Territoriality and time budgets in beavers during sequential settlement

BART A. NOLET

Institute for Forestry and Nature Research (IBN-DLO), P.O. Box 23, 6700 AA Wageningen, the Netherlands

AND

FRANK ROSELL

Department of Zoology, University of Trondheim, N-7055, Dragvoll, Norway

NOLET, B.A., and ROSELL, F. 1994. Territoriality and time budgets in beavers during sequential settlement. Can. J. Zool. 72: 1227–1237.

Beavers (*Castor fiber*) were sequentially released into a previously unoccupied area. The settlement of the animals approximated an ideal despotic distribution: they successively settled in rich habitat and then in poor habitat, and then became floaters. This pattern is regarded as evidence that territorial behavior limited density. The early arrivals showed a seasonal difference in territory size (small in winter, large in late spring and summer), which was expected from optimal territory size theory but which was not found in later arrivals. In the first 2 years, the beavers were swimming very large distances (up to 20.0 km per night), and were apparently undergoing a long-term decline in body condition. Body temperature decreased during swimming, especially in winter (daily amplitude 2.04°C). Each year, winter territories were about the size (7.9 ± 0.9 (SE) km, including 3.0 ± 0.4 km of wooded banks) that beavers could patrol daily without losing body condition. The number of territories established at any one time during the 5 years of study was only half the carrying capacity calculated on the basis of the current length of wooded banks within territories, in accordance with the prediction for sequential settlement in linear habitats. However, extensive no-man's-land was not present between territories, but early arrivals claimed larger territories than later ones. Social and thermoregulatory factors seem to play an important role in determining the costs of territory defense, and hence territory size. Overexploitation of the beaver's main food source, willow (*Salix* spp.), seems unlikely in this productive habitat.

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Des Castors européens (*Castor fiber*) ont été relâchés progressivement dans une aire préalablement inoccupée. Le type de colonisation utilisé se rapprochait d'une répartition despotique idéale : les castors ont d'abord envahi les habitats riches, puis les habitats pauvres et finalement les derniers arrivants étaient des vagabonds. Ce type de colonisation indique que le comportement territorial des castors en limite la densité. Chez les premiers arrivants, la taille des territoires était fonction de la saison (petits territoires en hiver, grands territoires au printemps et en été), ce qui correspond bien à la théorie de la taille optimale des territoires, mais ce pattern ne s'est pas répété chez les colonisateurs plus tardifs. Au cours des 2 premières années, les castors parcouraient de très grandes distances (jusqu'à 20,0 km par nuit) et semblaient prêts à subir une détérioration à long terme de leur condition physique. La température du corps baissait au cours de la nage, surtout en hiver (amplitude quotidienne de 2,04°C). Chaque année, les territoires d'hiver avaient à peu près les dimensions (7,9 ± 0,9 (erreur standard) km, dont 3,0 ± 0,4 km de berges boisées) que les castors pouvaient patrouiller chaque jour sans subir de détérioration de leur condition physique. Le nombre de territoires établis à un moment donné au cours des 5 années d'étude correspondait toujours à la moitié de la capacité théorique calculée en fonction de la longueur des berges boisées à l'intérieur des territoires, selon la théorie de la colonisation séquentielle dans des habitats linéaires. Cependant, il n'y avait pas de zones inoccupées très grandes entre les territoires, mais les premiers arrivants se sont appropriés des territoires plus grands que les arrivants plus tardifs. Des facteurs sociaux et thermorégulateurs semblent jouer un rôle important dans la détermination des coûts associés à la défense territoriale, et donc à la taille des territoires. La surexploitation de la principale source de nourriture des castors, les saules (*Salix* spp.), semble peu vraisemblable dans ce milieu très productif.

[Traduit par la Rédaction]

Introduction

Beavers (*Castor* spp.) live in family groups, which defend territories against other beavers (Bradt 1938; Djoshkin and Safonow 1972). Both the adult male and female participate in marking territorial boundaries at scent mounds, as do the yearlings (Aleksiuk 1968; Butler and Butler 1979; Svendsen 1980a). Aggressive encounters are not rare. For instance, bite wounds from conspecifics are the most important cause of death of adult beavers in a dense population of *Castor fiber* along the Elbe. Such deaths occur mostly in May at the time new territories are established (Piechocki 1977).

Aleksiuk (1968) regarded territoriality in beavers as a means of population regulation, thus preventing the depletion of food supply. However, the hypothesis that group territoriality limits density in beavers has never been tested. Moreover, the factors that determine group and territory size

have received little attention so far. The only experiment reported is that by Müller-Schwarze and Heckman (1980), who showed that beavers were less likely to colonize a vacant lodge if artificial scent mounds were constructed in its vicinity. A more fundamental understanding of territoriality in beavers is needed to predict the carrying capacity of a given area, which in turn is needed to model persistence time of an isolated beaver population (Goodman 1987).

Density is limited by territoriality when newcomers are prevented from settling by aggressive residents. One way to test the density-limiting hypothesis is by an experiment in which territory owners are removed. Subsequent observations can show whether the vacant territories are taken over by individuals that otherwise would have had a selective disadvantage (Davies 1978). Alternatively, one can sequentially add new pairs to a previously unoccupied area and check

whether the number of territories established is progressively smaller than the number of pairs attempting to settle. In more detail, it is predicted that animals first settle in rich habitat until it is full; this is followed by the occupancy of poor habitat (Fretwell and Lucas 1970). When all available habitats are occupied, new arrivals will be "floaters" without a territory (Davies 1978). This settlement pattern was termed the ideal despotic distribution by Fretwell (1972).

Cost–benefit models of territoriality argue that an optimal territory size should exist, and some have been successful in predicting territory size (Dill 1978; Pyke 1979). In these models, territory size affects the animal's food availability, its time budget, its distance moved, and the intruder pressure. Conversely, one can argue that these factors determine territory size.

In the Netherlands, beavers became extinct in 1826 (Van Wijngaarden 1966). In 1988–1993, a reintroduction experiment took place, with the sequential release of a total of 42 beavers (34 beavers >1 year old and 8 kits) (Nolet 1992). We studied the pattern of settlement of the beavers in detail. Territory sizes of new arrivals were assessed by radiotelemetry and those of settled beavers from the distribution of scent mounds. Habitat selectivity was determined in order to define rich and poor habitats. Food productivity as well as time budgets, daily distance moved, and body-temperature changes were recorded to obtain clues about the determinants of territory size.

Study area

The study was carried out in the Biesbosch (about 150 km^2) in the freshwater estuary of the rivers Rhine and Meuse in the Netherlands (51°45′ N, 4°50′ E). The central part is a nature reserve (about 50 km^2) intersected by creeks. It consists of willow coppices and reedbeds that are no longer exploited. The nature reserve is surrounded by agricultural fields and former creeks with more or less intact banks.

