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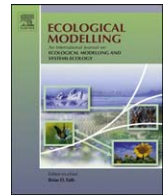Some of the authors of this publication are also working on these related projects:

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Simulation modeling to understand how selective foraging by beaver can drive the structure and function of a willow community

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ABSTRACT

Beaver–willow (*Castor-Salix*) communities are a unique and vital component of healthy wetlands throughout the Holarctic region. Beaver selectively forage willow to provide fresh food, stored winter food, and construction material. The effects of this complex foraging behavior on the structure and function of willow communities is poorly understood. Simulation modeling may help ecologists understand these complex interactions. In this study, a modified version of the SAVANNA ecosystem model was developed to better understand how beaver foraging affects the structure and function of a willow community in a simulated riparian ecosystem in Rocky Mountain National Park, Colorado (RMNP). The model represents willow in terms of plant and stem dynamics and beaver foraging in terms of the quantity and quality of stems cut to meet the energetic and life history requirements of beaver. Given a site where all stems were equally available, the model suggested a simulated beaver family of 2 adults, 2 yearlings, and 2 kits required a minimum of 4 ha of willow (containing about 10 stems m^{-2}) to persist in a steady-state condition. Beaver created a willow community where the annual net primary productivity (ANPP) was 2 times higher and plant architecture was more diverse than the willow community without beaver. Beaver foraging created a plant architecture dominated by medium size willow plants, which likely explains how beaver can increase ANPP. Long-term simulations suggested that woody biomass stabilized at similar values even though availability differed greatly at initial condition. Simulations also suggested that willow ANPP increased across a range of beaver densities until beaver became food limited. Thus, selective foraging by beaver increased productivity, decreased biomass, and increased structural heterogeneity in a simulated willow community.

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1. Introduction

Willow is ubiquitous in Holarctic riparian ecosystems and has likely coexisted with beaver (*C. canadensis* in North America and *C. fiber* in Eurasia) for millions of years (Baker and Hill, 2003). Willow is highly adapted to disturbed riverine environments and can sprout new stems in proportion to the number cut by beaver (Kindschy, 1989). Beaver are ecosystem engineers that can create positive interactions via physical and biological mechanisms (Jones et al., 1997). Beaver are unique herbivores that selectively forage willow to provide fresh food, stored winter food, and construction material for dams and lodges. Generally, plant–animal interactions can develop as mutalisms when foraging benefits vegetation growth

and the new growth benefits herbivores. The outcome of these interactions depends upon foraging intensity, food selection, and plant response to grazing. These interactions are poorly understood for beaver–willow communities. New insights about how selective foraging by beaver affects the structure and function of willow communities may arise from simulation modeling, which can represent complex interactions over a long period of time. We use a systems analysis approach to determine the outcome and condition of beaver and willow interactions. Model representation is based on well-defined mechanisms of species interactions. Interaction outcomes are described using comprehensive variables such as beaver body condition and willow morphology and productivity, which create some testable hypotheses from the simulations described below.

The SAVANNA ecosystem model is a management tool designed for large geographic areas with multiple habitat types and species interactions (Coughenour, 1992, 1994). The use of SAVANNA to predict the consequences of elk and vegetation management in RMNP revealed both its value and limitations for application to

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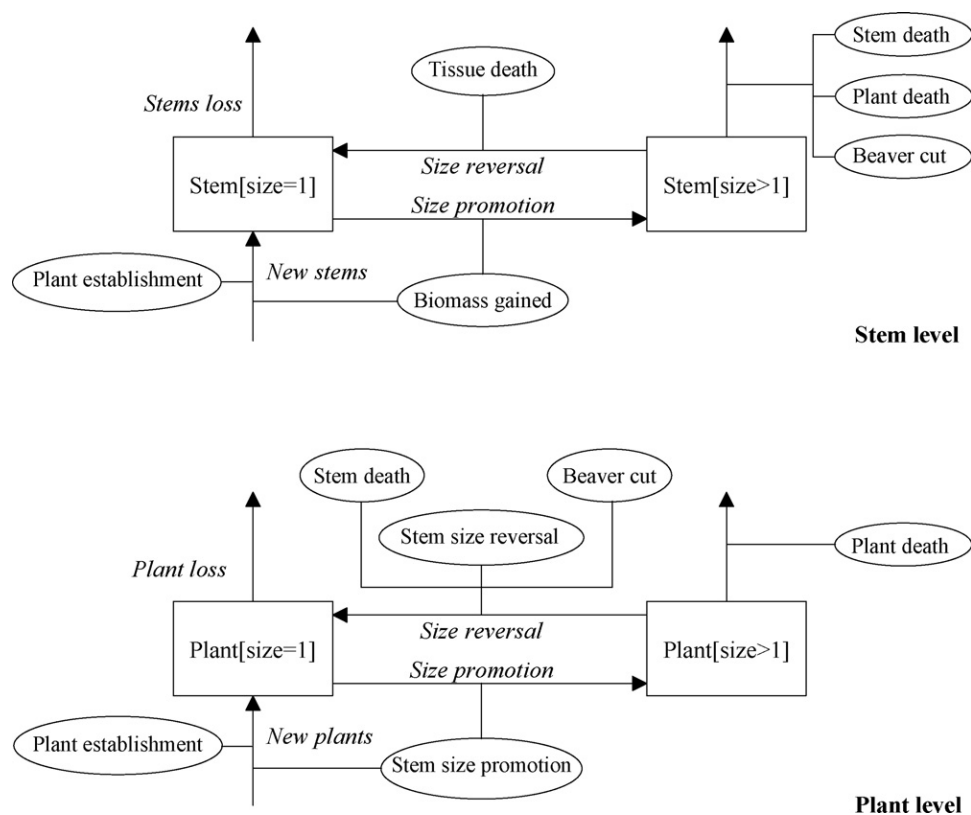*E-mail address:* rpeinett@jornada.nmsu.edu (H.R. Peinetti).

Fig. 1. Schematic of the willow model at both the stem and plant level. Processes represented at the stem and plant levels are interrelated. Stem dynamics are affected by plant establishment, death, and carbon balance (estimated at the plant level). Plant size promotion and reversal are the consequences of the growth and death of stems and the number and size of stems cut by beaver.

riparian ecosystems dominated by beaver and willow. Specifically, SAVANNA models herbivore foraging dynamics (e.g., ungulates) based on the assumptions that herbivores remove only a portion of current annual growth, herbivores entirely consume removed forage, browsing can occur at frequent time intervals, and response to herbivory can appropriately be measured at the plant level rather than the stem level. These assumptions are not valid for beaver because beaver remove entire stems near ground level, removal occurs at infrequent time intervals because stems need several years to recover suitability, stems are used as fresh food, stored food, and construction material, stems may not be fully used, and plants respond to cutting by sprouting new stems from belowground tissues. Thus, the existing SAVANNA model is unsuitable for beaver-engineered riparian ecosystems.

In this paper, we present modifications to the SAVANNA model that make it suitable for a beaver–willow community in RMNP. Then, we use the model to simulate how selective foraging by beaver can alter the willow community. Specifically, we modified the SAVANNA model by representing willow in terms of plant and stem dynamics, and beaver foraging in terms of the quantity and quality of stems used for food and construction activities. Beaver foraging was represented via a nested hierarchy of decision rules based on stem preferences and availability relative to a comprehensive simulation model of willow morphology. The model allowed beaver to select stems within plants, and tissues within stems, and it considered the seasonal differences in selection for use as fresh food, winter food, and construction material (Doucet et al., 1994). The model was used to simulate a small area that included a single beaver family and the willow-dominated riparian they affected. We used the model to determine the minimum area needed to sustain a beaver family based on their annual foraging requirements. Then, given this minimum area, we quantified the long-term con-

sequences of beaver foraging on the structure and function of the willow community and the persistence of beaver–willow interactions.

2. Methods

2.1. The SAVANNA Model

SAVANNA is driven by monthly weather data, and has a weekly time step for most processes (Coughenour, 1992, 1994). Weather variables can be corrected for position and elevation via spatial interpolation among weather stations. Alternatively, stochastic weather data can be created by random sampling of years from the weather files, and by adding an additional amount of random variation to these data. Weather data are used to calculate the water budget in conjunction with soil properties. The water budget includes terms for precipitation, interception, runoff, runon, infiltration, deep drainage, bare soil evaporation, and transpiration. Precipitation is calculated as snow if the temperature is below freezing. Melting during night and day is modeled separately. The decomposition submodel is based on the CENTURY model (Parton et al., 1987). It simulates the breakdown of plant material, animal feces, urine, nitrogen cycling, and the formation and turnover of soil organic matter. The landscape is represented in the model as an array of grid-cells. Within each grid-cell the model simulates vegetation patch types or "facets" defined by the fractional cover of three life forms: herbaceous, shrub and tree. A herbaceous facet contains only herbs, a shrub facet contains herbs and shrubs, and a tree facet contains herbs, shrubs, and trees. Facet locations are not modeled, only the fractions of grid-cells that are covered by the facet. Changes in facet cover are the dynamic outcome of vegetation growth, recruitment, and mortality. Within each

Table 1
Main parameters of the willow and beaver submodels.

