NRC Research Press

Linking time budgets to habitat quality suggests that beavers (*Castor canadensis*) are energy maximizers

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Abstract: According to optimal foraging theory, consumers make choices that maximize their net energy intake per unit of time. We used foraging theory as a framework to understand the foraging behaviour of North American beavers (*Castor canadensis* Kuhl, 1820), an important herbivore that engineers new habitats. We tested the hypothesis that beavers are energy maximizers by verifying the prediction that they allocate time to foraging activities independently of habitat quality in Kouchibouguac National Park of Canada in New Brunswick, where nearly five decades of unabated colonization by beavers led to family units established in habitats of varying quality. We observed the behaviour of 27 beavers at seven ponds from May to August 2001, at dusk and dawn. Habitat quality did not influence time that beavers allocated to foraging. This finding supported our hypothesis. The only factor in the best model explaining time spent foraging was the progression of spring and summer seasons (weekly periods). Limiting factors such as infrastructure maintenance and intermittent reactions to danger remain poorly understood for this important herbivore. Future research should focus on establishing the importance that habitat quality (food availability) and environmental stress (weather, predators) have on shaping its time budget and, consequently, its survival and reproductive success.

Key words: beaver, *Castor canadensis*, foraging, energy maximization, time minimization, New Brunswick.

Résumé : Selon la théorie de l'approvisionnement optimal, les consommateurs font des choix qui maximisent leur apport énergétique net par unité de temps. Nous avons utilisé la théorie de l'approvisionnement comme cadre pour comprendre le comportement d'approvisionnement du castor (*Castor canadensis* Kuhl, 1820), un important herbivore qui crée de nouveaux habitats. Nous avons testé l'hypothèse selon laquelle les castors sont des maximisateurs d'énergie en vérifiant la prédiction voulant que leur attribution de temps aux activités d'approvisionnement ne dépende pas de la qualité de l'habitat dans le parc national du Canada Kouchibouguac, au Nouveau-Brunswick, où près de cinq décennies de colonisation soutenue par les castors ont mené à l'établissement d'unités familiales dans des habitats de qualité variable. Nous avons observé le comportement de 27 castors dans sept étangs, de mai à août 2001, à la brunante et à l'aube. La qualité de l'habitat n'avait pas d'influence sur le temps alloué à l'approvisionnement par les castors. Cette constatation appuie notre hypothèse. Le seul facteur dans le modèle expliquant le mieux le temps alloué à l'approvisionnement est l'avancée du printemps et de l'été (périodes hebdomadaires). Des facteurs limitants comme l'entretien des infrastructures et des réactions intermittentes au danger demeurent mal compris pour cet important herbivore. Des travaux futurs devraient viser à établir le rôle que jouent la qualité de l'habitat (disponibilité de nourriture) et les stress environnementaux (météo, prédateurs) sur le budget-temps et, conséquemment, la survie et le succès de reproduction des castors. [Traduit par la Rédaction]

Mots-clés : castor, *Castor canadensis*, approvisionnement, maximisation énergétique, minimisation du temps, Nouveau-Brunswick.

Introduction

According to optimal foraging theory, consumers make choices that maximize their net energy intake per unit of time (Emlen 1966; MacArthur and Pianka 1966). The main assumption of optimal foraging theory is that energy maximization is related to individual fitness (Schoener 1971). Although alternative models have been developed (e.g., Herbers 1981), those based on optimization criteria have successfully explained the foraging behaviour of a wide array of consumers (Werner and Hall 1974; Belovsky 1978; Gallant et al. 2004). Energy maximization remains one of the main tenets of modern foraging theory, which also integrates compromises that animals make to fulfill other needs, such as predator avoidance (Basey and Jenkins 1995; Bednekoff 2007), territory defense (Jaeger et al. 1983), or return to a central place such as a shelter (Schoener 1979; Gallant et al. 2004).

One useful theoretical framework based on optimization criteria was proposed by Schoener (1971) and further developed by Belovsky (1978, 1981a, 1981b) for generalist herbivores. It considers

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Table 1. Sites where we performed behavioural observations on 27 North American beavers (*Castor canadensis*) and conducted vegetation surveys in Kouchibouguac National Park of Canada in 2001.