The climate is wet and mild. During 4 of the 5 study years the weather was extremely warm, with mean temperatures dropping to below 0°C on only 2–20 days compared with the normal 27 days. Only 1991 was normal in this respect.

Materials and methods

Six, 10, 11, and 7 European beavers >1 year old were sequentially released in October–November of 1988 through to 1991. We marked the animals with colored and aluminium ear marks for visual identification. Loss of aluminium ear marks was high (50%), but only 9% of the colored ear marks were lost. A radio transmitter was implanted intraperitoneally in 31 beavers (Davis et al. 1984). The transmitters weighed 52–92 g (always <0.6% of body mass). A radio frequency of 30 MHz was used because its signal is absorbed or reflected by water and vegetation to only a minor extent (Broekhuizen et al. 1980). The reception range was 300–600 m from a boat and 1–2 km from an airplane. The life-span of the transmitters implanted in 1988–1990 was, on average, 1.2 ± 0.2 (SD) years (N = 17, excluding 7 beavers that died before the transmitters expired). Thus, in the first 4 years of the study only new arrivals were radio-tracked. These animals were not reproducing during data collection. The seven transmitters implanted in the autumn of 1991 had a life-span of ca. 2 years, so that the four beavers which were radio-tracked in 1993 had been in the area for more than 1 year.

Pulse frequency was 20–30 min depending on body temperature. The temperature sensitivity of 10 transmitters was calibrated prior to implantation by measuring the pulse interval between 25 and 45°C (N = 14 temperatures). The pulse interval decreased curvilinearly with temperature (t). The constant, t and t^2, contributed significantly to the second-order regressions, and r^2 varied between 0.996 and 0.999. We rearranged the regression equations in order to estimate body temperature from the pulse interval. At 37°C the predicted mean was

37.0001°C, with a 95% confidence interval of ±0.155°C (N = 8). Three transmitters recovered after more than a year appeared to have had a drift of 0.002, 0.002, and 0.005°C · d^{-1}. We made no attempt to correct for this drift, and restricted the analysis to within-day variation in body temperature. Body temperatures of eight animals (one died and one disappeared shortly after release) were collected in 1990–1991. Air and water temperatures were recorded simultaneously.

During the first year after release the daytime resting site of each beaver was located, on average, every 7.2 ± 3.5 (SD) days (N = 31). On eight occasions an airplane was used to find beavers that had not been found by boat for 2 weeks. We regarded beavers that did not settle within the first 3 months as floaters. For each month we calculated the linear distance (i.e., as the crow flies) from a beaver's main resting site to that of its nearest neighbor.

During a freeze-up in February 1991, we made a continuous automatic registration of the presence or absence of two adult beavers at one den for 3 days. The reception range was 50 m.

In ice-free conditions, beavers were tracked at night by rowing boat. A beaver was mostly tracked for half a night, from prior to the moment it left its daytime resting place in the evening until midnight, or from midnight until after it entered the daytime resting place in the morning. An animal was located by homing-in on it. While on land, the beavers spent the greatest portion of their time within 1 m of the water's edge (Nolet et al. 1994), therefore it was possible to determine their location by taking the crossing of one bearing and the bank (White and Garrott 1986). Testing under field conditions revealed that the fix tended to lie slightly to the left of the position of the transmitter (average error 2.8° ± 6.4° (SD), N = 36). At the average distance between observer and beaver of 50 m (at right angles to the bank), this corresponds to an error of 2.4 ± 5.6 (SD) m. We did not correct for this, since it was small compared with the minimum segment length of bank types (see below). We focussed upon the animal with infrared binoculars or, when it was farther than 25 m away from the observer, with the aid of a lamp. The animal was located every 15 min (a total of 9350 fixes). We chose this time interval because time budgets and distance moved, as well as territory size, were to be derived from these measurements. The use of so-called independent fixes gives a tremendous underestimation of the time budget and distance moved (Reynolds and Laundre' 1990).

The distance between successive fixes was determined to an accuracy of 25 m following the waterways with an integrator on a 1 : 10 000 scale map. To assess a possible observer effect on distance moved per night, we tested whether the linear distance (i.e., as the crow flies) from the location at midnight to the resting place of the previous day was greater when the animal had been tracked during the first half of the night or when it was picked up in order to be tracked during the second half of the night. After correcting for individual differences, no significant effect of night half was found (regression analysis by factor beaver, $F_{(22,305)}$ = 4.37, P < 0.001, and night half, $F_{(1,304)}$ = 3.07, P = 0.081).

For each month we averaged the distances moved per 15-min period and summed these averages to obtain a daily distance moved in that month. During 15-min periods of nonstop swimming, beavers moved an average distance of 724 ± 12 (SE) m (N = 87). This is equivalent to a swimming speed of 2.9 km · h^{-1}, equal to the optimum swimming speed predicted from the beavers' body length (without tail) (Videler and Nolet 1990). We determined the duration of "swimming bouts" by counting the number of successive 15-min periods with a distance moved >375 m (equivalent to a displacement speed of 1.5 km · h^{-1}, so that the beavers swam for at least 50% of the time during a swimming bout).

From the steadiness of the signal from the transmitter, it was possible to determine whether an animal was inactive or active, and in the latter case, whether it was swimming. Every 15 min the behavior of the animal was classified into broad categories (inactive inside den, active inside den, swimming, on a bank). We assumed that when the animal was out of view on a bankside, the proportions of time it spent in foraging, grooming, and other activities were equal
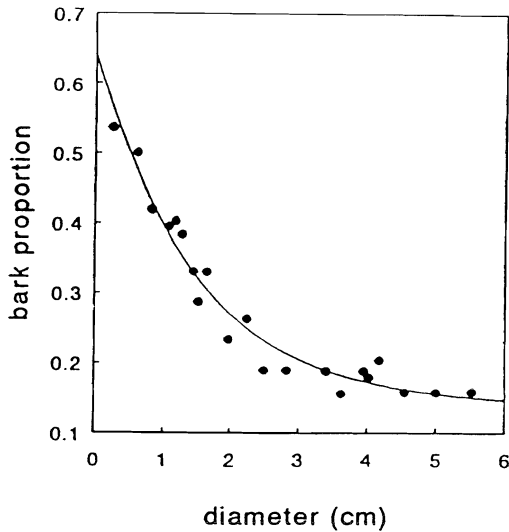
FIG. 1. Proportion of bark, p_{bark} (i.e.. bark mass/total mass), plotted against branch diameter in the willow *Salix alba*, with a fitted exponential curve.

to when it was in view. Because these data were collected from radio-tagged animals, the "pickup" bias involved was probably small in comparison with that in Rugg and Buech's (1990) study. The first part of the night tended to have been sampled slightly more than the second part, and we adjusted the time budget for this by weighting the observations accordingly.