Group	Symbol[a]	Description	Values
Willow stems	$FrNwSt$	Proportion of NPP allocated to development of new stems	.04
	$DrSt_m$	Nominal stem death rate (year^{-1}) (from size class $m = 1$–6)	.015, .015, .015, .015, .03, .03
	$RStB_m$	Biomass per stem (without leaves; g stem^{-1}) (size classes $m = 1$–6)	12, 34, 76, 160, 312, 620
Willow plants	$EfPlEstR$	Effect of plant density on establishment rate (plant density (plants ha^{-1}): reduction factor). X,Y pairs for linear interpolation	1800; 1.0, 2500; .6, 3000; .05
	$EfCCEstR$	Effect of canopy cover on establishment rate. X,Y pairs for linear interpolation	.2; 1.0, .3; .3, .7; .005
	$EstR$	Establishment rate (plants m^{-2} year^{-1}) as a function of water table depth (m) (mean of June and July). X,Y pairs for linear interpolation	.003; 0, 0; .3
	$DrPl_n$	Nominal plant death rate (year^{-1})	.15, .02, .004, .003, .002, .002
	$MNS_{m,n}$	Minimum number of stems of size m in a plant of size n. Values correspond to the following m,n pairs: 2,2; 3,3; 4,4; 5,5 and 6,6	10, 10, 20, 20, 20
	$PrResp$	Proportion of plant in the resprouting pool that resprout (week^{-1})	0.05
Beaver foraging	$PB1_{sp}$	Preference weights for species; grass and willow (dimensionless)	1, 99
	$PB2_{ts,sp}$	Preference weights for tissue within species (dimensionless). Leaf and tiller for grass, or leaf CAG and bark for willow	70 and 30, 45, 45, and 10
	PSt_m	Preference weights for willow stems when foraging for immediate food (dimensionless) (from size class $m = 1$–6)	2, 8, 30, 30, 20, 10
	$PStFC_m$	Preference weights for willow stem for food cache (dimensionless) (from size class $m = 1$–6)	0, 0, 6, 13, 27, 54
	$PStDam_m$	Preference weights for willow stems when foraging for dam construction (dimensionless) (from size class $m = 1$–6)	0, 1, 1, 1, 1, 5
	$PrWasteGr_{ts}$	Waste fraction of grass biomass. Ratio waste: intake of grass leaf and tiller	.05, .08
	$PrWasteWd_{ts,m}$	Waste fraction of woody biomass (willow). Ratio waste: intake of willow Leaf, CAG and Bark (from size class $m = 1$–6)	.05, .05, .05, .05, .05, .05,. . .,05, .05, .05, .05, .05, .05,. . .,08, .15, .80, 1.5, 3, 7
	$MxItk_{sp}$	Maximum intake rate of grass and willow biomass when beaver are foraging for summer food or cache food (winter) (g kg^{-1} day^{-1})	70, 50, 20
	$MxItkC_{sp}$	Maximum intake rate of willow for food cache (g kg^{-1} day^{-1})	70
	$MxItkDam_{sp}$	Maximum intake rate of willow for dam construction and maintenance (g kg^{-1} day^{-1})	20
	$Dig_{ts,sp}$	Dry matter digestibility (%) of grass tissue (leaf, tiller) and of willow tissue (leaf, CAG and bark) (Currier et al., 1960; Pearson, 1960; Hoover and Clarke, 1972)	40, 40, 65, 60, 60
Beaver energetics	CF	Energy to body weight conversion efficiency (MJ kg^{-1}) (Pearson, 1960)	3.8
	Met	Metabolizabilty of digestible forage as fraction of digestible biomass (dimensionless)	0.81
	GE	Gross energy content of plant tissues (MJ kg^{-1}) (McDonald et al., 1988)	18.5
	MD	Fraction reduction of metabolism during the winter (Aleksiuk and Cowan, 1969a,b)	.5
	$MWGain_i$	Maximum growth rate (kg kg^{-1} day^{-1}) of beaver (kits yearlings and adults)	.0072, .004, .0006
	$MWLoss_i$	Maximum weight loss (kg kg^{-1} day^{-1}) of beaver (kits yearlings and adults)	.0003, .0003, .0010
	$MnBvW_i$	Expected minimum body weight as fraction of expected maximum body weight (kits, yearlings, and adults)	.5, .5, .8
	$ExBvW_i$	Expected maximum body weight (kg) (kits, yearlings, and adults). $ExBvW$ for kits and yearlings corresponds to the time when individuals are aged	1, 5, 24

[a] Subscripts are: i = beaver age class; m = stem size class, n = plant size class, sp = plant species, and ts = plant tissue.

facet, the model simulates plant growth and soil water budgets. Facet cover is defined by rooted area, and soil water and nutrient budgets are computed on a soil volume basis. The vertical spatial structure of the model is defined by soil and plant canopy layers. The soil is divided into three layers. The top layer is the topsoil, which is a zone of potential bare soil evaporation as well as root uptake. The second layer is the deepest layer containing herbaceous roots. The bottom layer is occupied only by shrub and tree roots. Plant canopies are organized into strata to compute light intensity using Lambert–Beer's law. Vegetation is represented by two interrelated submodels: (1) a net primary production submodel that predicts plant biomass dynamics, and (2) a population submodel that predicts changes in the number of plants. Predators and other herbivores can be represented as separate submodels, but were not used in this particular application.

In this study, we expanded the SAVANNA model to represent a beaver–willow community in a montane riparian area (elevation 2500 m) of RMNP. The general structure of the new willow and beaver submodels is described below.

2.2. Willow submodel

The willow submodel represents the dynamics of willow stems and plants and their response to beaver herbivory. The model includes six willow stem size classes m; $m = \{1,. . .6\}$ within each of six plant size classes n; $n = \{1,. . .6\}$. Each stem size class is described in terms of biomass and length. Each plant size class is described in terms of height, canopy diameter, aboveground biomass, and belowground biomass. Processes occurring at different levels of organization are interrelated (Fig. 1). For example, plant carbon fixation is estimated at the plant level in the primary production routine of SAVANNA based upon total leaf area. The fixed carbon is then allocated to stem size classes in proportion to their contributions to total plant leaf area. Conversely, plant biomass and morphology are derived from the biomass of constituent stem size classes.

2.2.1. Stem dynamics

Stem number can increase by the development of new stems within an established plant or by the establishment of a new plant (Fig. 1). Stem number can decrease due to plant death, death of stems within an established plant, or beaver cutting. A fraction of the plant net biomass increment is allocated to the development of new stems ($FrNwSt$; Table 1), while the remainder is allocated to the growth of existing stems. Stems die at a nominal death rate ($DrSt_m$; Table 1). Stems are transferred between size classes based upon biomass per stem (StB_m). The net biomass increment of a stem size class depends on stem tissue growth and stem tissue loss due to death. It is assumed that biomass per stem in each size class is fixed ($RStB_m$; Table 1). Thus, when a stem size class gains biomass, a proportion of the stems must be promoted to the next larger size class in order to maintain the fixed biomass of the stem size class.

Likewise, the number of stems in the next larger size class must be such that the biomass per stem in that size class also remains fixed. For example, if biomass per stem in a size class has increased enough so that each stem equals the biomass per stem in the next larger size class, then all the stems in the smaller class are transferred. Proportionally fewer stems are transferred when biomass per stem is less than the biomass per stem in the next larger size class. When stems gain biomass, the fraction of stems promoted to the next larger size class is calculated as:

$$FrStPr_{m'+1,n,t} = (StB_{m'} - RStB_{m'}) * (RStB_{m'+1} - RStB_{m'})^{-1} \quad (1)$$

where m' is a subset of the stem size class m; $m' = \{1,\ldots,5\}$, and StB is stem biomass after growth. The number of stem promoted per unit of area is:

$$NStPr_{m'+1,n,t} = StN_{m',n,t} * FrStPr_{m'+1,n,t} \quad (2)$$

where StN is the number of stem by size in plants of size n per unit of area:

$$StN_{m'+1,n,t+1} = StN_{m'+1,n,t} + NStPr_{m'+1,n,t} \quad (3)$$

$$StN_{m',n,t+1} = StN_{m',n,t} - NStPr_{m'+1,n,t} \quad (4)$$

Conversely, a net loss of stem biomass results when stems are transferred to smaller size classes.

2.2.2. Plant dynamics

The distribution of stems within plants is declared at model initialization and subsequently is a dynamic output of the model. A plant in given size class n could be comprised of stems of any size class m. The following criteria were used to ascribe plants to size classes:

(1) A plant in a given size class greater than 1 must have a minimum number of stems of specified size $MNS_{m'',n''}$ where m'' is a subset of stem size class m: $m'' = \{2,\ldots,6\}$ and n'' is a subset of plant size class n: $n'' = \{2,\ldots,6\}$ (MNS; Table 1). Plants comprised of less than the MNS required to be in any size class greater than one are ascribed to size class $n = 1$. There is only one MNS value greater than zero for each plant size class n'', then MNS is a square diagonal matrix. The MNS greater than 0 of each plant size class n'' is considered hereafter as "reference MNS" value. For example, if a plant is in size class $n = 3$ and the reference MNS values for this size class is equal to 10 ($MNS_{3,3} = 10$), then the following condition must be true for $m = 3$ and $n = 3$:

$$NStN_{n,m} \geq 10 \quad (5)$$

where $NStN$ is a number of stem of size m in plant n:

$$NStN_{n,m} = StN_{n,m} * \text{Area} \quad (6)$$

where Area is the unit of area of which StN is measured.
(2) A plant in a given size class n can be composed of any number of stems of size smaller than the size of the stems of the reference MNS values of this plant size. For example a plant in size $n = 3$ could have any number of stem of size $m < 3$.
(3) A plant in a given size class $n < 5$ can be composed of stems of size bigger than the size of the stems of the reference MNS value of this plant size, but the number of bigger stems must be lower than the respective reference MNS values of plants of bigger size classes. For example if $MNS_{4,4} = 20$, $MNS_{5,5} = 20$, and $MNS_{6,6} = 20$ then the following condition must be true for a plant in size $n = 3$:

$$NStN_{m,n} < 20 \quad (7)$$

for all $m > 3$ and $n = 3$.