Pond name	Easting*	Northing*	Density of deciduous species/m²	Density of preferred species/m²	Number of studied beavers
Portage	0354501	5198855	14.06	0.56	3
Eric's pond	0353766	5197751	7.70	1.65	4
Cimetière	0348643	5189779	11.69	0.53	3
Patterson	0346464	5184028	8.43	0.34	5
Tweedie	0346518	5184731	1.16	0.03	4
Loggiecroft	0349530	5187061	8.25	0.38	2
Middle kouch 2	0348667	5185409	1.87	0.18	6

*Universal Transverse Mercator coordinate system, zone 20, NAD83.

that time is a limited resource, which animals have to allocate toward multiple opposing needs, most of which are related to fitness (e.g., foraging, grooming to get rid of parasites, resting to avoid thermal stress, building and maintaining structures used as refuge). Herbivores, thus, have to make a trade-off between minimizing time spent foraging so they can devote more time to other activities, and maximizing energy intake so they can reproduce or store food or fat for later use. Elucidating the foraging strategy that they use is an important step towards understanding their foraging behaviour (Santini and Chelazzi 1996; Bergman et al. 2001).

North American beavers (*Castor canadensis* Kuhl, 1820; hereafter beavers) are generalist herbivores (Roberts and Arner 1984; Gallant et al. 2004) that build dams in running streams using sectioned trees and mud. Determining the foraging strategy of beavers is important to wildlife management and biodiversity conservation because their foraging and dam-building activities shape entire ecosystems (Wright et al. 2002; Bailey et al. 2004; Rosell et al. 2005). The time that beavers devote to foraging has received little attention thus far, and the relative importance of energy maximization versus other needs in the foraging strategy of this ecologically important herbivore is not well understood. Forage choices and space use by beavers appear to be consistent with energy maximization goals (Fryxell 1992; Fryxell and Doucet 1993). However, behavioural observations confirming that beavers are energy maximizers are lacking, with the exception of Belovsky (1984), who collected behavioural data from a single beaver colony.

Habitat quality is a key factor in elucidating foraging trade-offs because it determines how quickly animals can meet their nutritional needs (Kirk et al. 2007; Ménard et al. 2013) and, ultimately, their survival and reproductive success (Fryxell 2001). Beavers in high-quality habitats can reach their nutrition and energy requirements relatively quickly by eating high-quality food such as trembling aspen (*Populus tremuloides* Michx.). This species is highly digestible and has a short retention time in the digestive system (Doucet and Fryxell 1993; Fryxell et al. 1994). In low-quality habitats, beavers are less selective in terms of tree size and forage species (Fryxell and Doucet 1993; Gallant et al. 2004). They have to rely on less nutritious species such as red maple (*Acer rubrum* L.), which take longer to digest (Doucet and Fryxell 1993; Fryxell et al. 1994). Consequently, they would need to spend more time eating larger quantities of low-quality food to satisfy their energetic needs.

We aimed to analyze beaver foraging within the framework of optimal foraging theory, specifically in terms of maximizing energy through time spent foraging in habitats with varying levels of food availability and quality. We tested the hypothesis that beavers are energy maximizers by verifying the prediction that time spent foraging by beavers is either independent of, or positively related to, habitat quality around ponds. According to this prediction, beavers should feed to satiation regardless of habitat quality, but may be able to spend even more time foraging in high-quality habitat because of trembling aspen's shorter retention time in the digestive system (Doucet and Fryxell 1993; Fryxell et al. 1994). We, therefore, analyzed the spring and summer behaviours of individual beavers in a protected area, where populations

increased to saturation levels (Slough and Sadleir 1977; Howard and Larson 1985; Barnes and Mallik 1997; Léger 2004). Under those conditions, beaver colonies could be found in both low- and high-quality habitats with varying levels of food availability.