On inspection by boat, the banks of waterways >5 m wide were classified as wooded, with herbs, with reeds, or barren, according to the dominant vegetation. The minimum segment length of a particular habitat type was 25 m. The banks were digitized from a 1 : 10 000 scale map into a GIS-system (ARC/INFO). The animals' locations were also digitized and plotted onto this map. We considered territories to be one- rather than two-dimensional, and we determined the length of banks within the extreme locations. Both banks were always included if a waterway was <100 m wide, because beavers frequently crossed such waterways and it was not always possible to tell along which bank they swam. For waterways >100 m wide, only the bank actually used by the beaver was included. Since beavers are mainly dependent on wooded banks for food and shelter, we classified territories that contained more or less than 25% wooded banks as rich and poor habitat, respectively. We quantified habitat utilization by attaching the bank type of the nearest bank to a beaver fix in the ARC/INFO coverage, including only those fixes in which the beavers were on a bank but away from the den.

Beavers were tracked during winter (November–December, later December–January), early spring (February–March, 1989 only), late spring (April–May), and summer (July–August). Within a territory, either one or both pair members were followed. Each beaver (pair) was tracked, on average, for 6.3 ± 3.1 (SD) nights (N = 46) per bimonthly period. To assess the effect of the number of tracking nights, five beaver pairs were tracked for 12 or 13 nights in a bimonthly period. We calculated their cumulative range (adding tracking nights in a random order) and fitted an exponential curve to the cumulative range on the number of tracking nights with pair as factor (accounting for 97.2% of the variance). A tracking effort of 6.3 nights yielded, on average, 71.1 ± 4.5% (SE) (N = 5) of the range covered after the theoretical maximum of 61 nights. We arbitrarily regarded this core area as the seasonal territory. In 1988–1992, 14 beavers (or beaver pairs) were eventually tracked in different seasons (winter as well as late spring and (or) summer) without their moving to another territory. We called these ranges year-round

TABLE 1. Ratio of the proportion of beaver fixes on banks located on wooded banks (p_{obs}) and the proportion of the territory consisting of wooded banks (p_{exp}); a ratio larger than 1 indicates that the the beavers preferred wooded banks

Year	p_{obs}/p_{exp}	N
1	1.72±0.04	480
2	1.72±0.41	780
3	2.25±0.59	694
4	1.61±0.06	569
Total	1.85±0.45	2523

NOTE: Ratios are given as the mean ± SD. N is the number of fixes on banks.

territories; they were based on an average of 20.6 ± 9.4 (SD) tracking nights.

In April to August 1993, all 13 territories present were mapped. Three beavers (or beaver pairs) were radio-tracked on 20.3 ± 0.6 (SD) nights, on average, and their ranges were delineated as outlined above. In addition, the study area was traversed each night by boat to spot ear-tagged beavers. The scent mounds in the study area were checked weekly. Scent mounds were assigned to a beaver family according to the nearest beaver sighting. The territorial boundaries were drawn on the basis of the locations (concentrations) of the scent mounds.

Primary productivity of *Salix alba* bark and twigs with leaves was measured in the winter and summer of 1992, respectively, in three coppices that had been cut 1, 2, or 3 years earlier. During the winter, six willows per coppice were randomly chosen. All the branches of each willow were sawn off, cut into parts, and divided into seven diameter classes between 0 and 6 cm. The total wet mass of the parts was determined, and this was converted to wet bark mass using a relationship between the proportion of bark (p_{bark}, i.e., bark mass/total mass) and branch diameter, derived by stripping bark from 21 samples of different diameters. This relationship was nonlinear and an exponential curve was fitted, which accounted for 95.4% of the variance (Fig. 1):

$$p_{bark} = 0.138 + 0.505 \times 0.510^{diam} \quad (F_{[2,18]} = 209.65, P < 0.001)$$

In the summer, six other willows per coppice were chosen. For each willow, we clipped all twigs with a diameter of 0.5 cm with their adhering leaves and weighed them.

Results

The beavers appeared highly territorial. Trespassing beavers always quickly swam through or along another beaver's territory, and in contrast with territory owners, did not spend much time on a bank. During encounters at a common boundary the beavers swam in circles and tail-slapped. Overt aggression was only observed twice. On one occasion, an adult female had entered her neighbor's territory and was chased by the resident male. On another occasion, a senile female had bite wounds on the face and flank 2 weeks after her mate had left her, and was apparently forced by newcomers into a remote corner of her former territory. Information about vacant territories was apparently rapidly available to nearby beavers. In two instances a subadult female was recorded to join a male in a neighboring territory 1.5 and 4 weeks, respectively, after the male's mate had died.

All beavers (or beaver pairs) that were tracked year-round showed a preference for wooded banks during their bank-related activities: the preference ratio (p_{obs}/p_{exp}) was,
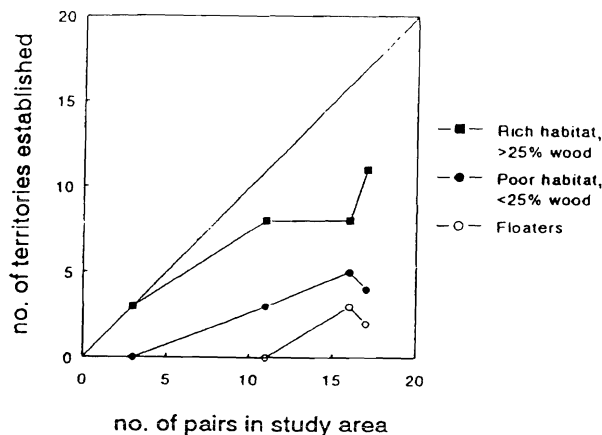
FIG. 2. Cumulative settling pattern of beavers in rich and poor habitats during four sequential releases. Floaters are beavers without a territory 3 months after release.

on average, 1.85 (Table 1), being >1 in all 14 cases (binomial probability at P ($p_{obs} > p_{exp}$) = 0.5 is $P << 0.001$). The preference ratio did not change with the year of study (regression analysis, $F_{[3,10]} = 1.79$, $P = 0.21$). The proportion of wooded banks within the territory therefore seems to be a reasonable measure of habitat quality. All first arrivals (3 pairs) settled in rich habitat. In the second year, another 5 pairs settled in rich habitat and 3 pairs settled in poor habitat. In the third year, only 1 pair settled in rich habitat and 5 pairs in poor habitat, and 3 animals became floaters. In the fourth year the corresponding numbers were 1, 2, and 2. Thus, in accordance with expectation, rich habitat filled up first, followed by occupancy of poor habitat and then the appearance of floaters (Fig. 2).

One beaver emigrated from the population 1 week after release in the fourth year of the study. Its route, which could be reconstructed from a sighting and cuttings, was about 50 km long. Four weeks later the beaver was caught and released again in rich habitat in the Biesbosch. It disappeared within 1 week, having probably emigrated again.