As with stems, the number of plants in each size class (Pl_n) is a dynamic output of the model, which is determined by the establishment, mortality, and transfer of individuals between size classes (Fig. 1). Establishment increases the number of plants in the smallest size class and death can decrease the number of plants in any size class. Annual willow establishment is affected by mean water table depth in June, July and August ($EstR$), existing plant density ($EfPlEstR$), and woody canopy cover ($EfCCEstR$; Table 1). Plant death is a function of the nominal death rate and growing conditions ($DrPl_n$; Table 1). Transfer of plants between size classes is calculated annually at the beginning of the growing season, after the size distribution of stems has been updated. The number of plants by size class per unit of area promoted to the next larger size ($NPlPr$) depends upon the number of stems promoted by unit of area (Eq. (2)) that corresponds with the reference MNS of a next upper size plant:

$$NPlPr_{n'+1,t} = NStPr_{m'+1,n',t} * MNS_{m'+1,n'+1}^{-1} \quad (8)$$

where n' is a subset of plant size class n; $n' = \{1,\ldots,5\}$, and the stem size class $m' + 1$ correspond with the size of the stem of the reference MNS of a plant in a size $n' + 1$. For example, if $n' + 1 = 4$, then $m' + 1 = 4$. If the annual number of stems in size $m' = 3$ in a plant of size $n' = 3$ that are promoted to size $m' + 1$ were equal to 10 stems m^{-2} ($NStPr_{4,3,t} = 10$) and $MNS_{4,4} = 20$; then 0.5 plants m^{-2} will be promoted from size $n' = 3$ to size $n' + 1 = 4$; providing that the number of plants in size $n' = 3$ is equal or higher than this value. That is:

If $Pl_{n',t} \geq NPLPr_{n'+1,t}$, then:

$$Pl_{n'+1,t+1} = Pl_{n'+1,t} + NPlPr_{n'+1,t} \quad (9)$$

$$Pl_{n',t+1} = Pl_{n',t} - NPlPr_{n'+1,t} \quad (10)$$

Instead, if $Pl_{n',t} < NPLPr_{n'+1,t}$ all plants in size n' are transferred to plant size $n' + 1$. Accordingly, a fraction or all of the stems ascribed to plant size n' are transferred to size $n' + 1$, depending upon the number of plants promoted. Promoted stems from Eq. (8) ($NStPr_{m'+1,n',t}$) are ascribed to the next upper plant size class ($n' + 1$), but if only a fraction of plants are promoted, then the rest of the stems in the size class remain in plant size n'. Stems in all other size classes in plant n' are transferred to plant size $n' + 1$ in proportion to a fraction of plant promoted ($NPLPr_{n'+1}/Pl_{n'}$). Similarly, a fraction of the plants in size classes n''; $n'' = \{2,\ldots,6\}$ are moved to smaller size classes when beaver cutting or old age causes the number of stems to be lower than the minimum number for that size class. Beaver may also remove the entire aboveground biomass of individual willow plants in high use areas. Under adequate growing conditions, willow plants cut by beaver can sprout new stems from belowground meristems and rapidly recover lost biomass (Kindschy, 1989; Baker et al., 2005). The model tracks the number of plants that have had their entire aboveground biomass removed as a "sprouting pool". Only a portion of plants in the sprouting pool is allowed to sprout during a single growing season (PrResp, Table 1), and the remainder sprout the following growing season. When a plant is allocated to the sprouting pool its root biomass is removed from the population until it sprouts, after which aboveground and belowground biomass is added back into the model as a new plant in size class $n = 1$.

2.2.3. Parameterization

Willow is represented as a functional group that is not differentiated by species. However, model parameters are based on species typical to the study area, such as *S. monticola* and *S. planifolia*. These species can reproduce either sexually or asexually, but are not rhizomatous or clonal. Parameters that represent plant biomass dynamics were those used in previous applications of the model to represent riparian willows in RMNP (Peinetti, 2000; Coughenour,

Table 2
Parameters used to represent willow morphological characteristics. Values were based on field measurements taken in Endo Valley, Rocky Mountain National Park, Colorado, USA, 1998.

	a. Plant size class					
	1	2	3	4	5	6
Height to top of canopy (m)	0.5	1.2	2.4	2.9	3.4	3.8
Height to bottom of canopy (m)	0.0	0.0	0.0	0.3	0.5	0.7
Canopy area (m²)	0.2	0.5	1.8	2.5	5.0	7.1
Aboveground live biomass (g)	200	400	1,500	3,900	9,000	21,000
Belowground live biomass (g)[a]	120	240	900	2,500	6,500	14,500

	b. Stem size class					
	1	2	3	4	5	6
Height of stem (m)	0.5	1.2	2.4	2.9	3.4	3.8
Woody biomass (g)[b]	10	30	70	150	300	600
Leaf biomass (g)	8	13	15	17	38	70
CAG biomass (g)	2	4	6	10	12	20
Number of stems in plant size 1[c]	20	0	0	0	0	0
Number of stems in plant size 2	9	10	0	0	0	0
Number of stems in plant size 3	30	6	10	2	0	0
Number of stems in plant size 4	25	10	9	14	2	0
Number of stems in plant size 5	17	10	12	14	17	1
Number of stems in plant size 6	12	12	12	15	17	20

[a] Belowground biomass was not measured.
[b] Total stem biomass excluding leaves and CAG.
[c] These values were used at model initialization.

2002). Parameters to represent willow plant and stem dynamics were based on field data collected by Peinetti (2000) and Peinetti et al. (2002) in Horseshoe Park, RMNP, and on model calibration (Tables 1 and 2).

2.3. Beaver submodel

The beaver submodel simulates the foraging activities of a single beaver family, which is often called a beaver colony. A beaver family typically consists of the parents (hereafter adults), the young of the year (hereafter kits), and 1 year olds (hereafter yearlings) (Muller-Schwarze and Sun, 2003); thus, the model considers individual beaver as either kits, yearlings, or adults. Each year the existing kits become yearlings, and new kits are added to maintain a constant number of beaver in the family unit. Adult numbers always remain constant; yearlings are assumed to disperse when they reach 2 years old. The family size is assumed to be constant at 6 individuals (2 adults, 2 yearlings, and 2 kits) if beaver energy balance is adequate, otherwise family size is reduced to maintain beaver body condition above the starvation level (see below).

Each age class has specific parameters associated with energy demands and growth, with an associated body weight equal to the mean body weight of all individuals in the class. Beaver foraging includes the use of herbs and willow stems for fresh food, stems for the construction and maintenance of a dam, and storage and consumption of stems in winter food caches. All foraging activities follow a fixed annual schedule. In all foraging activities, the amount of biomass removed primarily depends upon the intake rate of individuals in the family. The size and type of biomass removed depends upon beaver food preferences and stem availability. Different stem preference weights are specified for each foraging activity. Food selection includes two levels of decisions: (1) a selection for stem size and (2) a selection for stem tissue (bark, leaves, and current annual growth (CAG)).

2.3.1. Foraging activities

Intake of fresh food by plant species (sp) and tissue (ts) is calculated from the maximum intake rate of food by kg of beaver body weight per day ($MxItk_{sp}$, Table 1), and then scaled to the family using total numbers and body weights:

$$Itk_{ts,sp,t} = MxItk_{sp} * NPB_{ts,sp,t} \sum_{i=1}^{3}(NBv_{i,t} * WBv_{i,t}) * DT \tag{11}$$

where NBv and WBv are the number and mean weight of beaver in each size class (i), DT is the time step of the model, and NPB is the normalized preference weight based on the Ellis et al. (1976) diet selection model. First, the product of the input weights ($PB1$ and $PB2$, respectively; Table 1) times biomass availability for each plant species (sp) and tissue (ts) is calculated, and then scaled to 0–1 proportions in the diet, such that the proportions sum to 1.0:

$$PB'_{ts,sp,t} = TB_{ts,sp,t} * PB1_{sp} * PB2_{ts,sp} \tag{12}$$

$$NPB_{ts,sp,t} = \frac{PB'_{ts,sp,t}}{\sum_{sp}\sum_{ts}PB'_{ts,sp,t}} \tag{13}$$

Total number of willow stems needed to attain the resulting biomass intake of each tissue (bark, leaves, and CAG in Eq. (11)) is computed, and the maximum value is chosen. Tissue removal comprises intake plus waste, which is represented as a fraction of intake ($PrWasteWd_{ts,m}$, Table 1). The normalized preference weight for stems ($NPSt$) is used to determine the fraction of removal that comes from each stem size class (see below). The preliminary estimate of biomass removal of a tissue and associated stem ($RmvB'$) is:

$$RmvB'_{ts,m,t} = NPSt_{m,t} * Itk_{ts,t} * (1 + PrWasteWd_{ts,m}) \tag{14}$$

where Itk is the intake of willow tissues (Eq. (11); for the case of sp = "willow"). The preliminary estimate of number of stems cut for bark, leaves, or CAG is:

$$StCut'(ts)_{m,t} = \frac{RmvB'_{ts,m,t}}{StB_{ts,m,t}} \tag{15}$$

where $StB_{ts,m}$ represents the amount of tissue biomass per stem, by stem size class. The final number of stems cut is then:

$$StCut_{m,t} = \max[StCut'(ts)_{m,t}] \tag{16}$$

The tissue biomass removed is then:

$$RmvB_{ts,t+1} = \sum_{m=1}^{6}(StCut_{m,t} * StB_{ts,m,t}) \tag{17}$$

The number of willow stems cut by beaver is a function of stem preference ($NPSt$, Eq. (14)). $NPSt$ is calculated from the input preference weight for each stem size class (PSt_m; Table 1), and from availability of stems, following the same approach used to calculate NPB (see Eqs. (12) and (13)). The relative distribution of stem intake over the number of stems by size class is:

$$PSt'_{m,t} = PSt_m * \sum_{n=1}^{6} StN_{m,n,t} \tag{18}$$

$$NPSt'_{m,t} = \frac{PSt'_m}{\sum_{m=1}^{6}PSt'_m} \tag{19}$$

Stem preference $NPSt'_{m,t}$ is calculated based on the number of stems by size class, and is expressed as biomass because willow intake is estimated as biomass:

$$PSt''_{m,t} = NPSt'_{m,t} * \sum_{n=1}^{6}(StN_{m,n,t} * StB_{m,t}) \tag{20}$$

$$NPSt_{m,t} = \frac{PSt''_{m,t}}{\sum_{m=1}^{6}PSt''_{m,t}} \tag{21}$$

The intakes of stem size classes are distributed over plant sizes in proportion to the availability of stem sizes among plant size classes.