Materials and methods

Study area and species

The study took place in Kouchibouguac National Park of Canada (46°50′N, 65°00′W). This 239 km² park was established in 1969 (Parks Canada 2010). The park is located on the eastern shore of New Brunswick and is representative of the Maritimes Lowland ecoregion, which is characterized by a flat and gently seaward-sloping landscape, interspersed with ombrotrophic bogs, salt marshes, Acadian forest, and estuarine rivers (Desloges 1980). Freshwater covers 1% of the park area (Desloges 1980). Beavers in the park increased to saturation levels in the early 1990s and have steadily decreased since (Dubois et al. 1997; Léger 2004), as accessible stands of trembling aspen were depleted and pond sites became dominated by unpalatable woody vegetation, such as conifers (Canada Research Chair in Polar and Boreal Ecology, unpublished data). Following the park's creation, logging and agriculture stopped and old fields along rivers and streams started reverting to young forest stands, although very slowly (Pouzet 2007). Such sites favour colonization by beavers (Barnes and Mallik 1997), and in the park, they started to establish more colonies near old fields in the early 2000s (Canada Research Chair in Polar and Boreal Ecology, unpublished data). Black bear (*Ursus americanus* Pallas, 1780) and coyote (*Canis latrans* Say, 1823) are potential predators of beavers in the Park, in addition to American mink (*Mustela vison* Schreber, 1777 = *Neovision vison* (Schreber, 1777)) and river otter (*Lontra canadensis* (Schreber, 1777)), which potentially prey on kits (Jenkins and Busher 1979; Reid et al. 1994; Smith et al. 1994). The study area is described in detail in Graillon et al. (2000) and Gallant et al. (2004).

Sampling sites and habitat quality

We observed beaver activities at seven colonies consisting of well-developed beaver ponds where the lodges and dams were already built (Table 1). We identified beavers using colour-coded ear tags installed between 1998 and 2001, during the course of a concurrent study (C.H. Bérubé, unpublished data).

We measured habitat quality at the seven colonies by documenting woody vegetation around ponds, through transects perpendicular to their edges and at 50 m intervals. Ponds were of different sizes; therefore, the number of transects sampled per pond varied from three to eight. We concentrated sampling on the pond itself and, thus, did not sample vegetation downstream from the beaver dam and upstream from the pond. Along each transect, we sampled a 2 m × 2 m quadrat at 10, 30, 50, 70, and 90 m from the pond. Few beavers wander >100 m from their pond (Jenkins 1980; Gallant et al. 2004). Within each quadrat, we counted the number of stems and trunks for each woody-plant species. Using terrestrial woody vegetation to determine habitat

Table 2. Comparison of generalized linear mixed models describing proportion of observation time spent foraging by 27 North American beavers (*Castor canadensis*) at seven colony sites in Kouchibouguac National Park of Canada in 2001.

Model	−2·loglikelihood	Number of parameters (*K*)*	AIC$_c$	ΔAIC$_c$ (Δ$_i$)	Akaike weight (*w$_i$*)
Period	601.02	6	615.10	0.00	0.44
Density preferred	605.75	6	619.90	4.80	0.04
Density deciduous	606.05	6	620.20	5.10	0.03
Period + density preferred	599.12	7	616.07	0.97	0.27
Period + density deciduous	600.91	7	617.77	2.67	0.11
Period × density preferred	599.07	8	618.89	3.79	0.07
Period × density deciduous	600.38	8	620.19	5.09	0.03

*Includes the intercept, the dispersion parameter associated with the negative binomial distribution, and the zero-inflation parameter, as well as two random factors (beaver ID nested within pond ID). AIC$_c$, Akaike's information criterion corrected for small sample size.

quality was justified because beavers rely on caches of woody vegetation to survive year-round in temperate and boreal regions (Slough 1978; Doucet et al. 1994). Based on the wide variety of deciduous species cut by beavers, their general avoidance of conifers, and their preference for particular species in our study area (Gallant et al. 2004), we used two proxies for habitat quality in our analyses: (1) the density of deciduous species, calculated as the number of stems and trunks of deciduous species divided by the total area (m²) covered by sampled quadrats around ponds, and (2) the density of preferred species by beavers around each pond, calculated as the number of stems and trunks of trembling aspen, bigtooth aspen (*Populus grandidentata* Michx.), beaked hazelnut (*Corylus cornuta* Marshall), willows (species of the genus *Salix* L.), or pin cherry (*Prunus pensylvanica* L.f.) divided by the total area (m²) covered by sampled quadrats around ponds. These species are selected by beavers in our study area (Gallant et al. 2004).

