of positioning error on movement rate estimation. The distance moved per hour was equivalent between VHF and GPS collars (VHF:  $\bar{X} = 241 \pm 13$  m/h,  $N = 196$  movements; GPS:  $\bar{X} = 247 \pm 8$  m/h,  $N = 944$  movements,  $F = 0.12$ ,  $df = 1$ , 1138,  $p = 0.73$ ).

### *Activity budgets*

Variable-pulse activity sensors of VHF collars use mercury switches that add pulses to the base pulse rate of the collar each time the switch is triggered. The number of pulses above the base pulse rate indicates the degree of animal activity during the period when the pulses are counted (Coulombe et al., 2006). Transmitter signals of activity sensors were received and recorded continuously in a SRX-400 version W9 receiver-datalogger (Lotek Engineering, Newmarket, Ontario, Canada) connected to a multidirectional antenna, a battery, and a solar panel. The receiver-datalogger quantified pulse rate for approximately one minute and then saved a measure of average pulse rate. An average measure of pulse rate for each deer in a block was obtained approximately every 6 min continuously.

Validation studies of activity sensors have obtained mixed results in overall reliability (74–98% accuracy) and have demonstrated that it is necessary to validate methods used to measure activity budgets with direct animal observations (Gillingham & Bunnell, 1985; Beier & McCullough, 1990; Relyea et al., 1994). We conducted our own validation study with direct observations of deer in small enclosures (Coulombe et al., 2006). By combining the information of 3 successive scans, we correctly assessed 87% of all activity bouts (Coulombe et al., 2006). We used the following method to describe activity bouts: an inactive bout began when at least 3 inactive scans were observed, and to return to an active bout at least 3 active scans had to be observed. Activity data did not allow us to differentiate amongst different active or inactive behaviors, e.g., resting could not be differentiated from ruminating or eating from moving. Activity periods not corresponding to feeding activities (e.g., vigilance, social interactions), however, represent only 5–15% of time spent active in *Odocoileus* (Beier & McCullough, 1990; Gillingham et al., 1997) and, thus, are not a large part of the activity budget. Additionally, a decrease in plant quality is generally related to an increase in rumination time and, therefore, in time spent inactive (Mysterud, 1998; Pérez-Barbería & Gordon, 1999). Time spent inactive is, thus, an indication of rumination time. To analyze time budgets, we used the daily proportion of time spent active, the mean daily length of active and inactive bouts (that could vary independently) and the number of activity bouts per day (24 h).

We did not measure activity budgets for all deer in all years. In the 1st year of the controlled-density experiment (2002), we monitored deer activity

in July and August in block (A). In the 2nd year (2003), 2 blocks (A, C) were studied from July to September. In 2004, we monitored activity budgets of deer in block (C) from July to September. No deer were monitored for activity in block B. We monitored the activity budget of free-ranging deer from July to September 2003.

Because of the small sample size, we could not account for sex in the analyses. We chose to compare the effects of density between different age groups of both sexes because the effects of density may differ between growing individuals (i.e., yearlings) and adults as their activity budgets vary (Bunnell & Gillingham, 1985; Shi et al., 2003). However, to limit the potential effects of sex, we captured only 2 reproductive females and no large adult males for this study.

### *Analyses*

We tested if total plant biomass and biomass of the different species available to deer differed between densities (7.5 and 15 deer/km<sup>2</sup>), strata (cutblocks, forests) and years since the onset of the controlled-density experiment, using an analysis of variance with block as a random factor. We also tested whether plant biomass in the unfenced area differed from plant biomass in the controlled densities. We could not include estimates from the unfenced area in the same model as above because we had only 1 unfenced area, but we assessed the difference between natural and controlled densities by subtracting the average biomass of each plant species from the controlled densities to the corresponding value for that species in the unfenced area. Differences were tested in a model containing density and strata with block as a random factor. If the confidence interval of the estimated parameter included zero, we concluded that there was no difference between biomass in controlled deer densities and under natural densities.

We contrasted the mean distance moved and the proportion of time spent active between densities, periods of the day (dawn: 90 min before sunrise to 90 min after sunrise; day: 90 min after sunrise to 90 min before sunset; dusk: 90 min before sunset to 90 min after sunset; night: 90 min after sunset to 90 min before sunrise) and week with year as a random factor. We included all interactions in the models but to simplify the presentation of results, we only report interactions when  $p < 0.05$ . Because periods of the day and weeks were repeated for each deer, we used a repeated measures design

with density as the treatment and blocks (random) as replicates (Proc Mixed, SAS Version 9.1, SAS Institute, Cary, NC, USA). Mean length of active and inactive bouts and number of daily activity bouts were compared between densities and week for yearlings and adults with block and year as random factors and week as a repeated measure. To account for differences between years, we used simple contrast comparisons of the random factor 'block  $\times$  year' (McLean et al., 1991). After models were developed, we compared the means for adults and yearlings with a Z-test. As mixed models do not provide  $R^2$  values, we computed the explained variance for each significant slope with week as

$$R^2 = 1 - \frac{SSR}{SSTO},$$

where

$$SSR = \sum ((Y_{\text{observed}} - Y_{\text{predicted}})^2) \quad \text{and}$$

$$SSTO = \sum ((Y_{\text{observed}} - \bar{Y}_{\text{observed}})^2) \quad (\text{Xu, 2003}).$$

We could not include deer in the unfenced area in the models above because we had only one unfenced area that contained only adults. To test for differences between the adult activity budget in controlled densities and in the unfenced area, we subtracted each average value of activity from controlled densities to the corresponding value from the unfenced area, for each week and period of the day. Differences were tested in a model containing density, period of the day and week with block and year as random factors. If the confidence intervals of the estimated parameters included zero, we concluded that there was no difference between activity budgets in controlled densities and under natural densities.

Because temperature can influence deer activity patterns (Beier & McCullough, 1990), we verified its influence on deer movements and on the proportion of time spent active. We obtained mean hourly temperature from the Environment Canada meteorological station located on the western part of Anticosti Island. For each period of the day, we related the proportion of time spent active to the mean temperature for the period and tested if slopes significantly differed from zero as well as between densities.

After each analysis, residuals were examined for normality and variance homogeneity. Significance was set at 0.05 and all results, unless specified, are presented as means  $\pm$  standard error.

## Results

### *Forage abundance*

Contrarily to what we expected, total plant biomass did not vary with deer density ( $F = 0.03$ ,  $df = 1, 20$ ,  $p = 0.87$ ), but was greater in cutblocks 2 and 3 years after the onset of the controlled-density experiment than during the 1st year ( $F = 18.53$ ,  $df = 2, 20$ ,  $p < 0.01$ ; Table 1). Total biomass was greater in cutblocks than under forest cover 2 and 3 years after the onset of the experiment but not during the 1st year ( $F = 3.73$ ,  $df = 2, 20$ ,  $p = 0.04$ ; Table 1). Total plant biomass in forest stands was higher in the unfenced area than in the enclosures (Table 1).