Year-round territories of new arrivals were initially very large, but they roughly halved in size each year (Fig. 3a). Overlap with those of neighboring beavers was 14.5 ± 4.2% (SE) ($N = 14$). Seasonal territories also differed from year to year (regression analysis after logarithmic transformation of territory size, $F_{[1,45]} = 19.15$, $P < 0.001$) and between seasons ($F_{[2,43]} = 6.16$, $P = 0.005$). The beaver-pair factor did not significantly contribute to the regression model and was not incorporated. The interaction between year and season, however, was also significant ($F_{[2,41]} = 9.48$, $P < 0.001$), indicating that seasonal differences were not consistent among years. In the first year, winter territories were only one-fifth or one-sixth of late spring and summer ranges, but in the third and fourth years a seasonal pattern was no longer found (Table 2). Whereas late spring and summer ranges roughly halved each year, winter ranges peaked in the third year (Table 2). Winter ranges were, on average, 7.9 ± 0.9 (SE) km ($N = 19$). The lengths of wooded banks within winter ranges did not differ between years (Kruskal–Wallis one-way

TABLE 2. Seasonal territory sizes (km) of beavers in 4 consecutive years

Year	Winter	Late spring	Summer
	All banks		
1	6.1±2.0 (3)	36.5±7.8 (3)	29.3±3.1 (3)
2	7.6±2.1 (6)	17.1±2.2 (5)	21.0±5.1 (4)
3	10.8±0.7 (6)	8.5±2.2 (4)	10.0±2.8 (4)
4	5.6±0.4 (4)	6.4±1.0 (2)	6.4±1.1 (2)
	Wooded banks		
1	2.5±1.1 (3)	15.3±0.6 (3)	12.5±2.7 (3)
2	3.7±0.9 (6)	6.4±0.6 (5)	8.8±1.7 (4)
3	3.3±0.9 (6)	2.2±0.5 (4)	3.3±0.7 (4)
4	2.0±0.4 (4)	1.5±0.5 (2)	1.7±0.6 (2)

NOTE: Values are given as the mean ± SD, with the sample sizes in parentheses.

TABLE 3. Distance (km) as the crow flies to nearest-neighbor beaver pair within the first 3 months after release and after settlement in 4 consecutive years

Year	First 3 months after release ($N = 3$)	After settlement ($N = 9$)
1	1.44±0.23	2.06±0.12
2	1.95±0.05	2.02±0.05
3	1.74±0.15	1.83±0.09
4	1.53±0.16	1.62±0.03 (8)

NOTE: Values are given as the monthly mean ± SE. The number in parentheses is the only sample size that differs from 3 or 9.

ANOVA, $P = 0.53$), and were, on average, 3.0 ± 0.4 (SE) km ($N = 19$), or 38% of total bank length.

The monthly mean of the linear distance to the nearest neighbors was dependent on both the year of study (regression analysis, $F_{[1,45]} = 9.26$, $P = 0.004$) and a factor indicating whether more than 3 months had elapsed after release (after which most animals were settled; $F_{[1,44]} = 5.71$, $P = 0.021$) (Table 3). Excluding the first 3 months after release, the distance to the nearest neighbor clearly decreased with the year of study ($r^2 = 0.32$, $P < 0.001$, $N = 35$). However, in 1993 (the fifth year of the study), the territories of the early arrivals still appeared to be larger than those of later arrivals (Fig. 3b). All previously occupied 11 territories in rich habitat were still inhabited in 1993, but only 2 out of 10 previously occupied territories in poor habitat. In 1993, the average territory size was 12.8 ± 1.5 (SE) km, of which 4.8 ± 0.9 (SE) km was wooded ($N = 13$).

In a multiple regression model, the monthly means of the distance moved per night were dependent on the year of study ($F_{[1,22]} = 19.77$, $P < 0.001$) and season ($F_{[2,20]} = 6.97$, $P = 0.006$), but the interaction between year and season also contributed significantly ($F_{[2,18]} = 14.01$, $P < 0.001$). Except for winter, season did not have a significant effect, and the distance moved per night gradually decreased in the course of the study (linear regression of distance moved on year of study, $r^2 = 0.80$, $P < 0.001$, $N = 16$ months). In winter, however, the distance moved per night remained nearly the same ($r^2 = 0.26$, $P = 0.195$, $N = 8$ months), and was, on average, 5.2 ± 0.5 (SE) km. The maximum recorded distance covered per night was 20.0 km on 16 April 1989. When

TABLE 4. Time of exit from and return to the den by radio-tagged beavers in four seasons in MET: the daily time spent resting (T_r) is calculated as the difference between the average return and exit times

	Exit			Return				
	Mean time	SE (min)	N	Mean time	SE (min)	N	T_r	T_r (mean $\pm$ SD)[a]
Winter	17:57	8	47	06:05	14	32	11.9	12.04$\pm$0.4
Early spring	18:46	5	23	06:21	14	15	12.4	
Late spring	19:25	3	75	05:19	10	46	14.1	14.0$\pm$0.2
Summer	19:46	5	71	05:46	5	49	14.0	14.0$\pm$0.7

[a]Calculated for the 4 years of the study separately.

(a)

(b)
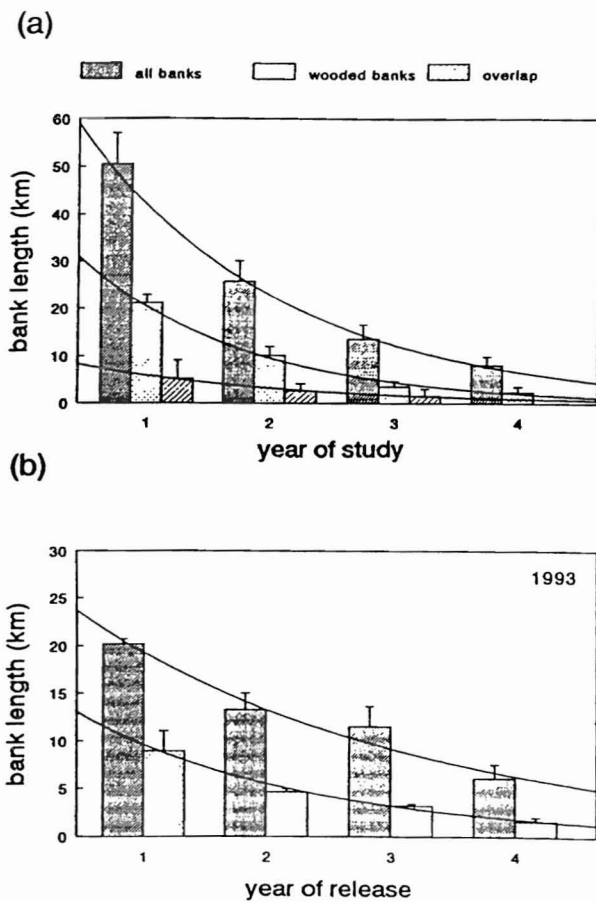
FIG. 3. (a) Year-round territory sizes, length of wooded banks within these territories, and overlap with neighboring territories (mean $\pm$ SE) for radio-tagged beavers in the course of the study ($N = 3, 5, 4$, and 2). (b) Territory sizes and lengths of wooded banks (mean $\pm$ SE) for all beavers in 1993 plotted against the year of release (of that member of a pair which was released first) ($N = 3, 4, 2, 3$). Exponential curves were fitted to the data.