Behavioural observations

We observed 27 individual beavers between 13 May and 23 August 2001 (Table 1), thus avoiding fall when beavers build their food cache (Busher 1996) and winter when they can be confined to the lodge and forced to feed on cached food (Aleksiuk 1970). We documented beaver behaviour during observation sessions, which occurred between 0500 and 0900 and from 1800 to 2200 (Atlantic daylight saving time), when beavers were most active (Belovsky 1984; Buech 1995), using Altmann's (1974) focal method. Sessions lasted from 1 to 2 h, starting when we arrived on site, and produced from 25 s to 2 h of continuous observations of beavers, during which we described their activities by whispering into handheld microcassette recorders. Recorded behaviours included swimming, patrolling (i.e., swimming with head held high above water), walking on land, swimming under water, exerting alert behaviour (i.e., standing still in observation), slapping tail on water, grooming, repairing the dam, interacting with family members, foraging, and staying in the lodge. We used Jeschke and Tollrian's (2005) definition of foraging, which includes all activities related to food ingestion, including traveling to reach food and provisioning activities such as cutting food items and bringing them back to the pond. Therefore, among travelling activities, only those clearly related to reaching food and bringing it back to the pond were considered part of foraging activities. Because studied ponds were already well established by beavers, we considered that tree cutting was motivated by foraging. Dam maintenance was mostly done by pushing mud against it. Except for speckled alder (*Alnus rugosa* (Du Roi) Spreng. = *Alnus incana* ssp. *rugosa* (Du Roi) R.T. Clausen), beavers stripped and ate the bark from stems and trunks of deciduous trees before using them for other purposes (D. Gallant, personal observations), which suggested that they were cut first and foremost for foraging.

For each observation session, we positioned ourselves at the same location at each pond to accustom beavers to our presence.

We performed 100 observation sessions of beaver behaviour. For approximately half of the sessions, we operated as a two-observer team, which allowed more beavers to be observed for their behaviour when several of them were active in the ponds. We used day (Leica® Trinovid 10 × 42 BN) and night vision binoculars (Newcon® BN-5 2.4×) to make observations and to identify individuals by their physical features and ear tags. Of the 100 sessions, we selected only those lasting ≥30 min because shorter ones did not give enough time to record appropriate information about the diverse behaviours of beavers in their colonies.

Statistical analyses

We analyzed how habitat quality and progression of the growing season influenced the proportion of observation time that beavers spent foraging by comparing the performance of various generalized linear mixed models (GLMM) that included different combinations of habitat quality ("density deciduous" and "density preferred"), period (weeks 1–15), and the interaction between these factors. We used the zero-inflated negative binomial probability distribution model because beavers did not forage during some observation sessions (zero values) and data were overdispersed. We set pond identity and beaver identity as random factors (individuals nested within ponds) and used the duration of observation sessions as an offset in the models. We fitted models using the package glmmADMB version 0.8.0 (Fournier et al. 2012) in R version 3.1.2 (R Core Team 2014).

We compared models using Akaike's information criterion (Burnham and Anderson 2002) corrected for small sample size (AIC$_c$) relative to the number of estimated parameters in the models to avoid overfitting problems (Hurvich and Tsai 1989). We also computed Akaike weights (*w$_i$*) to evaluate the level of support for each model.

Results

Collectively, the 27 beavers spent 18% of the observation time foraging. They spent the majority of their foraging time feeding on woody plants such as trees (45%) and shrubs (33%), and only 15% and 7% of their foraging time feeding on herbaceous and aquatic plants, respectively. This finding confirmed the critical importance of woody plants (78%) as a food source for beavers in our study area. Although foraging on nonwoody plants occurred less often, it was nonetheless widely distributed among ponds and individuals. Eleven beavers representing all seven ponds were observed eating herbaceous plants, while six beavers representing five ponds (Loggiecroft, Portage, Tweedie, Eric's Pond, Patterson; Table 1) were observed eating aquatic plants.