In cutblocks, *Abies balsamea*, *Cornus canadensis* and *Maianthemum canadense* were more abundant the 2nd year of the controlled density experiment than during the 1st year (Table 1). *Abies balsamea*, *Betula* sp., *Rubus pubescens*, *Cornus canadensis*, and *Maianthemum canadense* were more abundant in cutblocks the 3rd year of the controlled density experiment than during the 1st year (Table 1). *Betula* sp., *Picea glauca*, and *Rubus pubescens* were more abundant the 3rd year of the controlled density experiment than during the 2nd year. *Epilobium angustifolium* was also more abundant in cutblocks during the 3rd year of the experiment than before, but only in the L.D. enclosures (Table 1). Most estimates of biomass were similar between the unfenced area and the enclosures (Table 1). However, the biomass of *Cornus canadensis* in forests and *Cirsium* spp. in both strata were higher in the unfenced area than in the enclosures. In forest stands, the biomass of *Betula* sp., *Cornus canadensis* and *Maianthemum canadense* increased from the 1st to the 2nd year of the controlled-density experiment.

### *Movements*

Mean temperature did not affect deer movements or activity budgets during any period of the day (all  $p$ -values  $> 0.05$ ), we, therefore, did not include temperature in any analyses. We compared movement rates between controlled-densities and according to the number of years after the onset of the experiment to test if deer increase movement rates with increasing density or when plant biomass is lower. Movement rates were similar between controlled densities for both yearlings and adults (Table 2). In addition, movement rates did not differ between adults and yearlings ( $Z = 0.70$ ,

**Table 1.** Average biomass ( $\text{g}/\text{m}^2$ ;  $\pm$  standard error) of different plant species consumed by white-tailed deer in forests and cutblocks of Anticosti Island at 2 controlled densities (7.5 and 15 deer/ $\text{km}^2$ ) and in an unfenced area at  $>20$  deer/ $\text{km}^2$ .

	Year									
	1			2			3			
	7.5	15	>20	7.5	15	>20	7.5	15	>20	
<b>Tree seedlings</b>										
<i>Abies balsamea</i>	Forest	0.4 $\pm$ 0.1 <sup>b</sup>	0.6 $\pm$ 0.2 <sup>b</sup>	0.6 $\pm$ 0.2 <sup>b</sup>	0.4 $\pm$ 0.1 <sup>b</sup>	0.7 <sup>b</sup>	1.0 $\pm$ 0.5 <sup>b</sup>	0.8 $\pm$ 0.2 <sup>b</sup>		
	Cutblock	0.6 $\pm$ 0.2 <sup>b</sup>	0.7 $\pm$ 0.0 <sup>b</sup>	1.6 $\pm$ 0.8 <sup>a</sup>	1.4 $\pm$ 0.5 <sup>a</sup>	0.2 <sup>b</sup>	3.5 $\pm$ 1.1 <sup>a</sup>	1.6 $\pm$ 0.6 <sup>a</sup>		
<i>Betula</i> sp.*	Forest	0.0 $\pm$ 0.0 <sup>c</sup>	0.1 $\pm$ 0.0 <sup>c</sup>	0.1 $\pm$ 0.0 <sup>b</sup>	0.1 $\pm$ 0.1 <sup>b</sup>	0.1 <sup>b</sup>	0.2 $\pm$ 0.1 <sup>a</sup>	0.3 $\pm$ 0.2 <sup>a</sup>		
	Cutblock	0.1 $\pm$ 0.0 <sup>b</sup>	0.2 $\pm$ 0.1 <sup>b</sup>	0.5 $\pm$ 0.3 <sup>b</sup>	0.3 $\pm$ 0.0 <sup>b</sup>	0.1 <sup>b</sup>	3.3 $\pm$ 1.2 <sup>a</sup>	1.3 $\pm$ 0.7 <sup>a</sup>		
<i>Picea glauca</i>	Forest	— <sup>**</sup>	— <sup>**</sup>	1.8 $\pm$ 0.5 <sup>b</sup>	1.7 $\pm$ 1.2 <sup>b</sup>	0.7 <sup>b</sup>	1.2 $\pm$ 0.6 <sup>b</sup>	2.6 $\pm$ 2.5 <sup>b</sup>		
	Cutblock	— <sup>**</sup>	— <sup>**</sup>	1.1 $\pm$ 0.4 <sup>b</sup>	2.2 $\pm$ 0.5 <sup>b</sup>	0.6 <sup>b</sup>	5.1 $\pm$ 1.4 <sup>a</sup>	4.9 $\pm$ 2.2 <sup>a</sup>		
<b>Large forbs</b>										
<i>Rubus idaeus</i> *	Forest	0.0 $\pm$ 0.0 <sup>a</sup>	0.0 $\pm$ 0.0 <sup>a</sup>	0 $\pm$ 0.0 <sup>a</sup>	0.0 $\pm$ 0.0 <sup>a</sup>	1.8 <sup>a</sup>	0 $\pm$ 0.0 <sup>a</sup>	0.0 $\pm$ 0.0 <sup>a</sup>		
	Cutblock	0.8 $\pm$ 0.8 <sup>a</sup>	0.3 $\pm$ 0.3 <sup>a</sup>	20.6 $\pm$ 20.5 <sup>a</sup>	8.5 $\pm$ 8.5 <sup>a</sup>	1.6 <sup>a</sup>	48.0 $\pm$ 44.9 <sup>a</sup>	41.6 $\pm$ 41.5 <sup>a</sup>		
<i>Rubus pubescens</i>	Forest	0.6 $\pm$ 0.3 <sup>b</sup>	1.8 $\pm$ 0.9 <sup>b</sup>	1.3 $\pm$ 0.6 <sup>b</sup>	1.5 $\pm$ 0.5 <sup>b</sup>	1.7 <sup>b</sup>	1.6 $\pm$ 0.8 <sup>b</sup>	1.8 $\pm$ 0.7 <sup>b</sup>		
	Cutblock	0.7 $\pm$ 0.3 <sup>b</sup>	2.0 $\pm$ 0.9 <sup>b</sup>	4.0 $\pm$ 1.2 <sup>b</sup>	3.6 $\pm$ 0.5 <sup>b</sup>	1.6 <sup>b</sup>	12.9 $\pm$ 2.1 <sup>a</sup>	9.1 $\pm$ 2.8 <sup>a</sup>		
<i>Epilobium angustifolium</i>	Forest	— <sup>**</sup>	— <sup>**</sup>	0.0 $\pm$ 0.0 <sup>c</sup>	0.0 $\pm$ 0.0 <sup>c</sup>	0.0 <sup>c</sup>	0.0 $\pm$ 0.0 <sup>c</sup>	0.0 $\pm$ 0.0 <sup>c</sup>		
	Cutblock	— <sup>**</sup>	— <sup>**</sup>	5.3 $\pm$ 5.2 <sup>b</sup>	0.1 $\pm$ 0.1 <sup>b</sup>	0.0 <sup>b</sup>	12.4 $\pm$ 6.4 <sup>a</sup>	0.1 $\pm$ 0.1 <sup>b</sup>		

Table 1. (Continued).