Stems used for the winter food cache and dam are represented with a similar approach by using the offtake rates for these activities (Table 1). In the case of the food cache, only CAG and bark are considered in the offtake equations. We assume that construction of a single dam occurs only during the first year when the family establishes the site, and maintenance of the dam occurs in the following years. The model does not include estimates for stem needed to build and maintain beaver lodges or additional dams. In reality, the number and size of dams and lodges used by a single beaver family depends upon the physical and biological conditions of the site, which varies greatly (Baker and Hill, 2003). We also assume that beaver continue to cut willow stems until all the required biomass is collected. As in other foraging activities, stems selection is based on preference weights and stem availability. Stem preference for the construction of a dam reflects their need for a variety of stem sizes (Barnes and Mallik, 1996). The model forces beaver to collect a fixed amount of biomass comprised of small (size 2), medium (size 3 and 4), and large stems (size 5 and 6). Stem size class 1 was excluded because it was considered too small to justify the energetic costs of transporting cut stems to the dam. Stem preference indices are applied within each size class in the case of medium and lager size stems. For example, the fraction of biomass from medium stems could include any proportion of stems from size class 3 or 4.

2.3.2. Energy balance and growth

Biomass consumed by beaver is transformed to metabolizable energy intake (FME: food metabolic energy), by considering the dry matter digestibility of each tissue (Dig), the gross energy content of plant tissues (GE), and the ability to metabolize digested forage (Met; Table 1). FME is calculated as:

$$FME_t = \sum_{sp=1}^{n}\sum_{ts=1}^{m}(Itk_{ts,sp,t} * Dig_{ts,sp,t} * GE * Met) \tag{22}$$

Family energy balance is determined by comparing the energy acquired (FME) to the metabolic energy required (MER). Thus,

energy balance affects body weight. A positive energy balance produces an increase in mean body weight, while a negative energy balance produces weight loss. MER is calculated as:

$$MER_t = (BMR_t + BAR_t + ERC_t) * MD_t \tag{23}$$

where BMR is the basal metabolic requirement, BAR is the activity requirement, ERC is the energy required for construction of the dam and a winter food cache, and MD represents metabolic depression during winter (scaled 0–1; Table 1). BMR is estimated from an allometric equation of energy and body size (W) (Novakowski, 1967; Belovsky, 1984).

$$BMR_t = 70 * W_t^{0.75} \tag{24}$$

BMR is increased by 12% in the case of kits (MacArthur, 1989). BAR is 1.5 times BMR in the case of kits, and 2.0 times BMR in the case of yearlings and adults. The energetic cost associated with cutting and moving stems of different sizes is estimated by adapting Eq. (7) of Belovsky (1984). Periods of low metabolic rate occur when adult and yearling beaver are using food from their winter food cache (November–April); periods of high metabolic rate occur for kits during winter and for beaver of all age classes during the remainder of the year. Weight gain occurs only if FME is higher than MER. The potential increase in body mass is calculated as:

$$Gr_{t+1} = (FME_t - MER_t) * CF \tag{25}$$

where CF represents the efficiency of energy conversion by body mass. The increase in body mass in each time step (WBv) depends upon the following conditions: (a) yearlings and adults can increase their body mass only during the period of high metabolic rate, but kits can grow throughout the year (albeit at a different rate) because we assume that kits are less affected by metabolic depression than other age classes; (b) weight gain and loss are limited to maximum values ($MWGain$ and $MWLoss$; Table 1), with the exception of a period of food shortage followed by high energy inputs where the actual growth rate could be slightly above $MWGain$, which allows recovery of weight lost; and (c) when the energy gained is not sufficient to support the $MWGain$, the growth is partitioned between age classes. Conversely, body weight is reduced when there is a negative energy balance. The energy lost (MER − FME) is transformed to mass units using the efficiency of conversion of energy to body mass. As with growth, the rate of weight loss is limited to a maximum value ($MWLoss$). Animal nutritional status is evaluated using a 0–1 condition index. The condition index is calculated by comparing the actual body weight of individuals in each age class to the maximum and minimum body weight for that size class ($ExBvW_i$ and $MnBvW_i$, Table 1):

$$CI_{i,t} = (BvW_{i,t} - MnBvW_i) * (ExBvW_i - MnBvW_i)^{-1} \tag{26}$$

The $ExBvW$ for kits and yearlings varies throughout the year as individuals are increased in size, in contrast the $ExBvW$ of adults remains constant. At each weekly time step, the $ExBvW_i$ of kits and yearlings are updated by adding the $MWGain$; they are reset to initial values once each year when individuals are aged. The $MnBvW_i$ is calculated as a fraction of the $ExBvW_i$.

2.3.3. Parameterization

The beaver submodel was parameterized using observational data from the study site, existing knowledge and data from the literature, and model calibration. Foraging activity is an important energetic parameter for beaver that varies seasonally, especially in cold climates where ponds freeze during winter (Aleksiuk, 1970). During the late summer and autumn, beaver cut and store woody vegetation in food caches for use as winter forage (Aleksiuk and Cowan, 1969a). Activity levels and forage requirements are also

high during the spring and early summer as herbaceous and woody vegetation becomes green and succulent. The model reflects these seasonal changes by weighting activity from May to October with higher values (Aleksiuk and Cowan, 1969a,b; Novakowski, 1967). The intake rates for fresh food ($MxItk_{sp}$) were obtained by calibrating the model to maintain the beaver condition index near the value of 1.0. The parameter values we obtained in this manner were similar to the measured values for beaver in northern latitudes (Brenner, 1962; Aleksiuk and Cowan, 1969b). We assumed that beaver consumed only edible material (grass, willow leaves, and willow twigs and bark) as fresh food, and that some edible and inedible material was removed but unused. The amount of woody material discarded by beaver was based the calculations of Baker and Cade (1995). We also assumed a small amount of fresh food was discarded by beaver (Table 1). The total biomass removed as fresh food included the sum of intake and waste biomass, as shown in Eq. (14). Similarly, the intake rate for the food cache ($MxItkC_{sp}$) considered the amount of stored food necessary to maintain the family during the period of low activity from November to April, and assumes that beaver only rely in food from the cache during this period. Intake rates for construction are difficult estimate because the vegetation used for dam construction is not always differentiated from that used for feeding (Doucet et al., 1994). In addition, the size and number of dams constructed by beaver depends on many highly variable site conditions, such as stream channel morphology, water velocity, and slope. We estimated the maximum intake rate for the beaver dam ($MxItkDam$) in the model was 2 Mg of woody biomass that was cut by beaver during 60 days in the early fall, which is consistent with field data for RMNP (Baker, B.W., unpublished data).

We estimated parameters representing beaver preferences for different size stems from field observations in RMNP. Because stem size class preferences may differ in other locations, we evaluated how sensitive the model was to stem selection criteria. Preferences for willow vary with the type of foraging activity. We assumed that beaver prefer medium size stems when foraging for fresh food, and larger size stems for transport to and storage in the food cache (Table 1). These preferences are based on the central place foraging behavior of beaver, which are explained in more detail in Section 3.1.

Parameters used to represent beaver energy balance and growth were obtained from the literature. Metabolic energy (Eq. (22)) was based on the dry matter digestibility of each tissue (Dig) (Currier et al., 1960; Pearson, 1960; Hoover and Clarke, 1972), the gross energy content of all plant tissues (*GE*) (McDonald et al., 1988), and metabolizable digested forage (Met) (ARC, 1980) (Table 1). Basal metabolic rate (BMR) was estimated from Eq. (24), which was corroborated for beaver by MacArthur (1989). Basal metabolic activity (BMA) was based on experiments with beaver maintained in captivity (Pearson, 1960). The energetic cost associated with moving stems to be stored in a food cache or for construction was added to BMR and BMA using Eq. (23). This cost was estimated considering the energy demand for walking, swimming, and hauling (Schmidt-Nielsen, 1972; Belovsky, 1984), the mean distance traveled in a trip (150 m), and the biomass of stems moved as estimated by the foraging routine of model. A scaling factor was used to account for the ability of beaver to carry multiple smaller stems (15, 6, 3, 2, 1, and 1 stems per trip for size classes 1–6, respectively). We considered that beaver in our study site reduced their metabolic rate during the period of low activity (November–April), as has been observed for beaver in northern latitudes (Aleksiuk and Cowan, 1969a, b) (Table 1). The expected body size and growth rates of kits, yearlings, and adults were based on Pearson (1960), Novakowski (1967), Aleksiuk and Cowan (1969a, b), and MacArthur (1989). Parameters use to convert energy to body weight were based on Pearson (1960) and Coppock et al. (1986).

2.4. Model settings and evaluation

We configured SAVANNA (Peinetti, 2000; Coughenour, 2001, 2002) for our application to a beaver–willow community in RMNP via the parameters described above. Observational data suggested the willow community had received a low level of elk and beaver herbivory for many decades; empirical foraging data were unavailable. The site was characterized based on the field data in terms of biomass, density, and size distribution of willow stems and plants (Table 2). Willow stem biomass was 610 g m^{-2}, plant density was 3200 plants ha^{-1}, and the frequency distribution for stem size classes 1–6 was 0.210, 0.409, 0.175, 0.122, 0.064, and 0.020, respectively (Peinetti, 2000). We negated the effects of unknown levels of prior herbivory by running the model with elk and beaver absent until the aboveground net primary production (ANPP) for willow had stabilized, which occurred after 50 years. Thus, we could initialize different model runs via both a browsed (field data) or unbrowsed (field data after 50 simulated years) condition. The study area was modeled as spatially homogeneous in terms of physical conditions, vegetation, and beaver use; thus, all willow stems were equally available to beaver. Simulations used weather data from local weather stations and SNOTEL sites in and near RMNP.