FIG. 4. Distance moved per night versus seasonal territory size (mean $\pm$ SE) for radio-tagged beavers during 12 bimonthly periods. The line indicates a ratio of 1:1.

distance moved is plotted against territory size (Fig. 4), it is clear that the beavers were not patrolling all the banks within their territory daily in the late spring and summer of the first 2 years. Later, the ratio of territory size to distance moved approached 1, suggesting a daily patrol of territories.
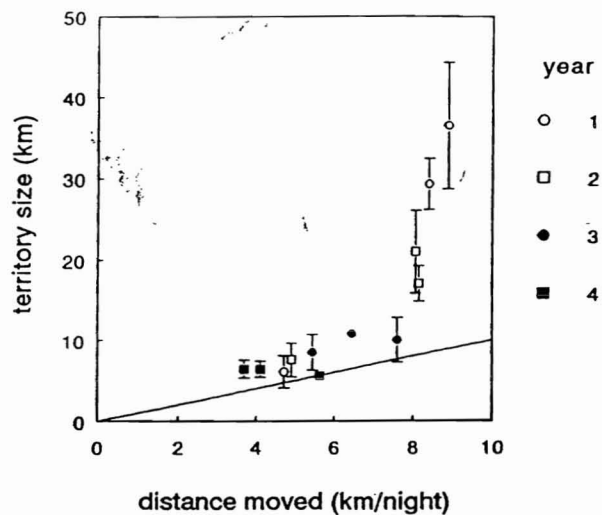
The time-budget data from 4 years of study and three seasons were analyzed using a regression model with year as variable and season as factor. The year × season interaction did not contribute significantly to any of the time–budget variables and was excluded from the model. The time spent resting did not vary among years ($F_{[1,8]} = 0.03, P = 0.87$), but it did among seasons ($F_{[2,9]} = 13.56, P = 0.003$): during ice-free conditions in winter, beavers rested less than in late spring or summer (Table 4). The time spent foraging also differed between seasons ($F_{[2,9]} = 11.46, P = 0.004$): in ice-free winters, the beavers spent, on average, 7.7 ± 0.6 (SE) h ($N = 4$) per night foraging, but in late spring and summer this was reduced to 5.0 ± 0.2 (SE) h ($N = 8$). No trend was observed among years ($F_{[1,8]} = 0.51, P = 0.50$). Surprisingly, we found no seasonal difference in the time spent swimming ($F_{[2,9]} = 1.37, P = 0.31$), but the differences between years were significant ($F_{[1,8]} = 5.68, P = 0.044$). In the first 2 years of the study, the beavers spent considerable time exploring their new surroundings, the maximum being 6.3 h $\cdot$ d^{-1} in early spring 1989. Excluding these years, the daily time spent swimming significantly differed among seasons ($F_{[2,3]} = 9.54, P = 0.05$), increasing from 2.9 ± 0.2 (SE) h ($N = 2$) in winter to 4.2 ± 0.2 (SE) h ($N = 4$) in late spring and summer. During the 3 days of recording ice conditions in early spring 1991,
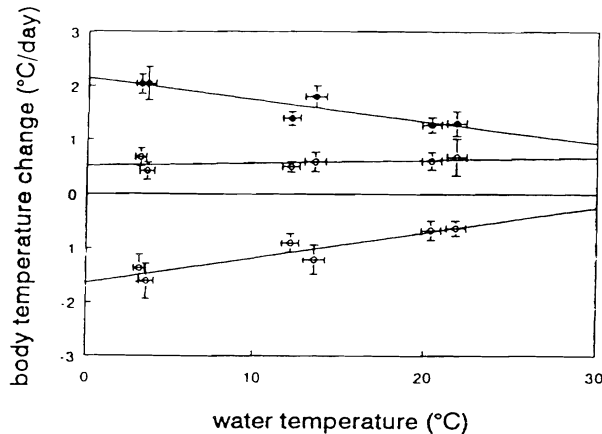
FIG. 5. Daily body temperature change (mean ± SE) in relation to water temperature over 6 months (N = 9, 14, 11, 14, 9, and 6). ●, difference between daily maximum and minimum body temperatures; ○, difference between daily maximum (upper data points) or minimum (lower data points) body temperature, respectively, and value at resting site.

the beavers were inside the den for as much as 19.7 h · d^{-1} and otherwise foraged close to the den, spending very little time swimming beneath the ice. In winter and early spring, the daily time spent swimming was negatively related to water temperature (r^2 = 0.82, P < 0.02, N = 6).

Swimming bouts were shorter in winter and early spring than in late spring and summer. The maximum duration was 60 min in the winter (N = 118 swimming bouts) and early spring (N = 43). In the late spring and summer of 1989, it was 165 (N = 66) and 135 min (N = 70), respectively. This coincided with a greater change in body temperature per day in winter than in summer: the daily amplitude was, on average, 2.04°C in midwinter and only 1.27°C in midsummer (Fig. 5). Body temperature increased during nonforaging sessions on the bank (presumably mainly grooming) and decreased during swimming (Fig. 6), rising 0.6°C above body temperature during the daytime in both winter and summer, but dropping more in winter (−1.5°C) than in summer (−0.6°C) (Fig. 5).

Bark and leaf production was high (Table 5). Yearly bark production was maximal after two growing seasons, whereas yearly leaf production was already maximal after one growing season.

Discussion

Time allocation and optimization criterion

Pyke (1979) used a cost–benefit model to predict the optimal territory size of nonreproducing sunbirds (*Nectarinia reichenowi*). He found good agreement with observed values, assuming the birds were minimizing their energy expenditure. Earlier, Dill (1978) showed that optimal territory size should vary with the optimization goal used by the defender. In particular, an animal maximizing its energy gain (G) should defend larger territories than an animal minimizing its energy expenditure. The animal's optimization criterion might alter in the course of the year. Masman et al. (1988) showed that European kestrels (*Falco tinnunculus*) switch their optimization criterion from minimization of energy expenditure in winter

TABLE 5. Yearly production (kilograms wet mass per tree per year) of bark and twigs with leaves of willow (*Salix alba*) in coppices after one, two, or three growing seasons

Growing season	Production	
	Bark	Twigs with leaves
1	1.62±0.37	4.63±1.04
2	2.84±0.64	3.54±0.70
3	1.80±0.34	2.51±0.91

NOTE: Values are given as the mean ± SE (N = 6).

to maximization of energy gain during reproduction in summer. This could be a general phenomenon in seasonally reproducing animals.