		Year											
		1			2			3					
		7.5	15	7.5	7.5	15	>20	7.5	15	15			
Small forbs													
<i>Cornus canadensis</i>	Forest	5.5 ± 2.1 <sup>c</sup>	4.5 ± 1.8 <sup>c</sup>	11.0 ± 3.2 <sup>b</sup>	10.7 ± 4.4 <sup>b</sup>	19.3 <sup>a</sup>	8.6 ± 2.7 <sup>b</sup>	11.1 ± 2.8 <sup>b</sup>					
	Cutblock	5.0 ± 2.1 <sup>c</sup>	5.4 ± 1.1 <sup>c</sup>	12.0 ± 4.1 <sup>b</sup>	11.3 ± 2.3 <sup>b</sup>	4.0 <sup>c</sup>	13.9 ± 3.0 <sup>b</sup>	10.8 ± 2.6 <sup>b</sup>					
<i>Maianthemum canadense</i> *	Forest	1.3 ± 0.3 <sup>d</sup>	1.3 ± 0.4 <sup>d</sup>	2.6 ± 0.8 <sup>c</sup>	3.1 ± 1.2 <sup>c</sup>	2.7 <sup>c</sup>	2.8 ± 0.5 <sup>c</sup>	21.8 ± 0.3 <sup>c</sup>					
	Cutblock	0.6 ± 0.2 <sup>b</sup>	0.6 ± 0.2 <sup>b</sup>	2.4 ± 1.1 <sup>a</sup>	1.8 ± 0.3 <sup>a</sup>	0.7 <sup>b</sup>	1.6 ± 0.1 <sup>a</sup>	1.5 ± 0.4 <sup>a</sup>					
<i>Trientalis borealis</i>	Forest	— <sup>***</sup>	— <sup>***</sup>	0.3 ± 0.1 <sup>a</sup>	0.1 ± 0.0 <sup>a</sup>	0.2 <sup>b</sup>	0.3 ± 0.1 <sup>a</sup>	0.1 ± 0.0 <sup>a</sup>					
	Cutblock	— <sup>***</sup>	— <sup>***</sup>	0.1 ± 0.0 <sup>b</sup>	0.1 ± 0.0 <sup>b</sup>	0.0 <sup>b</sup>	0.0 ± 0.0 <sup>b</sup>	0.0 ± 0.0 <sup>b</sup>					
<i>Grass spp.*</i>	Forest	19.6 ± 10.5 <sup>b</sup>	15.5 ± 3.6 <sup>b</sup>	5.0 ± 2.4 <sup>b</sup>	9.9 ± 0.5 <sup>b</sup>	15.4 <sup>b</sup>	4.9 ± 2.6 <sup>c</sup>	6.8 ± 2.3 <sup>c</sup>					
	Cutblock	22.3 ± 7.7 <sup>a</sup>	30.1 ± 5.4 <sup>a</sup>	57.5 ± 6.4 <sup>a</sup>	45.7 ± 2.8 <sup>a</sup>	64.1 <sup>a</sup>	44.6 ± 16.1 <sup>a</sup>	43.2 ± 23.4 <sup>a</sup>					
<i>Cirsium spp.</i>	Forest	1.1 ± 0.6 <sup>c</sup>	1.4 ± 1.3 <sup>c</sup>	5.3 ± 2.7 <sup>c</sup>	3.6 ± 3.5 <sup>c</sup>	29.3 <sup>a</sup>	3.3 ± 2.0 <sup>c</sup>	1.1 ± 0.6 <sup>c</sup>					
	Cutblock	6.6 ± 5.3 <sup>b</sup>	8.4 ± 4.2 <sup>b</sup>	22.4 ± 13.5 <sup>b</sup>	24.7 ± 12.2 <sup>b</sup>	32.1 <sup>a</sup>	15.6 ± 7.9 <sup>b</sup>	15.1 ± 10.4 <sup>b</sup>					
Total	Forest	28.7 ± 9.0 <sup>b</sup>	25.1 ± 5.2 <sup>b</sup>	26.0 ± 2.5 <sup>b</sup>	29.4 ± 5.5 <sup>b</sup>	71.4 <sup>a</sup>	22.5 ± 6.3 <sup>b</sup>	23.7 ± 3.0 <sup>b</sup>					
	Cutblock	36.8 ± 12.3 <sup>b</sup>	47.7 ± 7.5 <sup>b</sup>	126.4 ± 23.3 <sup>a</sup>	97.4 ± 4.5 <sup>a</sup>	104.5 <sup>a</sup>	156.0 ± 63.9 <sup>a</sup>	124.3 ± 63.6 <sup>a</sup>					

For each species, different letters indicate differences observed between densities, years and stratum at  $p < 0.05$ .

\* Because of the heterogeneity of variance between strata, separate comparisons for forests and cutblocks were done for these species.

\*\* Not sampled the first year of the controlled-density experiment.

**Table 2.** White-tailed deer summer movement rates according to density, age class, week and period of the day in 2002 and 2003.

	Factor	Parameter	Estimate error	Standard	<i>N</i>	df	<i>F</i>	<i>p</i>
Adults ( <i>N</i> = 9)	Density	7.5 deer/km <sup>2</sup>	124.1	7.6	75	1, 5	0.29	0.61
		15 deer/km <sup>2</sup>	102.6	6.7	58			
	Week		0.3*	0.4	133	1, 108	1.39	0.24
	Period of the day	Dawn	128.6	13.7	34	3, 15	1.46	0.26
		Day	116.6	7.9	37			
		Dusk	120.6	11.0	25			
Night		102.1	10.3	37				
Yearlings ( <i>N</i> = 12)	Density	7.5 deer/km <sup>2</sup>	120.0	5.9	77	1, 5	2.84	0.15
		15 deer/km <sup>2</sup>	97.1	6.9	53			
	Week		-0.4*	0.4	130	1, 101	0.02	0.89
	Period of the day	Dawn	118.4	9.0	31	3, 15	1.42	0.28
		Day	105.8	6.8	38			
		Dusk	120.6	11.0	25			
Night		102.1	10.3	36				

We compared movements (m/h) between densities and weeks for adults and yearlings with block (3 sites) and year as random factors and period of the day and weeks as repeated measures. Each sample (*N*) corresponds to a specific period of the day, week, density and block.