We verified the willow model by comparing model predictions to field data for the variable plant density. Field data were collected during fall 1998 from inside and outside a 30 m × 48 m elk exclosure that had been constructed in fall 1994 in Endo Valley to study browsing effects on willow (Peinetti et al., 2001; Zeigenfuss et al., 2002). Plants were placed into the same 6 size classes used in the model, thus differences in the size class distribution between fenced and unfenced willow represented differences in willow growth 4 years after release from ungulate browsing. The characteristics of unfenced willow (browsed) were used as initial condition. The model was run for 4 years using actual RMNP weather records from 1994 to 1998. We compared the size distribution of willow plants in the fenced site with model predictions after 4 simulated years.

The performance of the beaver model was evaluated by considering how the model represented beaver foraging and energetics in a stable willow riparian environment. To determine the sustainable density of beaver in this environment, we estimated the minimum area of willow habitat needed to sustain a complete beaver family for 150 years while maintaining their condition index near 1.0 for the entire simulated time period. This was achieved by introducing adults, yearlings, and kits (in that order) into range of different size areas. We found that 1 ha sustained 1 adult, 2 ha sustained 2 adults, 3 ha sustained 2 adults and 2 yearlings, and 4 ha sustained a complete family of 2 adults, 2 yearlings, and 2 kits. We used the 4-ha minimum area to run simulations representing a stable beaver–willow community with a single beaver family. We estimated the annual foraging requirements of the beaver family in terms of the number and size distribution of willow stems used as fresh food, a stored winter food cache, and woody material to build and maintain a beaver dam. We used the same simulated conditions to develop an annual energy budget for the family in terms of energy balance and growth by age class.

Finally, we evaluated the sensitivity of the model to variations in beaver preferences for different size willow stems. The *estimated preferences* we used in our model were based upon field observations, which suggested that beaver preferred medium and large size stems ($PrSt_m$, Table 1). We compared this "standard" preference weighting with four alternative preference scenarios to evaluate model sensitivity for the following willow variables: (1) number and size distribution of stems, (2) woody biomass, and (3) ANPP.

2.5. Simulated experiments

We simulated willow communities with beaver absent and beaver present to better understand how selective foraging affects willow population dynamics, productivity, and system stability. We compared the long-term dynamics of two willow populations with contrasting initial conditions (browsed and unbrowsed) to determine how beaver foraging affected community structure. Finally, we evaluated how willow productivity (ANPP) varied over a range of beaver densities.

3. Results

3.1. Model performance

We verified the ability of the model to predict willow growth rates by comparing model output and field data for plant density by size class (Fig. 2). In the browsed condition (unfenced willow), plant size class 1 (height < 0.5 m) dominated the site with a density of 3400 plants ha^{-1}. In contrast, after 4 years of protection from elk browsing the paired fenced site was dominated by plant size classes 2 and 3. The density of plants in size classes 4–6 was similar in the fenced and unfenced sites, perhaps because four growing seasons was not enough time for plants to reach the larger size classes (Baker et al., 2005). Simulated data were consistent with observed data after 4 years, which suggests the model accurately predicted plant growth after release from browsing.

Mean stem density of willow in the 4-ha site averaged about 10 stems m^{-2} (401,000 total live stems) during the last 50 years of a 150-year model run in a stable beaver–willow community (Table 3). Willow had 65.3 Mg of aboveground woody biomass with a mean ANPP of 21 Mg year^{-1}. Beaver cut 5.5% of available woody biomass each year for use as fresh food and a winter food cache, which equaled 18% of willow ANPP. Grasses comprised <1% of the annual diet. Beaver used 2.0 Mg of woody biomass to construct a single dam during their first year of occupancy and 0.4 Mg year^{-1} thereafter to maintain the dam. Combined use of woody biomass totaled 28% of willow ANPP in the first year and 20% in remaining years. The relatively large differences between the amounts of woody biomass removed and consumed as fresh and winter food

Table 3
Foraging dynamics of a beaver family (2 adults, 2 yearlings, and 2 kits) in a simulated willow community in Rocky Mountain National Park, Colorado, USA. Values are means of the last 50 simulated years and indicate totals for the 4-ha unbrowsed willow site during stable equilibrium.

	Biomass (Mg)				Number of stems
	Leaves[a]	CAG[b]	Woody[c]	Total[d]	
Willow availability	12.49	9.55	65.26	N/A	401,000
Fresh food					
Removed	0.15	0.19	2.30	2.45	13,000
Consumed	0.14	0.18	0.38	0.52	N/A
Winter food					
Stored in a cache	0.09	0.15	1.31	1.40	2,350
Removed from cache	N/A	0.13	1.16	1.16	N/A
Consumed	N/A	0.12	0.27	0.27	N/A
Dam					
Construction	0.08	N/A	2.0	2.08	6,000
Maintenance	0.02	N/A	0.4	0.42	1,200

[a] Leaves at peak biomass.
[b] Current annual growth (CAG) biomass at the end of the growing season.
[c] Stem biomass at the end of the growing season (excluding leaves but including CAG).
[d] Total does not equal the sum of leaves, CAG, and woody because leaves are reported at peak biomass, which occurred before the end of the growing season, and thereafter leaf biomass was allocated to CAG and older woody tissues.

(Table 3) reflect the relative values of bark and small twigs as food and waste. However, the model did not consider the use of peeled stems as construction material for the dam, which often occurs in natural beaver populations. The beaver family used more stems for fresh food than for the winter food cache (Table 3), and stems for fresh food represented a more diverse size structure (Fig. 3a). Most stems cut for the winter food cache were from the largest size class (Fig. 3b). Stem availability in the simulated habitat was sufficient to meet demands for dam construction. The largest stems (size class 6) dominated dam construction material, although all other size classes were used except size class 1 (stems <0.5 m tall) (Fig. 3c). Size differences of stems used for fresh food and the food cache reflected the central place foraging behavior of beaver. In general, stems cut for fresh food are consumed at the nearest safe place, but stems cut for food caches must be large enough to justify the energetic costs of transportation from the cut site to the cache site in the fall and from the cache to the lodge in the winter (Baker and Hill, 2003). Thus, the interaction of beaver preference indices and dynamic stem availability created a steady-state condition in terms of number and size of willow stems cut by beaver.

The energy gained by the family in a steady-state condition was proportional to increase in body size (mostly yearlings and kits) during May–October, when beaver were most active and food availability was high (Fig. 4a and b). The food metabolic energy (FME) gained was greater than metabolic energy required (MER) without growth costs during most of the year. The greatest differences were in May–October when kit and yearling growth rates were highest. This demonstrates that the simulated 4-ha area was capable of supporting the complete annual needs of the family, as the model was calibrated to have an energy balance with intake close to demand (MER plus growth costs). The condition index (ratio of simulated and expected weights; see Eq. (26)) was higher for adults and yearlings than for kits. The condition index of kits averaged slightly below 1.0 for the entire year and was the lowest near the end of April (Fig. 4), which was after ice-out but before spring green-up when high-energy food was scarce and demands of growth increased as beaver became more active.

How sensitive was the beaver–willow model to variation in beaver preferences for willow stems of different sizes ($PrSt_m$)? We found the model scenario that used *estimated stem preferences*
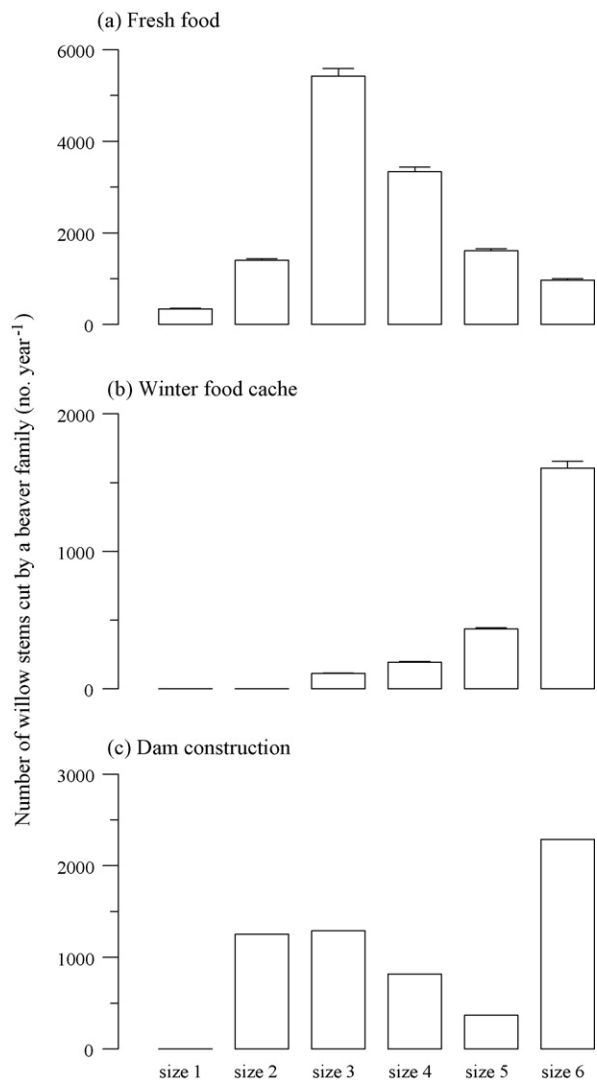

Fig. 2. Comparisons of different willow treatments to quantify how model simulations predict willow growth patterns. "Field data - unfenced willow" represents a site browsed by ungulates in Rocky Mountain National Park, Colorado. "Field data - fenced willow after 4 years" represents a paired site 4 years after fencing to exclude ungulate browsing. "Unfenced willow after 4 years of simulated time" represents field data from an unfenced willow (i.e., browsed) site after 4 years of simulated time. Comparisons reflect how well the model predicts willow growth after release from browsing.