In summer, beaver food is abundant and of high quality (Simonsen 1973; Svendsen 1980b; Roberts and Arner 1984; Histøl 1989; B.A. Nolet, P.J. van der Veer, E.G.J. Evers, and M.M. Ottenheim, in preparation). In this season, the diet of beavers reflects energy gain maximization (Belovsky 1984). In winter, however, beavers are not only faced with poor-quality food (B.A. Nolet, P.J. van der Veer, E.G.J. Evers, and M.M. Ottenheim, in preparation), but also with cold water. The lower critical water temperature is about 20°C for *Castor canadensis* (MacArthur and Dyck 1990). Below this, beavers drop their body temperature between 1.0 and 2.5°C and heat up again in the den or on the bank in more or less regular cooling–heating cycles (MacArthur and Dyck 1990; Smith et al. 1991; Dyck and MacArthur 1992; this study). In extreme cold, activity falls to very low levels and beavers confine themselves to the den and its immediate surroundings (Novakowski 1967; Aleksiuk and Cowan 1969; Lancia et al. 1982).

To gain some insight into the energetic consequences of the time allocation of different behaviors, we expressed daily metabolizable energy intake and daily energy expenditure as functions of the time budget (see the Appendix). The calculated daily energy expenditure decreased from 6755 ± 122 (SE) kJ · d^{-1} in winter (N = 4) to 5823 ± 120 (SE) kJ · d^{-1} in late spring (N = 4) to 5397 ± 128 (SE) kJ · d^{-1} in summer (N = 4). Using MacArthur's (1989) estimate of basal metabolic rate (BMR; 1.70 W · kg^{-1}), this corresponds to 2.3, 2.0, and 1.8 × BMR, respectively. The free-ranging beavers thus expended considerably more energy than the 1.7 × BMR measured in *Castor canadensis* held under simulated ice-free winter conditions (Dyck and MacArthur 1993). The discrepancy was probably due to the fact that the captive beavers were confined to a small tank.

Subsequently, we constructed maintenance lines (G = 0) in the foraging time – swimming time plane. We also expressed the potential daily swimming time as a function of foraging time, assuming a fixed time required for coprophagy, and a requisite body cooling–heating cycle. The maintenance lines and to a lesser extent the potential daily swimming time are dependent on water temperature. We defined the optimal daily swimming time as the potential daily swimming time at which no long-term loss of body condition occurs. For a given water temperature, it is found at the intersection of the maintenance line and the potential daily swimming time.

Under ice-free conditions in the winter, most data points were close to the optimal swimming time (Fig. 7). Beavers
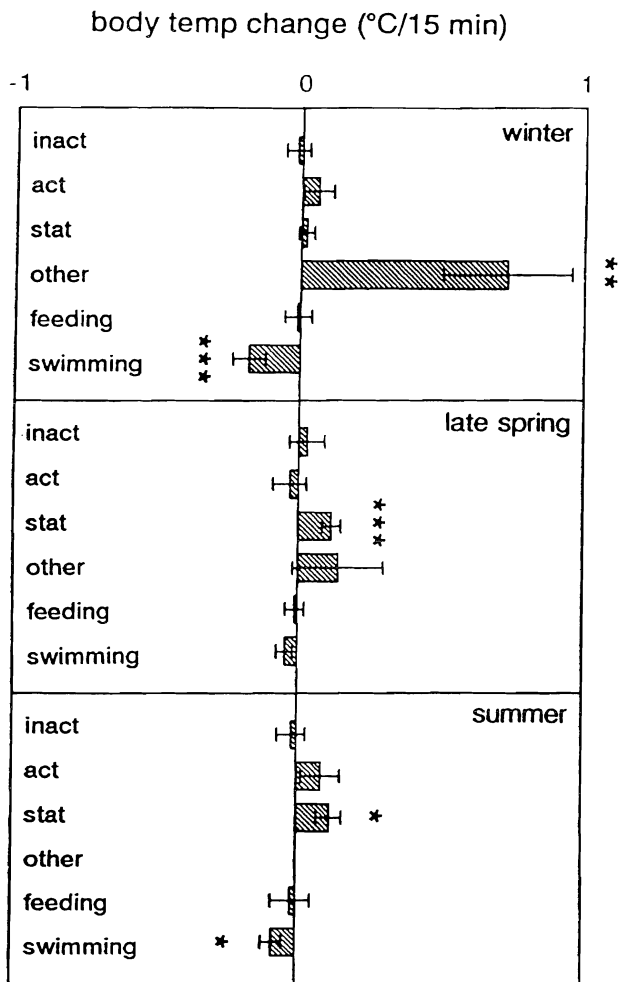
body temp change (°C/15 min)

FIG. 6. Change in body temperature (mean ± SE) of radio-tagged beavers in relation to behavior in winter (total N = 495), late spring (N = 448), and summer (N = 173). Behavioral categories are as follows: inactive inside den (inact), active inside den (act), stationary on bank (stat), other behavior, feeding, and swimming. Difference from zero tested with a t test: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

seemed to maximize their swimming time while remaining at maintenance, swimming for 2.7–4.1 h·d⁻¹. This is more than the immersion time of 2.3 h·d⁻¹ found by Dyck and MacArthur (1993) in captive *C. canandensis* held in a small tank at similar ambient temperatures. Two notable exceptions were early spring of the first year and winter of the second year, when the beavers were probably willing to accept loss of body condition in order to explore their new surroundings. When ice prevented the beavers from swimming much in early spring of the third year, they needed less food in order to assimilate as much energy as they expended. They minimized their energy expenditure (a calculated 4141 kJ·d⁻¹, or 1.4 × BMR) and did not have to eat into their body reserves.

In late spring and summer, conditions are much more favorable for swimming large distances. In late spring, three of the four data points were on the right of the maintenance lines: the beavers benefitted from the good food conditions

and gained in body condition. The data points are close to the line of potential swimming time, which suggests that swimming time was constrained by thermoregulatory requirements (Fig. 7). Only in the late spring of the first year did beavers spend a lot of time swimming and they were probably losing body condition, again as a result of exploration. This loss of body condition did not, however, cause higher mortality in these beavers (B.A. Nolet and J.M. Baveco, in preparation). In the summer, food conditions were already deteriorating and data points were close to the optimal swimming time (Fig. 7).