\* For week, the estimate corresponds to the slope of movements (m/h) over weeks.

*p* = 0.50). Movement rates did not change according to the number of years after the onset of the controlled-density experiment for both yearlings (1 year:  $\bar{X} = 109 \pm 7$  m/h, *N* = 38 daily periods; 2 years:  $\bar{X} = 111 \pm 6$  m/h, *N* = 92; *F* = 0.00, df = 1, 106, *p* = 1) and adults (1 year:  $\bar{X} = 107 \pm 11$  m/h, *N* = 19; 2 years:  $\bar{X} = 116 \pm 6$  m/h, *N* = 114; *F* = 0.08, df = 1, 113, *p* = 0.78) or according to periods of the day or number of weeks since the beginning of the summer (Table 2).

#### *Proportion of time spent active*

We compared activity budgets between deer densities, according to the number of years after the onset of the controlled-density experiment, and with date during summer to test how deer responded to changes in intraspecific competition and plant biomass. Adults at L.D. were about 16% more active than at H.D. (Table 3). Yearlings were active about 73–75% of the

**Table 3.** Proportion of time that white-tailed deer spent active in summer at 2 controlled densities on Anticosti Island, Québec.

	Factor	Parameter	Estimate	Standard error	<i>N</i>	df	<i>F</i>	<i>p</i>	
Adults ( <i>N</i> = 9)	Density	7.5 deer/km <sup>2</sup>	0.73	0.03	98	1, 4	24.9	0.03	
		15 deer/km <sup>2</sup>	0.63	0.04	60				
	Week		0.0045*	0.0150	147	1, 138	0.51	0.48	
	Week × density		-0.0306**	0.0190	147	1, 138	11.12	0.03	
	Period of the day	Dawn		0.63 <sup>a</sup>	0.04	42	3, 12	0.78	0.53
		Day		0.69 <sup>a</sup>	0.04	41			
		Dusk		0.82 <sup>a</sup>	0.04	39			
Night			0.59 <sup>a</sup>	0.04	36				
Yearlings ( <i>N</i> = 12)	Density	7.5 deer/km <sup>2</sup>	0.75	0.03	102	1, 5	0.98	0.34	
		15 deer/km <sup>2</sup>	0.73	0.03	72				
	Week		0.0027*	0.0140	174	1, 153	0.24	0.62	
	Week × density		-0.0018**	0.0180	174	1, 153	2.37	0.13	
	Period of the day	Dawn		0.70 <sup>b</sup>	0.03	47	3, 15	3.22	0.05
		Day		0.75 <sup>b</sup>	0.03	44			
		Dusk		0.90 <sup>a</sup>	0.03	44			
Night			0.62 <sup>c</sup>	0.04	39				

The proportion of time spent active was compared between densities, weeks since the beginning of summer and periods of the day for adults and yearlings with block (3 sites) and year as random factors and periods of the day and week as repeated measures. Each sample (*N*) corresponds to a specific period of the day, week, density and block. Values of proportion of time spent active between periods of the day with different letters are statistically different ( $p < 0.05$ ).

\* For week, the estimate corresponds to the slope of the proportion of time spent active over weeks.

\*\* For week × density, the estimate corresponds to the difference between slopes at 7.5 and 15 deer/km<sup>2</sup>.

time, both in L.D. and H.D. enclosures (Table 3). F.R. adults were as active ( $\bar{X} = 0.72 \pm 0.01$ ,  $N = 21$  daily periods) as those in controlled density enclosures (L.D.:  $t_2 = 1.23$ ,  $p = 0.34$ ; H.D.:  $t = -2.34$ ,  $df = 2$ ,  $p = 0.14$ ; Table 3). Yearlings were more active than adults at H.D. ( $Z = -1.98$ ,  $p = 0.05$ ), but not at L.D. ( $Z = -0.44$ ,  $p = 0.66$ ). The proportion of time spent active by adults at L.D. decreased from the 1st to the 3rd year after the onset of the controlled-density experiment (L.D.: 1 vs. 2 years:  $F = 0.74$ ,  $df = 1, 90$ ,  $p = 0.39$ ; 1 vs. 3 years:  $F = 4.26$ ,  $df = 1, 90$ ,  $p = 0.04$ ; 2 vs. 3 years:  $F = 2.39$ ,  $df = 1, 90$ ,  $p = 0.13$ ; Figure 1a). For yearlings, time

spent active was similar through years (1 vs. 2 years:  $F = 0.93$ ,  $df = 1$ , 158,  $p = 0.33$ ; 1 vs. 3 years:  $F = 1.84$ ,  $df = 1$ , 158,  $p = 0.18$ ; 2 vs. 3 years:  $F = 1.21$ ,  $df = 1$ , 158,  $p = 0.27$ ; Figure 1a). For adults, the proportion of time spent active decreased throughout summer at L.D. ( $t = -2.14$ ,  $df = 138$ ,  $p = 0.03$ ,  $r^2 = 0.07$ ) but not at H.D. ( $t = 0.96$ ,  $df = 1$ , 38,  $p = 0.34$ ; interaction week  $\times$  density in Table 3, Figure 2a). For yearlings, time spent active did not change through summer at both densities (Table 3, Figure 3a). F.R. adults spent less time active during July than adults at L.D. ( $F = 4.14$ ,  $df = 1$ , 36,  $p = 0.05$ ,  $r^2 = 0.25$ ), but no differences occurred in other months or with deer at H.D. Yearlings were more active at dusk and less active at night than during any other period of the day (Table 3). Although adults were 39% more active at dusk than at night, the difference was not significant (Table 3).