Fig. 3. The number of willow stems predicted to be cut by a beaver family (2 adults, 2 yearlings, and 2 kits) in a steady-state condition. Foraging represents (a) stems cut to be consumed as fresh food, (b) stems cut and stored in a winter food cache, and (c) stems cut and used as construction material for a single beaver dam. Values represent means of the last 50 simulated years (error bars are standard deviations), and are the consequence of stem availability and beaver preference indices for stem sizes.

(Table 4) resulted in a total stem density of about 10 stems m^{-2} after the 200-year simulation. There were more stems in classes 1–3 in this scenario, but stems were distributed relatively evenly within size classes 1–3 and 4–6 (Fig. 5a). Results for the *equal stem preference* scenario (Table 4, Fig. 5b) closely mirrored those for the

Table 4
Preference indices for stem sizes used to represent different beaver foraging preferences.

Foraging preferences	Size 1	Size 2	Size 3	Size 4	Size 5	Size 6
Estimated[a]	2	8	30	30	20	10
None	1	1	1	1	1	1
Larger stem sizes[b]	5	5	5	5	40	40
Medium stems sizes[c]	5	5	40	40	5	5
Smaller stems sizes[d]	40	40	5	5	5	5

[a] Inferred from general field observations. It corresponds to $PrSt_m$ values in Table 1.
[b] Preferences for stem size 5 and 6 were 8 times greater than for other sizes.
[c] Preferences for stem size 3 and 4 were 8 times greater than for other sizes.
[d] Preferences for stem size 1 and 2 were 8 times greater than for other sizes.

estimated preference scenario. The *large stem preference* scenario (Table 4, Fig. 5c) increased the total stem density and decreased the proportion of the largest (class 6) stems. The *medium stem preference* scenario (Table 4, Fig. 5d) decreased total stem density and increased the proportion of small and medium size stems. The *small stem preference* scenario (Table 4, Fig. 5e) decreased total stem density to <5 stems m^{-2}, and paradoxically increased the proportion of the smallest stems as beaver were forced to cut a larger number of willow stems to meet their energy requirements, and sprouting of new stems replaced cut stems. Willow biomass decreased and ANPP increased in all scenarios during the first 20 simulated years as the willow community adjusted to beaver foraging activity (Fig. 6). Thereafter, woody biomass and ANPP remained stable except for the *small stem preference* scenario, which became unstable as biomass removed by beaver became greater than ANPP. Thus, we found the model was relatively robust to changes in stem size preferences of beaver in terms of woody biomass and ANPP, but preference indices had an important effect in determining the size class distribution of willow plants over the long term.

3.2. Simulation experiments

How did beaver foraging affect the productivity and population structure of the willow community? We compared ANPP and plant architecture in model runs with beaver absent and beaver present in the 4-ha site with a steady-state balance between beaver and willow (Fig. 7). Initially, unbrowsed willow ANPP was about 3.0 g m^{-2} and the size class distribution was dominated by plants in a larger size class (Fig. 7a). When beaver were absent ANPP slightly declined over the long term as more plants were promoted to larger size classes. After 100 simulated years productivity declined to about 2.5 g m^{-2} and >80% of plants were taller than 2.0 m (Fig. 7b). Willow ANPP increased from 3.0 to over 5.0 Mg ha^{-1} during the first 20 years after beaver introduction. Beaver annually removed about 20% (1.0 Mg ha^{-1} year^{-1}) of available ANPP. Selective foraging by beaver created a more balanced distribution of plants that was dominated by intermediate sizes but still included many large plants (Fig. 7c). Under these conditions beaver and willow persisted in a stable equilibrium. Removal of beaver from the system resulted in a rapid decrease in ANPP until it stabilized near the level with beaver absent. The trajectory of decreased ANPP with beaver absent mirrored the trajectory of increased ANPP with beaver present. We also examined the effects of beaver on belowground productivity (BNPP). We found BNPP attained stable equilibria both with and without beaver, but values stabilized at 6.0 Mg ha^{-1} with beaver present and 5.0 Mg ha^{-1} with beaver absent. Thus, the willow community developed a more diverse plant architecture and increased productivity in response to beaver herbivory.

How does the initial condition of a willow community affect how beaver foraging can alter community structure in the long term? We introduced beaver into two willow communities (browsed and unbrowsed) with different initial conditions in terms of available willow biomass and found that selective foraging created similar stable equilibria after about 100 years of simulated time (Fig. 8). Woody biomass increased from 6.4 to 16.4 Mg ha^{-1} with the browsed initial condition and decreased from 27.0 to 16.4 Mg ha^{-1} with the unbrowsed initial condition. The combination of selective foraging pressure relative to stem availability likely explained the convergence of willow biomass from different initial conditions. Stem use depended upon availability, and large stems were more preferred than small stems. More large stems were available in the unbrowsed condition than in the browsed condition at the start of the simulation, thus more large stems were utilized. Removal of large stems increased the proportion of small stems as plants replaced stems to recover root:shoot ratios. Also, large stems contain a lower proportion of biomass from bark and small twigs (Baker
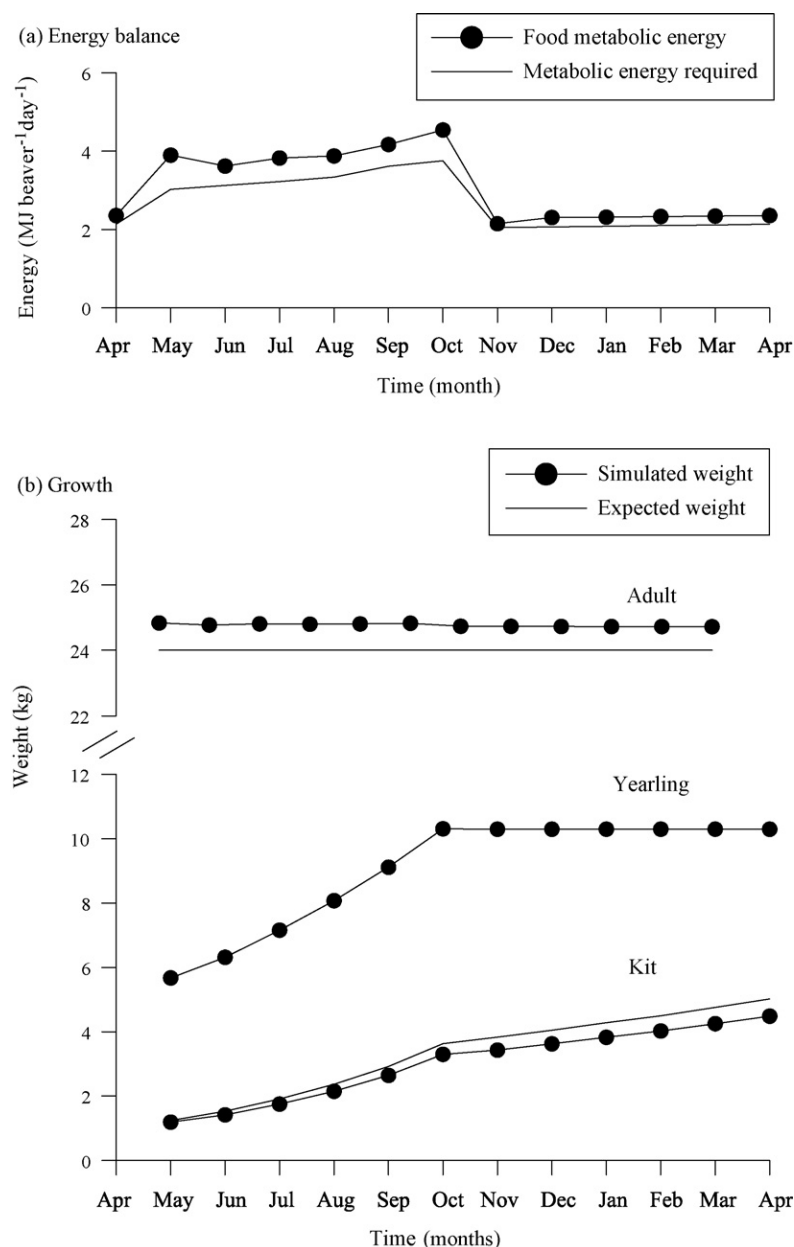
Fig. 4. Energy balance averaged for the six individuals in the family (a) and growth by age class of beaver (b) when foraging in a steady-state condition. Values represent means of 50 simulated years. A positive energy balance suggests the configuration of the model in terms of food intake was sufficient to maintain body condition of beaver.

and Cade, 1995), thus more non-food biomass is discarded from large stems. In contrast, the browsed treatment had fewer large stems available at time zero. Fewer large stems were selected relative to smaller stems, which reduced total cut biomass and waste biomass. Release from ungulate browsing can increase the standing crop of willow given suitable physical conditions (Baker et al., 2005), thus woody biomass may have increased in our model simulations with or without beaver present. The interesting results in this simulation are that the introduction of beaver into a willow community can either increase or decrease woody biomass relative to initial condition, and that similar stable equilibria can develop regardless of initial condition.