The best model describing trends in the proportion of observation time that beavers spent foraging included "period" as the single factor (Table 2). Beavers increased their foraging time as the season progressed (Table 3, Fig. 1). Eight of the nine beavers that

Table 3. Regression results of a generalized linear mixed model showing the effect of period (weeks) on proportion of observation time spent foraging by 27 North American beavers (*Castor canadensis*) at seven colony sites in Kouchibouguac National Park of Canada in 2001.

Coefficient	Coefficient estimate	Standard error	Z	P
Intercept	−2.14	0.25	−8.44	0.000
Period	0.06	0.03	2.39	0.017

Note: Variance and standard deviation for random factors "pond ID" and "individuals within pond IDs" were $4.76 \times 10^{-8} \pm 2.18 \times 10^{-4}$ and $2.28 \times 10^{-9} \pm 4.78 \times 10^{-5}$, respectively. Estimates and standard errors for the negative binomial dispersion parameter and the zero-inflation parameter were 1.71 ± 0.36 and 0.15 ± 0.05, respectively.

we successfully observed during both the first 7 weeks and the last 8 weeks of the 15 week study period increased the proportion of observation time that they allocated to foraging and, collectively, they represented all ponds except Cimetière (Table 1). Nonetheless, correlation between fitted and observed values was low (Pearson correlation = 0.39, *n* = 47), indicating that the best model only explained part of the variability observed in the proportion of observation time that beavers spent foraging (Table 2).

Habitat-quality factors "density deciduous" and "density preferred" were correlated (Pearson correlation = 0.77, *n* = 47); thus, we alternated between them in model comparisons. Habitat quality had no influence on the proportion of observation time that beavers spent foraging, as all models including "density deciduous" or "density preferred" did not perform better than the model with "period" as the single factor (Table 2, Fig. 2). Habitat quality did not influence the rate of increase of the proportion of observation time that beavers spent foraging as the summer progressed, as shown by the lack of improvement of model performance when the interaction between "period" and habitat-quality factors was included (Table 2). These results fitted the prediction that time spent foraging by beavers was independent of habitat quality around ponds, thus supporting the energy maximization hypothesis.

Discussion

Our results, based on direct observations of the behaviour of individual beavers, showed that they spent as much time foraging in high-quality habitat as they did in low-quality habitat. Given that lower quality food takes more time to pass through the gut of herbivores (Doucet and Fryxell 1993; Fryxell et al. 1994), it would be expected that energy-maximizing foragers in lower quality habitat spend less time foraging than in high-quality habitat. Despite high provisioning costs, results by Jeschke and Tollrian (2005) suggest that beavers can usually reach satiation when foraging in nature. However, satiation may not limit beavers, which are central-place foragers (Gallant et al. 2004) that can continue to forage when satiated. Several aspects of their foraging behaviour appear to confirm that they can continue provisioning activities for later nutritional needs. Beavers cut more trees than they can consume in the short term, and they often leave a substantial part of the bark and foliage on felled trees for preferred species such as aspen and cherry (species of the genus *Prunus* L.) trees. They do so as well for less preferred ones, such as paper birch (*Betula papyrifera* Marshall), oaks (species of the genus *Quercus* L.), and maples (species of the genus *Acer* L.) (Aldous 1938; Jenkins 1980). We observed this behaviour for aspens in our study area (L. Léger and D. Gallant, personal observations). In addition, beavers potentially cut and leave uneaten branches of less palatable species in the pond for days to leech-out phenolic compounds (Müller-Schwarze et al. 2001). In temperate regions, provisioning behaviour culminates in the building of the food cache during fall (Slough 1978; Doucet et al. 1994; Busher 1996). Thus, beavers may maximize time spent foraging and go beyond daily satiation needs, which