#### *Number of activity bouts*

The number of daily activity bouts did not differ with density or weeks since the beginning of the summer for both yearlings and adults (Table 4). Similarly, the number of daily activity bouts did not differ between F.R. deer ( $\bar{X} = 8.8 \pm 2.2$ ,  $N = 15$  weeks) and those in controlled-density enclosures (Table 4; L.D.:  $t = -0.04$ ,  $df = 4$ ,  $p = 0.97$ ; H.D.:  $t = 1.99$ ,  $df = 4$ ,  $p = 0.12$ ). Yearlings and adults had a similar number of activity bouts (L.D.:  $Z = 0.62$ ,  $p = 0.54$ ; H.D.:  $Z = -0.16$ ,  $p = 0.88$ ). Yearlings had more activity bouts 3 years after the onset of the controlled-density experiment than after 1 or 2 years (1 vs. 2 years:  $F = 0.20$ ,  $df = 1$ , 34,  $p = 0.66$ ; 1 vs. 3 years:  $F = 83.62$ ,  $df = 1$ , 34,  $p < 0.01$ , 2 vs. 3 years:  $F = 75.32$ ,  $df = 1$ , 34,  $p < 0.01$ ) and adults had more activity bouts 3 years after the onset of the controlled-density experiment than 2 years after it (1 vs. 2 years:  $F = 1.01$ ,  $df = 1$ , 34,  $p = 0.32$ ; 1 vs. 3 years:  $F = 1.34$ ,  $df = 1$ , 34,  $p = 0.26$ ; 2 vs. 3 years:  $F = 6.28$ ,  $df = 1$ , 34,  $p = 0.02$ ; Figure 1b). Despite a small sample size, we detected a gradual decrease in the number of activity bouts for F.R. deer during the summer. F.R. deer had more activity bouts than deer at L.D. until the end of July, but less bouts at the end of August (week  $\times$  week:  $F = 12.95$ ,  $df = 1$ , 8,  $p < 0.01$ ,  $r^2 = 0.49$ ; Table 4, Figure 2b).

#### *Length of active and inactive bouts*

The length of active bouts did not differ with density for yearlings (Table 4). For adults, it was also similar for all densities, including F.R. deer ( $\bar{X} =$

**Table 4.** Number of daily activity bouts and length (min) of active and inactive bouts during summer of yearling and adult white-tailed deer at 2 controlled densities on Anticosti Island, Québec.

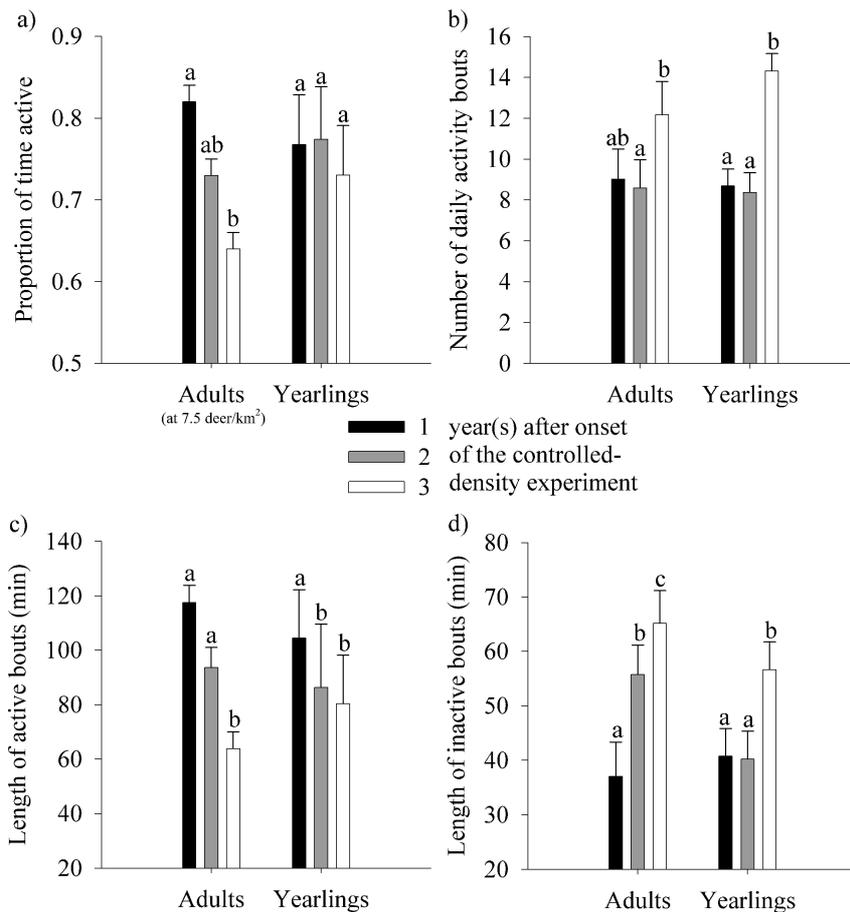
	Factor	Parameter	Estimate	Standard error	<i>N</i>	df	<i>F</i>	<i>p</i>
Number of bouts								
Adults ( <i>N</i> = 9)	Density	7.5 deer/km <sup>2</sup>	8.9	1.1	8	1, 4	2.04	0.23
		15 deer/km <sup>2</sup>	10.2	1.1	8			
	Week		-0.05*	0.20	16	1, 30	0.35	0.56
Yearlings ( <i>N</i> = 12)	Density	7.5 deer/km <sup>2</sup>	10.1	1.5	20	1, 4	0.60	0.48
		15 deer/km <sup>2</sup>	9.9	1.5	18			
	Week		0.06*	0.13	38	1, 30	0.02	0.89
Length of active bouts								
Adults ( <i>N</i> = 9)	Density	7.5 deer/km <sup>2</sup>	104.6	18.1	29	1, 7	0.85	0.39
		15 deer/km <sup>2</sup>	68.3	20.0	23			
	Week		-0.60*	2.40	52	1, 41	0.06	0.81
Yearlings ( <i>N</i> = 12)	Density	7.5 deer/km <sup>2</sup>	77.3	16.0	29	1, 7	3.07	0.12
		15 deer/km <sup>2</sup>	104.6	17.3	24			
	Week		-4.52*	3.00	53	1, 42	0.88	0.35
Length of inactive bouts								
Adults ( <i>N</i> = 9)	Density	7.5 deer/km <sup>2</sup>	50.5	6.1	28	1, 5	3.51	0.12
		15 deer/km <sup>2</sup>	58.2	6.3	22			
	Week		-0.60*	0.99	50	1, 41	0.08	0.78
Yearlings ( <i>N</i> = 12)	Density	7.5 deer/km <sup>2</sup>	43.7	6.1	29	1, 5	2.72	0.16
		15 deer/km <sup>2</sup>	48.9	6.7	20			
	Week		1.93*	0.90	49	1, 40	0.46	0.50
	Week × density		-3.01**	1.14	49	1, 40	7.24	0.01

The number of activity bouts and length of active and inactive bouts were compared between densities and weeks since the beginning of summer for yearlings and adults with block (3 sites) and year as random factors and weeks as repeated measures. Each sample (*N*) corresponds to a specific week, density and block.

\* For week, the estimate corresponds to the slope of the number of activity bouts or length of bouts over weeks.