Increasing beaver densities from zero to 1.5 beaver ha^{-1} (1 family in 4 ha) resulted in increasing levels of willow ANPP from 2.3 to 5.3 Mg m^{-2} (Fig. 9). Beaver persisted at 1 family in 4 ha for the entire 100-year model run, and ANPP reached a sustainable steady state. Simulations with higher beaver densities caused ANPP to decrease until beaver were excluded by food limitation when their den-

sity reached 2.0 beaver ha^{-1}. Thus, willow productivity was higher under all levels of sustainable beaver herbivory.

4. Discussion and conclusions

4.1. Model performance

The model estimated that a beaver family in a willow-dominated riparian area cut about 70 willow stems per day during its first year of occupancy, when one dam and one winter food cache were constructed. Beaver foraging requirements generally vary in response to local biological and physical site characteristics. For example, a beaver family in boreal forest at Isle Royale, Michigan, cut about 30 plants per day from a mixed community that included *Alnus*, *Acer*, and *Betula* (Belovsky, 1984). Beaver annually used 4% of available willow stems at our RMNP study site (Table 3), whereas Eurasian beaver (*C. fiber*) used 1–5% of available willow (*S. alba*)
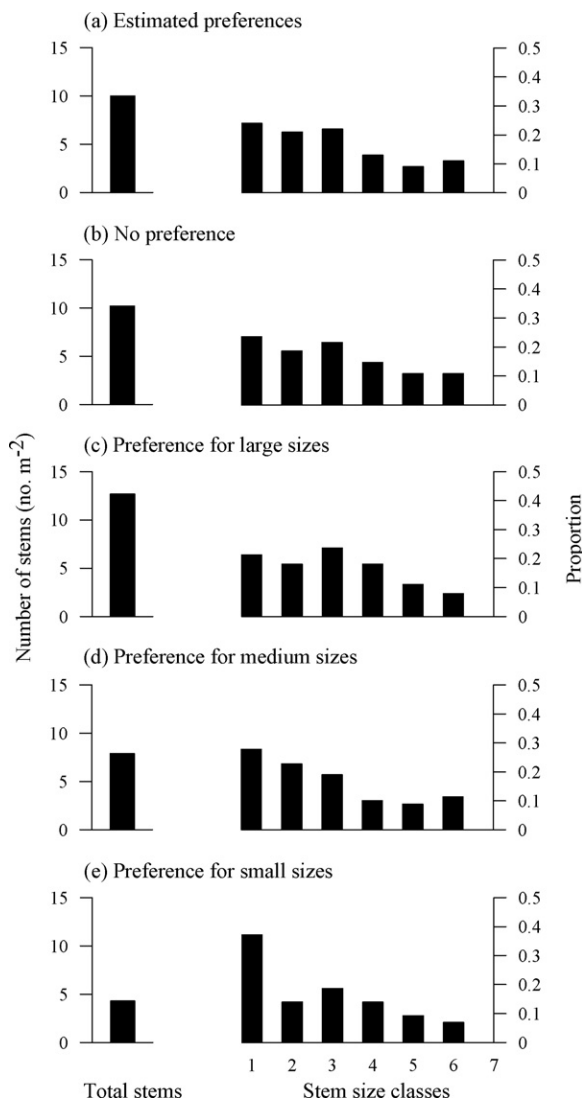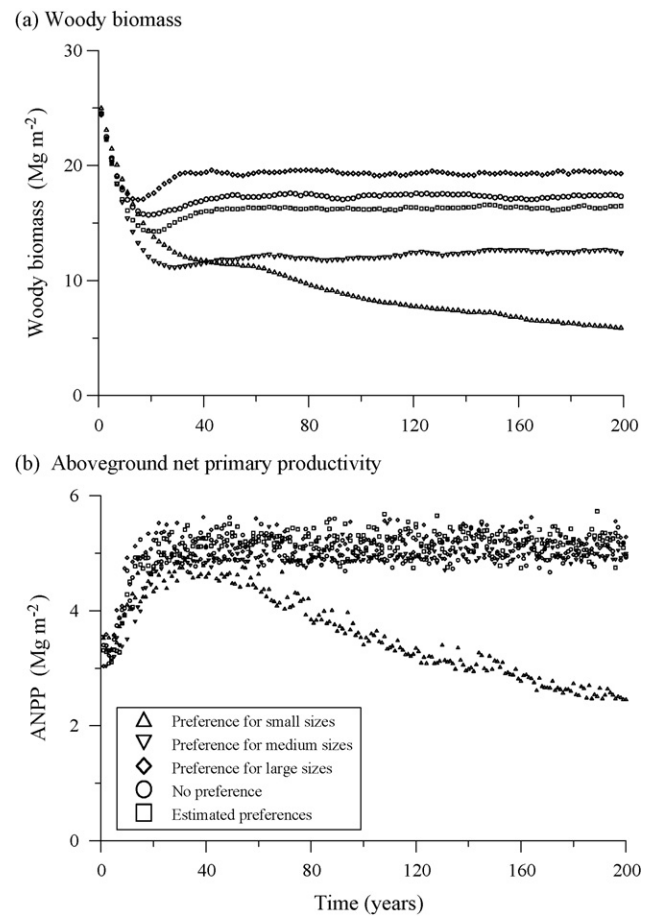
Fig. 5. Model sensitivity to variation in beaver preferences for stems of different sizes. Values represent the long-term effects of stem cutting by beaver on the total number and the proportional size class distribution of willow stems. The large (c), medium (d), small (e) stem size preference categories represent size classes 5 and 6, 3 and 4, and 1 and 2, respectively. Results suggest the "preference parameter" is relatively robust with respect to size class, except that preferences for small sizes (e) greatly reduced the total number of stems and increased the proportion of the smallest stems.

Fig. 6. Model sensitivity to variation in beaver preferences for stems of different sizes. Values represent the long-term effects of stem cutting by beaver on (a) woody biomass and (b) aboveground net primary productivity (ANPP) of willow. Note that the model was most sensitive when there was a preference for small sizes.

in the Netherlands (Nolet et al., 1994). Beaver energetic needs can also differ for wild and captive populations. Our model included estimates for energy expended to obtain and transport stems, construct and maintain a single dam and store winter food; thus, it predicted higher energy demands for beaver than has been found in studies of captive beaver (Pearson, 1960; Woodard, 1994). Captive beaver consumed 30–40% less biomass than predicted by our model (Aleksiuk and Cowan, 1969a,b; Woodard, 1994). The construction needs of beaver can substantially increase their minimum area requirements, but are difficult to predict because the number and size of dams and lodges built by beaver depend on local geomorphology, hydrology, and other site-specific conditions (Doucet et al., 1994). Beaver used 2.5 Mg of willow to build and maintain a dam in our simulated RMNP study site. Site sustainability can be increased and area needs decreased if beaver dams contain a high proportion of stems from non-food species, peeled stems, dead stems, woody debris, or rocks and other non-plant materials (Doucet et al., 1994; Barnes and Mallik, 1996). Our model assumed the simulated beaver

dam consisted entirely of intact willow stems, as no information was available to quantify other construction material. Beaver use fewer stems in sites where they do not build and maintain dams, such as in lakes or large rivers, or when they use abandoned dams that require maintenance only (Johnston and Naiman, 1990). Beaver can adapt to many different environmental conditions, thus modeling assumptions that reflect site-specific conditions will yield better predictions.

We found a single beaver family required a minimum of 4 ha of willow (containing about 10 stems ha^{-2}) to persist indefinitely ($\geq$150 years) in a site where all stems were equally available. Assuming a 4-ha riparian willow zone is 50 m wide by 800 m long, and contains suitable physical features, it is likely the site could indefinitely sustain a single family that was free to move their dams, lodges, and foraging areas upstream or downstream as needed (Baker and Hill, 2003). However, quantitative field data were not available to verify these predictions. Qualitative data from a beaver telemetry study in RMNP suggests predictions are realistic for sites (e.g., Wild Basin) subjected to minimal additional herbivory (Baker, B.W., unpublished data).

Our model represented foraging dynamics at the stem level rather than the plant level, which was recommended by Woodard (1994:210) in her field studies and modeling of beaver populations at Sagehen Creek, California. The constraints within our model assumed a spatially uniform environment, and excluded the effects of beaver on willow establishment and survival processes. In reality, this is an overly simplistic view that captures only a portion
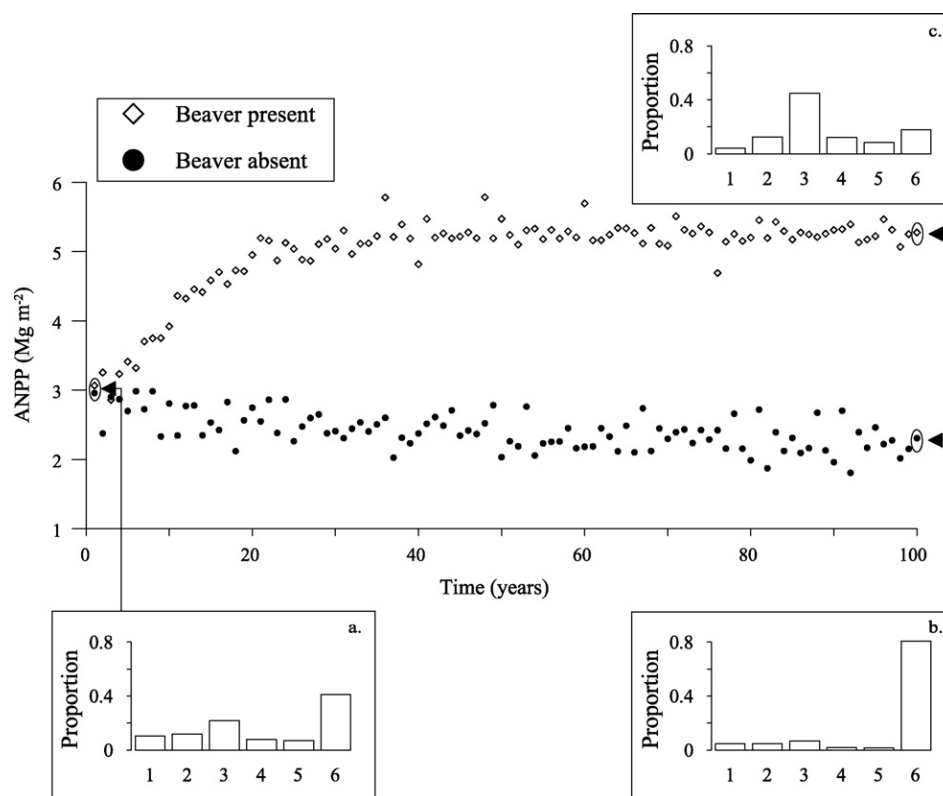
Fig. 7. Comparisons of beaver present and beaver absent for the aboveground net primary productivity (ANPP) and the proportional size distribution of willow plants (boxes a, b, and c). The initial condition (Time = 0) represents a willow community without beaver or ungulate herbivory for 50 years (unbrowsed condition). Note that ANPP increased rapidly during the first 20 years of beaver presence. The results for willow size class distribution suggest that selective foraging by beaver increased the proportion of willow plants in the intermediate size classes (compare "b" and "c" relative to "a").