In summary, during ice conditions beavers truly minimized their energy expenditure by practically refraining from swimming. Territorial patrol was probably not feasible or necessary, because the beavers would rapidly lose body condition when swimming large distances. Under ice-free conditions in the winter, as well as in the summer, beavers maximized their swimming times while assimilating just enough energy for maintenance. Beavers only gained energy during good food conditions in late spring. Swimming is probably mainly associated with territorial patrol. In the first 2 years, when the beavers were exploring the area, they apparently underwent a long-term decline in body condition. We conclude that time allocation, and hence the seasonal differences in territory size, are largely determined by the interaction between the optimization goal and thermoregulatory constraints.

Sequential settlement and carrying capacity

In this study, we showed that sequentially released beavers successively established territories in rich and poor habitats, and finally became floaters, settling into a pattern approximating the ideal despotic distribution (Fretwell 1972). This can be regarded as evidence that territorial behavior is limiting for density in beavers, as postulated by Aleksiuk (1968). Maynard Smith (1974) modeled sequential settlement in territorial species. According to his model, newcomers would not settle between two established territories when the no-man's land in between is not large enough for a new territory. He concluded that in the worst case, the density in linear habitats would be only half that reached during simultaneous settlement. Stamps (1992) showed that the density does not have to be less after sequential settlement, because animals might be attracted to settle next to already established territories.

It is difficult to estimate the carrying capacity of the study area on the basis of our results. However, we found that the seasonal difference in territory size of newcomers (small in winter, large in late spring and summer), which was expected from optimal territory size theory, gradually disappeared in the course of the study. We furthermore found that winter territories were about the size a beaver can daily patrol, and that the length of wooded banks within winter territories did not differ between years. We therefore expect that all territories will eventually shrink to the present winter territory size and contain, on average, 3.0 km of wooded banks.

In the study area, which comprised 128.6 km of wooded banks, there was space for about 43 territories (128.6/3.0). Only 21 territories, i.e., only half this number, had been occupied at any one time during our study, in accordance with Maynard Smith's model. However, no evidence was found for an extensive no-man's-land between territories. Early arrivals appeared to claim larger year-round territories than later ones. The mere
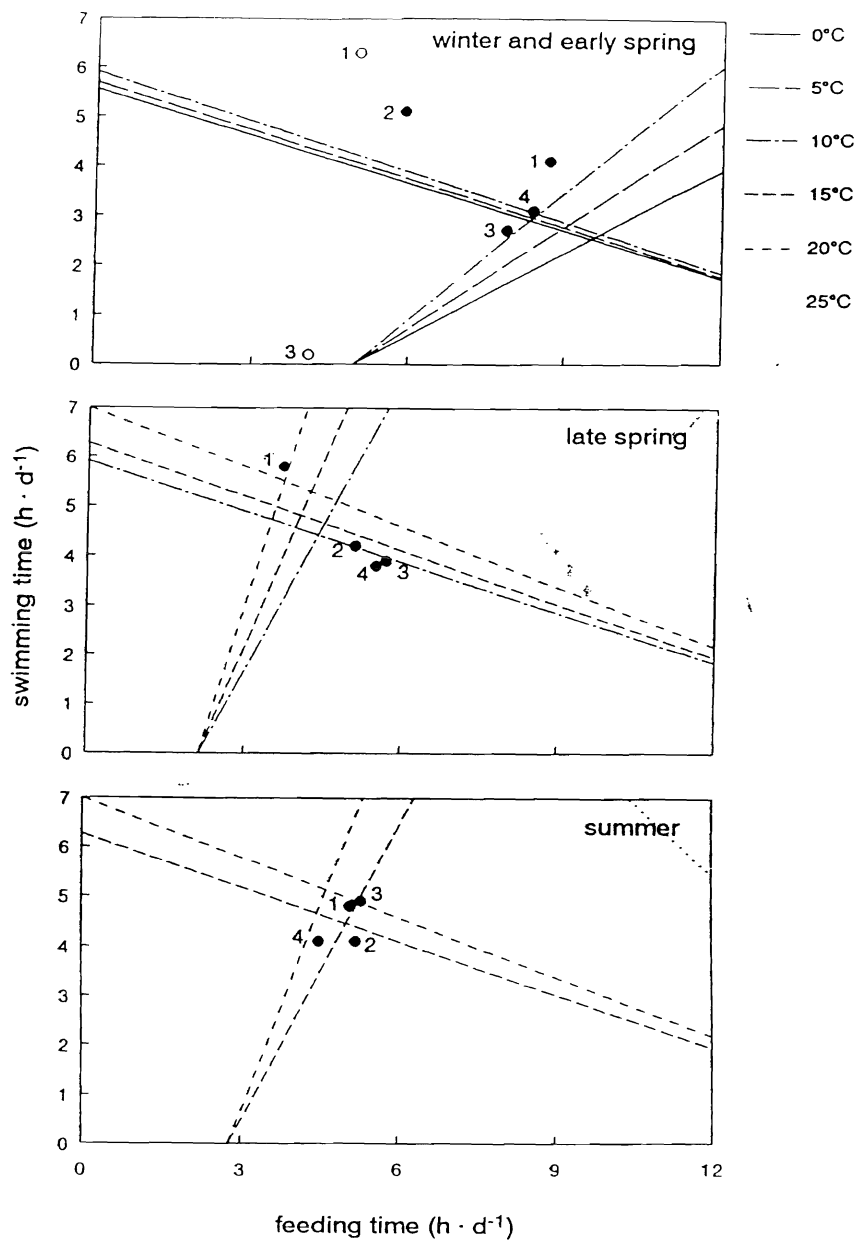
FIG. 7. Daily foraging time versus swimming time during four seasons: winter (●) and early spring (○), late spring, and summer. Numbers indicate the year of study. Maintenance lines (increasing from left to right) and lines of potential swimming time (decreasing from left to right) are given for three representative water temperatures per season. The maintenance line of 25°C is equal to that of 20°C.

fact that the early arrivals were territory owners before the newcomers arrived apparently put them at an advantage. This is corroborated by the high mortality (33–44%/year) of newcomers that were confronted with territory owners, compared with that of already settled animals (4–18%/year) (Nolet 1992). We conclude that the extent to which territoriality limits density depends on the sequence in which beavers colonize an area.

In temperate regions, beaver territories are generally less than half the size of the present average territory in the

Biesbosch. Heidecke (1986) gives densities of the beaver population in Germany and these correspond to linear territory sizes of 3.1–6.5 km. Davis (1984) radio-tracked *C. canadensis* in South Carolina, and the two territory sizes he recorded, expressed as bank length, were 3.9 and 5.2 km. Surprisingly, his beavers moved, on average, only 1.7 and 3.3 km/night, respectively. This suggests that these beavers did not patrol their territories daily. In his study, however, beavers were located only once an hour and therefore the distances were probably underestimated.