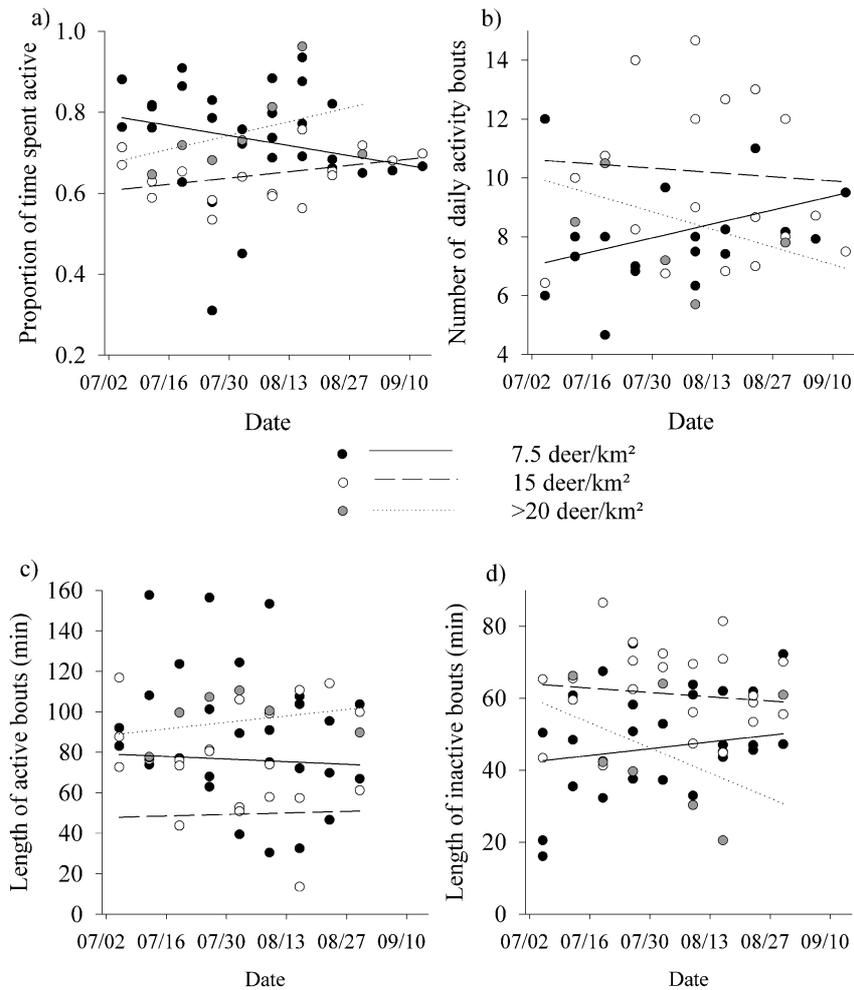
\*\* For week × density, the estimate corresponds to the difference between slopes at 7.5 and 15 deer/km<sup>2</sup>.

93.0 ± 3.8 min, *N* = 15 weeks; L.D. vs. H.D.: Table 4; L.D. vs. F.R.:  $t = -0.12$ , *df* = 5, *p* = 0.91; H.D. vs. F.R.:  $t = -1.16$ , *df* = 5, *p* =



**Figure 1.** Summer activity budgets of white-tailed deer on Anticosti Island, Québec, according to the number of years since the onset of a controlled-density experiment. Data were pooled between two controlled deer densities (7.5 and 15 deer/km<sup>2</sup>). We compared results in a model accounting for density, period of the day and weeks since the beginning of the summer with block and year as random factors. Bars with different letters are statistically different between years.

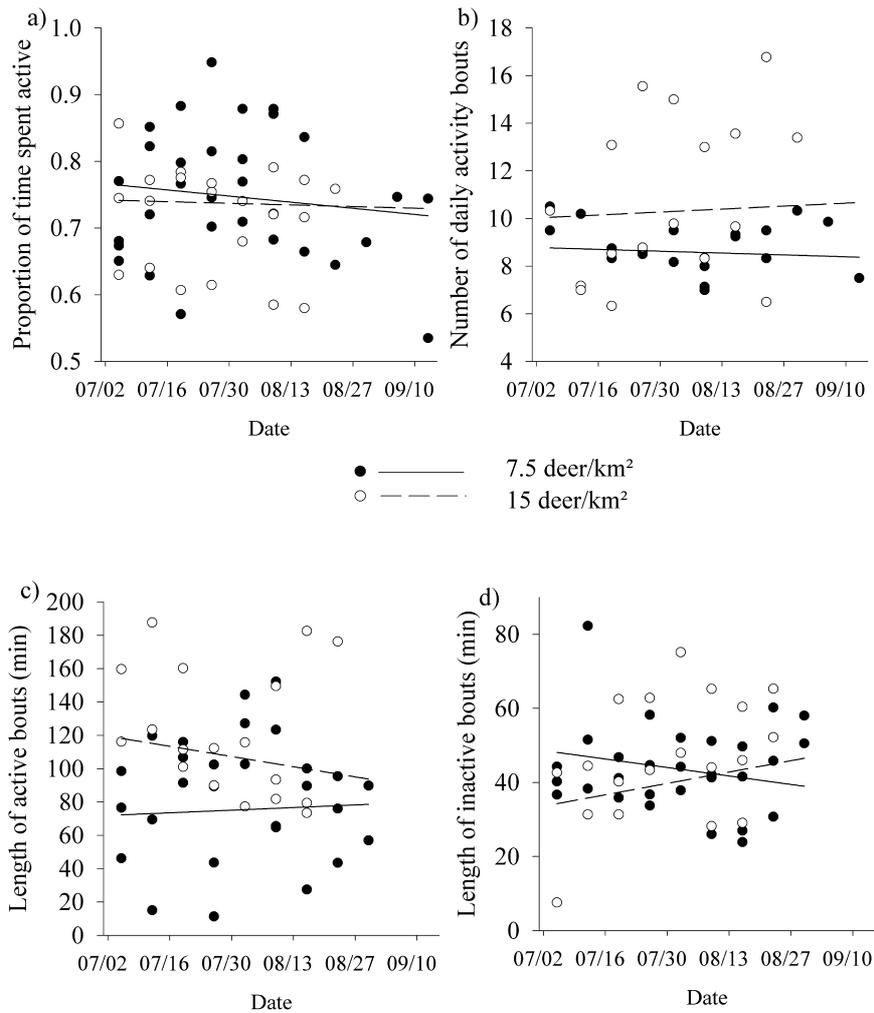
0.30). Adults and yearlings also had active bouts of similar lengths (L.D.:  $Z = 1.13$ ,  $p = 0.26$ ; H.D.:  $Z = -1.37$ ,  $p = 0.17$ ; Table 4). Active bouts were longer 1 and 2 years after the onset of the controlled-density experiment than 3 years after it for adults (1 vs. 2 years:  $F = 1.21$ ,  $df = 1, 48$ ,  $p = 0.28$ ; 1 vs. 3 years:  $F = 8.40$ ,  $df = 1, 48$ ,  $p < 0.01$ ; 2 vs. 3 years:  $F = 5.56$ ,  $df = 1, 48$ ,  $p = 0.02$ ; Figure 1c) and longer the 1st year than the 2nd and



**Figure 2.** Proportion of daily time spent active (a), number of daily activity bouts (b), length of active (c) and inactive bouts (d) in summer for adult white-tailed deer on Anticosti Island, Québec, pooled across years. Each circle corresponds to the observed mean for 1 block-density during 1 week. Regression lines were drawn from predicted values (Tables 3 and 4).