Fig. 1. Proportion of observation time spent foraging as a function of period (weeks) during 47 observation sessions on 27 North American beavers (*Castor canadensis*) at seven colony sites in Kouchibouguac National Park of Canada. The relationship is described by negative binomial smoothing curves spanning weeks from 13 May to 23 August in 2001 (for model results see Table 3).
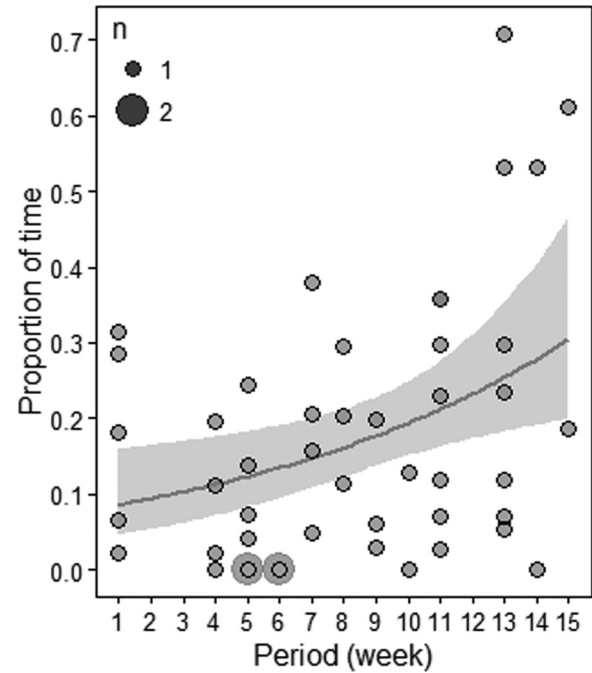
Fig. 2. Proportion of observation time spent foraging during 47 observation sessions on 27 North American beavers (*Castor canadensis*) at seven colony sites with varying densities of trunks and stems of deciduous woody plants (for details see Materials and methods) in Kouchibouguac National Park of Canada.
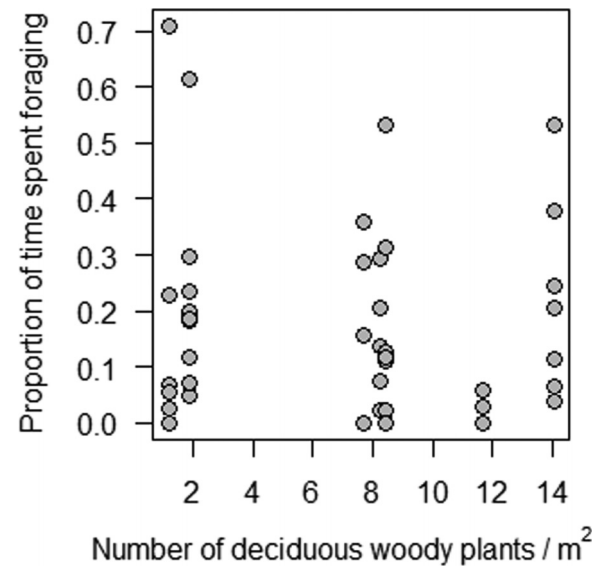
leads to the provisioning of surplus food that helps maximize future energy intake.

Some of our observations of beaver behaviour came from ponds that were almost completely dominated by conifers (i.e., Tweedie and Middle Kouch 2; Table 1), and probably near the threshold at which beavers cannot sustain themselves and have to emigrate. The proportion of observation time that beavers spent foraging at

these ponds was comparable to the other ponds (Fig. 1), which suggests that beavers do not change tactics and remain energy maximizers until depletion of resources. Because handling time is probably more important than searching time for foraging beavers, they may respond directly to the abundance of the food that they seek rather than to its density. In our study, food density is probably highly correlated to its availability because the food density gradient among our studied sites included some ponds almost completely dominated by unpalatable conifers. Also, length of dams (available from 2002 for six out of our seven studied ponds) was uncorrelated to density of preferred species (Pearson correlation = −0.07, *n* = 6), which suggests that pond size did not influence food availability.