TABLE 6. Values used in calculating metabolizable energy intake[a]

| | Bark (winter) | Twigs with leaves | |
		Late spring	Summer
q	0.515	0.719	0.719
E (kJ · g^{-1} dry mass)	18.5	19.5	19.1
p	0.845	0.732	0.679
DM (g dry mass · g^{-1} wet mass)	0.48	0.40	0.35
I_{wet} (g wet mass · h^{-1})	213	416	416

[a]From B.A. Nolet, P.J. van der Veer, E.G.J. Evers, and M.M. Ottenheim (in preparation).

Aleksiuk (1968) also postulated that territorial behavior was a self-regulating mechanism which prevented food depletion. However, overexploitation of food sources by beavers is a common phenomenon in boreal forests (e.g., Johnston and Naiman 1990). In our opinion, therefore, whether a territory is depleted of food depends on the productivity of the food. Regrowth in willows is high after they have been cut by beavers (Kindschy 1985). In fact, the exploitation of a coppice is based on this ability of willows to regrow.

The density of willows on wooded banks in the Biesbosch was measured in 1989 and 1992 (0.090 and 0.113 tree/m^2; Nolet et al. 1994). Mean daily intake of bark and twigs with adhering leaves measured in captivity was 0.0549 ± 0.0036 (SE) (N = 11) and 0.0952 ± 0.0032 (SE) kg wet mass/kg body mass (N = 27), respectively (B.A. Nolet, P.J. van der Veer, E.G.J. Evers, and M.M. Ottenheim, in preparation). We assume that beavers avoided 1-year-old regrowth because of high concentrations of phenolglycoside compounds in these juvenile-form branches (cf. Basey et al. 1988). In the Biesbosch, the beavers regularly feed up to 6 m from the water's edge (Nolet et al. 1994). Using these data, we calculated that an average family of 4.6 beavers (Heidecke 1984) in a territory with 3.0 km of wooded banks would clip 32% of the 2-year-old regrowth of the willows within 6 m of the water's edge (1.8 ha). In areas without wolf predation, beavers feed regularly up to 20 m from the water's edge (McGinley and Whitham 1985), and in that case they would cut only 10% of the willow regrowth. Overexploitation therefore seems to be unlikely in this productive temperate forest.

Appendix

Calculation of maintenance lines

We assumed that beavers were feeding on bark in winter and on twigs with adhering leaves in late spring and summer (B.A. Nolet, P.J. van der Veer, E.G.J. Evers, and M.M. Ottenheim, in preparation). So far, no metabolic measurements have been done for *Castor fiber*, so we used data on *Castor canadensis* instead. We assumed a body mass (M) of 23 kg (B.A. Nolet, P.J. Van der Veer, E.G.J. Evers, and M.M. Ottenheim, in preparation). Air temperatures were taken from Gilze-Rijen weather station approximately 20 km from the study area. Water temperatures were measured in the Biesbosch by the Water Storage Corporation.

Maintenance requires that

$$[1] \quad G \text{ (kJ · d}^{-1}) = \text{MEI [kJ · d}^{-1}] - \text{DEE [kJ · d}^{-1}] = 0$$

where G is the daily energy gain, MEI is the daily metabolizable energy intake, and DEE is the daily energy expenditure. We expressed MEI as a function of observed foraging time (T_f; h · d^{-1}) as

$$[2] \quad \text{MEI} = q \times E \times p \times T_f \times \text{DM} \times I_{wet},$$

where q is the assimilation quotient, E is the energy content, p is the proportion of the observed foraging time that was actually spent gnawing the food (i.e., excluding selecting and gathering of food), DM is the dry-matter content of the food, and I_{wet} is the fresh-intake rate (Table 6).

We calculated DEE as

$$[3] \quad \text{DEE} = \text{RMR}_{air(tn)} \times T_r + 2 \times \text{RMR}_{air(tn)} \times (T_f + T_h) + \text{WMR} \times T_w$$

where T_r, T_h, and T_w are the time (h · d^{-1}) spent resting, heating up, and in water, respectively, RMR$_{air(tn)}$ is the resting metabolic rate in air in the thermoneutral zone (17.2 × $M^{0.67}$ kJ · h^{-1}; MacArthur 1989), and WMR is the metabolic rate in water. Air temperatures were normally above the lower critical air temperature for a given season (Coles 1967; MacArthur 1989). During foraging and heating up, we assumed a metabolic rate of twice RMR$_{air(tn)}$. Because the average displacement speed was half the optimum swimming speed, we assumed that beavers swam at their optimal speed only half of the time in water and floated during the other half. WMR was thus calculated as

$$[4] \quad \text{WMR (kJ · h}^{-1}) = 0.5 \times \text{GMR} + 0.5 \times \text{RMR}_{water} + \text{PMR}$$

where GMR is the gross metabolic rate, RMR$_{water}$ is the resting metabolic rate in water, and PMR is the surplus cost of postponed recovery. We derived GMR from the equation of Videler and Nolet (1990) for "other submerged swimmers," which we modified for surface swimming and temperatures below thermoneutrality:

[5] $GMR \ (kJ \cdot h^{-1}) = Q_{10}^{((t-t_w)/10)} \times W \times 11.9 \times M^{1.05}$

where Q_{10} is the increase in GMR per 10°C (0.57, from data on muskrat; Fish 1983), t_w is the water temperature (°C), t_{wl} is the lower critical temperature in water (20°C; MacArthur and Dyck 1990), and W is the surplus cost due to the wake on the surface (1.33, from data on muskrat; Fish 1982). MacArthur and Dyck (1990) measured RMR_{water} (kJ $\cdot$ h^{-1}) below t_{wl} as (35.3 − 0.698 × t_w) × $M^{0.67}$, and PMR (kJ $\cdot$ h^{-1}) as (11.6 − 0.413 × t_w) × M^1.

Calculation of potential daily swimming time

The daily time budget can be written as

[6] $24 \ (h \cdot d^{-1}) = T_c + T_f + T_w + T_h$

where T_c is the time spent on coprophagy (6.55 h $\cdot$ d^{-1}; B.A. Nolet, P.J. van der Veer, E.G.J. Evers, and M.M. Ottenheim, in preparation). Both cooling rate (C) and heating rate (H) were dependent on water temperature (derived from MacArthur and Dyck 1990):

[7] $\dot{C} \ (°C \cdot h^{-1}) = 3.344 − 0.1190 \times t_w \ (r^2 = 0.95, N = 4)$

and

[8] $\dot{H} \ (°C \cdot h^{-1}) = 1.560 − 0.0457 \times t_w \ (r^2 = 0.79, N = 4)$

We calculated the time that beavers had to spend heating up as

[9] $T_h \ (h \cdot d^{-1}) = \dot{C} / \dot{H} \times T_w$

The potential swimming time $(T_{w_{max}})$ is therefore

[10] $T_{w_{max}} \ (h \cdot d^{-1}) = (24 − 6.55 − T_f)/(1 + \dot{C}/\dot{H})$

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