3rd year for yearlings (1 vs. 2 years:  $F = 4.80$ ,  $df = 1, 49$ ,  $p = 0.03$ ; 1 vs. 3 years:  $F = 4.03$ ,  $df = 1, 49$ ,  $p = 0.05$ ; 2 vs. 3 years:  $F = 0.40$ ,  $df = 1, 49$ ,  $p = 0.53$ ; Figure 1c). The length of active bouts did not change through summer in any age-class or density (Table 4; Figures 2c and 3c).

The length of inactive bouts did not vary with density for both yearlings and adults (Table 4). In the unfenced area, the length of inactive bouts ( $\bar{X} =$



**Figure 3.** Proportion of daily time spent active (a), number of daily activity bouts (b), length of active (c) and inactive bouts (d) in summer for yearling white-tailed deer on Anticosti Island, Québec, pooled across years. Each circle corresponds to the observed mean for 1 block-density during 1 week. Regression lines were drawn from predicted values (Tables 3 and 4).

$50.3 \pm 5.9$  min;  $N = 10$  weeks) was similar to L.D. ( $t = 1.38$ ,  $df = 3$ ,  $p = 0.26$ ; Table 4), but deer at H.D. had longer inactive bouts than F.R. deer ( $t = 3.20$ ,  $df = 3$ ,  $p = 0.05$ ; Table 4). The length of inactive bouts was also similar for adults and yearlings (L.D.:  $Z = 0.80$ ,  $p = 0.42$ ; H.D.:  $Z =$

1.04,  $p = 0.30$ ; Table 4). The length of inactive bouts, however, gradually increased from the 1st to the 3rd year after the onset of the controlled-density experiment for adults (1 vs. 2 years:  $F = 9.72$ ,  $df = 1, 46$ ,  $p < 0.01$ ; 1 vs. 3 years:  $F = 20.09$ ,  $df = 1, 46$ ,  $p < 0.01$ ; 2 vs. 3 years:  $F = 11.72$ ,  $df = 1, 46$ ,  $p < 0.01$ ; Figure 1d). For yearlings, inactive bouts were also longer the 3rd year than during the 2nd ( $F = 3.85$ ,  $df = 1, 45$ ,  $p = 0.05$ ) and the 1st year ( $F = 3.87$ ,  $df = 1, 45$ ,  $p = 0.05$ ) after the onset of the controlled-density experiment (Figure 1d). For adults, the length of inactive bouts did not vary with time at L.D. and H.D. (Table 4; Figure 2d), but F.R. deer had longer inactive bouts compared to deer at L.D. until the end of July, but shorter inactive bouts after (week  $\times$  week:  $F = 6.10$ ,  $df = 1, 19$ ,  $p = 0.02$ ,  $r^2 = 0.44$ ; Figure 2d). The length of inactive bouts tended to decrease throughout the summer for yearlings at L.D. ( $t = -1.60$ ,  $df = 40$ ,  $p = 0.12$ ,  $r^2 = 0.05$ ), and increase at H.D. ( $t = 2.15$ ,  $df = 40$ ,  $p = 0.04$ ,  $r^2 = 0.07$ ; Figure 3d).

## Discussion

We expected that population density would influence deer foraging behavior as increased density is often related to a decrease in forage abundance. Forage abundance did not differ significantly between 7.5 and 15 deer/km<sup>2</sup> during the course of our study, and deer density had limited impacts on their time-budgets. However, as demonstrated by differences in activity budgets observed through years and comparisons with free-ranging deer, when forage abundance was lower, deer activity budgets changed considerably, likely to compensate for a decrease in available energy.

### *Influence of population density*

Observational studies have found that concentrate feeders such as white-tailed deer spend 20 to 68% of their time active in summer (Bunnell & Harestad, 1990). Depending on density and age, we found that deer spent 63 to 75% of their time active in summer. Compared to other studies, these activity values are high. Extra time needed for foraging, because of the low abundance of vegetation generated by long term heavy browsing on Anticosti Island (Potvin et al., 2003), might generate such high activity rates. High activity values were observed even when biomass availability had significantly

increased, e.g., in low-density enclosures 2 and 3 years after the onset of the experiment.

We used adjacent and ecologically comparable enclosures and found that there was no influence of population density on deer movement rates. Similarly, in agricultural and forested landscapes differing in population density, Rouleau et al. (2002) monitored movements of white-tailed deer and found that variations in movement rates were related to ecological differences between landscapes but not to population density. Conversely, for mule deer (*Odocoileus hemionus*) movement rate decreased at low density where forage was more abundant (Wickstrom et al., 1984; Bartmann et al., 1992). Although plant biomass increased from the 1st to the 2nd year of the treatment, we did not observe any difference in movement rates.

There was an error associated with telemetry positions but movement rates of a deer measured with both GPS (high precision) and VHF (low precision) collars were comparable. Perhaps fences limited deer movements so that we did not detect differences between densities. Deer fitted with GPS collars in nearby unfenced cutblocks, however, moved at a much lower rate ( $\bar{X} = 78 \pm 33$  m/h;  $N = 4$  deer; data not shown) than deer in the enclosures (Table 2). Consequently, it appears that the fence did not restrain deer movements.

Flexible time-activity budgets also allow animals to circumvent the effects of declining food abundance at high population density (Cederlund et al., 1989; Beier & McCullough, 1990; Borkowski, 2000). In winter, for example, cervids usually reduce activity in response to food scarcity (Moen, 1978; Georgii, 1981; Risenhoover, 1986). Contrarily to our prediction, adults were more active at low density than at high density. During the growing season, high plant biomass, especially at low density, may allow adult deer to be more selective in their search of plant species or plant parts (Owen-Smith & Novellie, 1982; Belovsky, 1984). At low density, adult deer could, thus, increase time spent active because high quality food is more abundant and is then more cost-effective to search for (Trudell & White, 1981; Moncorps et al., 1997). As we found no difference in plant biomass between low and high-density enclosures, the decrease in the proportion of time spent active at high density appears to be better explained by an increase in intraspecific competition than by differences in vegetation abundance. Borkowski (2000) also found that sika deer (*Cervus nippon*) reduced activity at high-density compared to low-density. As they did not measure foraging conditions, they could only suggest that deer spent less time active at high density than at low

density either because the average lignin concentration of winter forage was higher at high-density than at low density and took longer to ruminate, or because of an increase in intraspecific competition that forced some deer to use suboptimal habitats where high-quality forage was less abundant. In our study, because plant biomass did not vary with deer density in the enclosures, we conclude that the foraging conditions were similar at both densities. Adult deer, thus, most likely increased time spent inactive at high density in response to an increase in intraspecific competition. Flexible time-activity budgets are also illustrated in the observation of free-ranging deer that had access to a greater proportion of less palatable species such as *Cirsium* spp. and had longer rumination periods and, thus, inactive bouts, in comparison to controlled-density deer.