The proportion of observation time that beavers spent foraging varied considerably from late May to late August (Fig. 1). Hall (1960) also recorded such within-year variability. This variability may be due to the tree-cutting habits of beavers. Once large trees have been felled, they can potentially be used for several days during which less effort is required to obtain food because part of the provisioning process is already done. We hypothesize that the increase in time spent foraging as the summer progressed, which was independent of habitat quality, is linked to increased tree cutting and provisioning in anticipation of building the food cache. An alternative hypothesis is that temporal variability in time spent foraging is due to changes in the necessity of dam and lodge maintenance that limit the time that beavers can spend foraging. This necessity is typically greater in spring due to increased water flow after snowmelt and quickly diminishes as summer progresses (Eimers et al. 2008). Nonetheless, our best model, which involved a temporal variable, only explained part of the variability observed in the data, which suggests that other unmeasured factors also play a role in determining the time that beavers allocate to foraging.

Provisioning costs of beavers foraging on land increase as a function of tree size (Belovsky 1984; Fryxell and Doucet 1993) and distance from the pond (Fryxell and Doucet 1991, 1993). It takes under 1 h to cut a tree 10–15 cm in diameter, but 4 to 6 h for a tree 25 cm in diameter (Belovsky 1984). In our study area, Gallant et al. (2004) found that beavers travelled up to 80 m on land to reach trembling aspens. Although we documented beaver activities when they were most active (dusk and dawn) (Belovsky 1984; Buech 1995) and under less thermal stress (Belovsky 1984) or predation risk (see farther below), foraging rarely surpassed one-third of the time that we observed beaver behaviour. It is unlikely that beavers only spend the time necessary to feed to satiation with the rest being lay time, like in the model proposed by Herbers (1981) to explain idle time in animals. Along with time spent in the lodge avoiding thermal stress in summer (Belovsky 1984), other essential activities, like infrastructure building and maintenance (dams, lodges, burrows, and food caches), occupy a large part of the time budget of beavers (Buech 1995).

Nonwoody species, such as grasses and aquatic plants, often become very important sources of food for beavers in summer (Northcott 1971; Svendsen 1980). Our behavioural observations showed that these seasonal food sources were of lesser importance in our study area, but they were not negligible. Occasional foraging on herbaceous plants occurred in all the ponds that we studied, whereas foraging on aquatic plants occurred in ponds with habitat quality ranging from the highest (i.e., Portage and Eric's Pond) to the lowest (Tweedie), as defined by the density of deciduous species and preferred species (Table 1). These observations suggest that the subset of time spent foraging on nonwoody plants was not correlated with our measurement of habitat quality. However, because we did not measure the availability of this resource, it is not clear whether this seasonal resource influences time that beavers allocate to foraging.

Basey and Jenkins (1995) found that when facing predation risk, beavers trade off maximization of energy intake against minimi-

zation of predation risk when selecting trees to cut based on their size and distance from the pond. Based on Schoener (1974), Jenkins (1980) proposed that if predation risk is high, beavers can become time minimizers instead of energy maximizers, but this has never been verified. Some beavers in our study area travelled up to 80 m on land to access trembling aspen (Gallant et al. 2004), which would normally expose them to high predation risk (Basey and Jenkins 1995). However, they constituted a small part of the diet of coyote, the most potent predator in the park (Dumond et al. 2001). This suggests that encounter rates between beavers and predators were low and would not have differed substantially among ponds. Whether perceived danger can substantially influence time that beavers devote to foraging, as opposed to forage choices (see Basey and Jenkins 1995), is not clearly understood.

In our study, foraging represented only a portion of the time budget of beavers, and habitat quality did not influence the proportion of observation time spent foraging. Thus, our results suggest that (*i*) beavers strive to optimize time spent foraging independently of habitat quality and (*ii*) there are factors unrelated to habitat quality, such as infrastructure maintenance, and intermittent reactions to perceived dangers that limit the time beavers can devote to maximizing energy intake. A future research angle to understand the population dynamics of this important herbivore should decipher how much habitat quality (i.e., food availability) and environmental stress (e.g., weather, predators) may shape its time budget and, consequently, its survival and reproductive success.

Acknowledgements

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