Because of their smaller mass and digestive system, higher metabolic rate and energetic demands of growth, yearlings generally spend more time active than adults (Bunnell & Gillingham, 1985; Shi et al., 2003). For yearlings, we found no difference in the proportion of time spent active, number of daily activity bouts or length of active and inactive bouts between controlled densities. Yearlings already spent a larger part of their diel time active in high-density enclosures than adults, and it may not have been possible for them to increase time spent active in low-density enclosures, where intraspecific competition was reduced.

#### *Annual differences*

Plant biomass was higher the 2nd and 3rd year after the initiation of the controlled-density experiment than during the 1st year (Table 1). The partitioning of time of deer between active and inactive bouts also varied through years. Indeed, when plant biomass increased, the length of active bouts decreased while the length of inactive bouts and the number of daily activity periods increased (Figure 1). The decrease in the length of active bouts was probably due to an increase in plant biomass rather than to an improvement of diet quality. Indeed, as biomass increased through years, deer could fill their rumen faster before entering a rumination bout, which could also explain the higher number of daily activity bouts 3 years after the initiation of the experiment compared to the 1st year. Longer inactive bouts may be related to the possibility to reduce exposition to adverse environmental conditions (Mysterud, 1998; Pérez-Barbería & Gordon, 1999). Alternatively, if

the abundance and diversity of available plant species increase, individuals may select more digestible forage and, thus, the extra time spent searching for higher quality food may be compensated by the higher net energy gain (Cederlund et al., 1989). On a daily basis, as deer select better forage, they require less time to process vegetation and can spend more time searching for highly digestible plants or plant parts (Bartmann et al., 1992; WallisDeVries, 1996). Under this scenario, we should have expected inactive bouts to decrease in length as the active bouts increase in length, the opposite of what we found (Figure 1c and 1d). Additionally, if deer increase selectivity as biomass increases in enclosures, we should have expected movement rates to increase (Gates & Hudson, 1983; Kohlmann & Risenhoover, 1994). Movement rates, however, did not change. We, therefore, conclude that deer responded to an increase in plant biomass the 2nd and 3rd year of the experiment by reducing the time necessary to fill their rumen and increasing the number of foraging bouts per day. These changes in plant biomass and in their foraging behavior allowed them to gain about 25% more mass during summer than deer under natural conditions on the island, i.e., at a density of  $>20/\text{km}^2$  (Simard et al., data not shown).

#### *Seasonal differences*

Forage quantity and quality normally vary during and between seasons. On Anticosti, the vegetation-growing season begins when snow melts in early May, the new shoots are then rich in protein and easily digestible (Van der Wal et al., 2000). Through the growing season, vegetation increases in structural compounds and decreases in protein content and, thus, digestibility decreases (Robbins, 1983; Van Soest, 1994).

Activity gradually decreased during summer for adults at low density. Abundance of vegetation gradually increases through summer and adult deer may need to spend less time active, searching and eating vegetation as the season progresses. Forage biomass as of mid-July may exceed deer metabolic demands and they could, thus, meet their energy requirements by foraging fewer hours per day (Beier & McCullough, 1990). This is consistent with our interpretation of annual differences that as biomass increases, the amount of time required for deer to fill their rumen decreases.

Until the end of July, deer under natural density ( $>20$  deer/ $\text{km}^2$ ) spent less time active and had longer inactive bouts, likely to digest less palatable forage. This is consistent with our prediction that deer should increase

time spent inactive at high density. Plant biomass of several species differed between the unfenced area and the controlled-density enclosures such as a greater proportion of *Cirsium* spp. in the unfenced area. However, as the abundance of forage increased through summer, deer in the unfenced area increased the proportion of time spent active and, consequently, inactive bouts decreased in length. An increase in foraging time and length of activity bouts could be expected if deer increased selectivity as vegetation became more abundant (Wickstrom et al., 1984).

During summer, juveniles and adults responded differently to an increase in forage abundance and to a decline in plant digestibility. An increase in time spent feeding through the plant growing season is normal for young individuals and has been reported for the mouflon (*Ovis musimon*; Moncorps et al., 1997) and feral goats (*Capra hircus*; Shi et al., 2003). As yearlings grow during summer, their energy requirements also increase and they need more forage and, thus, increase feeding time (Bunnell & Gillingham, 1985). For yearlings in our study, however, the proportion of time spent active did not increase during summer in either density. This may have been caused by a decrease in vegetation quality and, thus, an increase in processing time. The proportion of time spent active was constantly high at both densities and, thus, yearlings might not have had time available to increase time spent active through summer.

#### *Diel activity pattern*

For yearlings at both densities, the proportion of time spent active was higher at dawn but especially at dusk and lower during the night than during daytime. Peaks of activity at dawn, but especially at dusk, have been largely documented in deer and are part of their diurnal foraging-ruminating cycle (Kammermeyer & Marchinton, 1977; Beier & McCullough, 1990). Foraging bouts usually occur following and before periods of darkness, so deer may gather food in periods of daylight, when foraging is more profitable. As in many other studies, we found that peaks of activity at dawn were not as constant as those at dusk (Skogland, 1983; Beier & McCullough, 1990), and they probably occurred just after dawn (Beier & McCullough, 1990). The hour and a half interval we used before and after sunrise may also be too large to detect differences between dawn and daytime. We did not detect statistically higher activity rates at dawn and dusk for adults, but activity was nonetheless 19 to 39% higher at dusk than during other periods of the day (Table 3).

Our results illustrate that controlled-density experiments, where population density is directly manipulated, may greatly help improving our understanding of the foraging behavior of herbivores in relation to available resources. Forage quality is another important factor that can determine deer foraging behavior, and coupling it with forage abundance can be a useful approach to estimate carrying capacity of deer habitats (Hobbs & Swift, 1985). Further research should investigate how forage quality combined to forage abundance can influence deer foraging behavior in relation to population density.

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