of the true complexity in beaver–willow interactions. For example, cut stems can sometimes sprout adventitious roots and become established as new individuals (Cottrell, 1995). Beaver dams can create bare moist sediment and raise the water table, which affects the growth rates and survival of willow (Baker and Hill, 2003). Beaver are central place foragers that can select stem sizes based on hauling distance. As distance increases selection favors the smaller trunks of larger trees, such as aspen, and the larger stems of smaller shrubs, such as willow (Woodard, 1994). The foraging and dam building activities of beaver create heterogeneous plant communities that form complex patches in the landscape (Sturtevant, 1998; Westbrook, 2005; Westbrook et al., 2006). Therefore, selective foraging by beaver, although important and complex, represents only one of several beaver activities that can help drive the structure and function of a willow community.

4.2. Plant response to beaver foraging

The model suggested willow ANPP was higher under all sustainable levels of simulated beaver herbivory. The trend suggested ANPP increased until beaver densities reached 0.25 colonies ha^{-1} and decreased with higher densities until food limitation excluded beaver at densities of ≥ 0.33 colonies ha^{-1}. BNPP was slightly higher with all sustainable beaver densities. Beaver herbivory altered plant architecture by creating a more balanced and diverse size structure that included a large proportion of plants in the intermediate and tall sizes. The absence of beaver allowed plants to continue to grow in size as they aged, and unlimited growth developed a homogeneous community of larger willow that was only half as productive as the more structurally heterogeneous beaver–willow community. Simulations showed the standing crop of woody biomass was 27.0 Mg ha^{-1} without beaver and 16.4 Mg ha^{-1} with beaver.

These patterns were largely the dynamic consequence of stem availability, beaver size preferences for food and construction material, increased stem turnover rate, and sprouting following stem removal.

Response to beaver foraging depends on plant life history traits. Beaver typically cut stems near the ground level, which can stimulate the growth of vigorous new shoots from the root collar or remaining stem segment. Red willow (*S. lasiandra*) in Oregon increased stem production in proportion to the number of stems cut per plant, with a stem elongation rate of 3.3 cm day^{-1} on cut plants and 0.4 cm day^{-1} on controls (Kindschy, 1985, 1989). Mountain willow (*S. monticola*) plants in RMNP recovered 148.4% of their pre-cut stem number during the first growing season after all stems were removed to simulate beaver herbivory (Baker et al., 2005). Cottonwood trees (*Populus fremontii*) subjected to repeated beaver cutting developed a shrub-like growth form that had 3 times more basal branches and were only 25% as tall as uncut trees (McGinley and Whitman, 1985). Beaver cutting can stimulate vigorous suckering in clonal species such as aspen (*Populus tremuloides*) and coyote willow (*Salix exigua*) (DeByle, 1985). Thus, plant response to beaver foraging varies by growth form (tree vs. shrub) and reproductive strategy (sprouting vs. seed; clonal vs. non-clonal).

How does beaver foraging increase structural heterogeneity and productivity in a willow community? A diverse canopy structure can increase productivity if it includes more stems and younger stems. A large proportion of solar radiation is intercepted by the stems and branches of woody plants, which is greatly affected by their spacing (Cannell et al., 1987). Productivity is higher in leaves than in stems and the leaf area index is higher when leaves are distributed throughout both the horizontal and vertical planes of the canopy, which increases the efficiency of intercepting solar radiation. Small stems have a low leaf area index and large stems
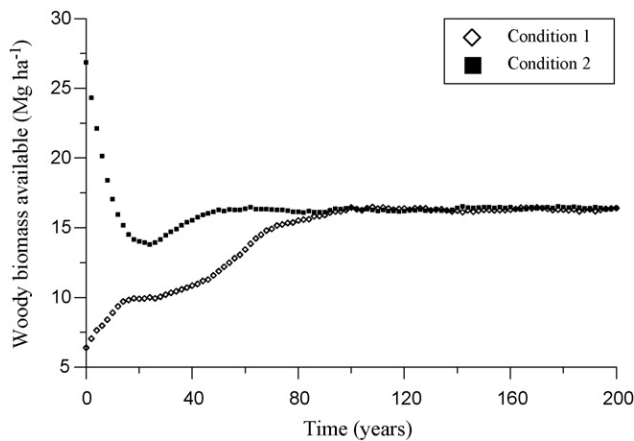
Fig. 8. Comparison of the change in available woody biomass for 200 simulated years given two different initial conditions and beaver introduced to the 4-ha willow community at Time = 0. Condition 1 represents a site protected from ungulate browsing for 50 years and Condition 2 represents a site lightly browsed by ungulates for 50 years. Note that both sites developed similar stable state conditions after about 100 years regardless of available willow biomass at initial condition (Time = 0).

have a high proportion of non-photosynthetic tissues, so optimum productivity often occurs in intermediate size stems. If beaver foraging thins out some larger stems and creates a more balanced size structure, then it may increase the ratio of photosynthetic to non-photosynthetic tissue. Thus, mechanisms that result from vigorous sprouting and a diverse plant architecture suggest a hypothesis that partially explains how beaver herbivory may increase willow productivity.

4.3. Overcompensation

The grazing optimization hypothesis suggests plants can overcompensate in response to herbivory (McNaughton, 1983). The debate created by this hypothesis has formed its own 3-decade body of evidence, but not consensus (Belsky, 1986; Briske, 1993). Our beaver–willow model provides some insights for a unique her-
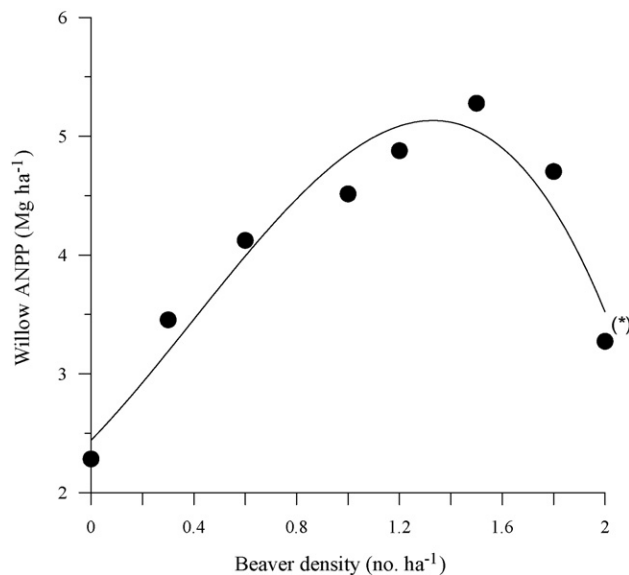
Fig. 9. Change in aboveground net primary productivity (ANPP) under increasing foraging intensity by beaver, as represented by increasing beaver density. Values represent a mean of the last 50 simulated years after the model had reached a steady-state condition. Note (*) that the system was not sustainable when the density of beaver was $\geq 2.0\,\text{ha}^{-1}$.

bivore in an optimum and controlled riparian environment. We found the response of willow ANPP to beaver cutting closely mirrored the classic theoretical pattern expected for overcompensation (McNaughton, 1983). Belsky (1986) suggested root productivity should decline in response to herbivory, however, we found willow BNPP slightly increased in response to beaver. Aboveground woody biomass declined as younger and smaller stems replaced mature stems cut by beaver. Thus, beaver foraging increased productivity but decreased biomass.

Does increased willow productivity in response to beaver infer a fitness benefit to willow? Asexual reproduction via spouting or suckering is an important evolutionary and life history strategy in willows. Most willow species evolved in highly disturbed riverine environments (Karrenberg et al., 2002) and are well adapted to beaver disturbance. Cut stem sections can sprout new roots and shoots, which perpetuates individual genomes. Willows are long-lived plants (>100 years) and beaver-cut plants can sprout vigorously from the root collar or the stem below the cut; however, it is unknown how repeated but intermittent stem removal typical in beaver systems affects plant lifespan. Intermittent cutting can allow the time needed for new shoots to mature and produce seed, but it is unknown how stem removal and regrowth affects the lifetime reproductive success of plants. The dams, ponds, and canals built by beaver can benefit the physical environment of willow and can place water and sediment in locations that floods cannot reach (Westbrook, 2005; Westbrook et al., 2006). If beaver foraging optimizes willow productivity, and beaver construction optimizes willow establishment and survival processes, then perhaps beaver can improve the fitness of some willow populations.

4.4. Beaver–willow persistence

Experimental studies to evaluate long-term species interactions under a wide set of conditions are ordinarily unfeasible. This makes modeling a good approach to quantitatively assess conditions for long-term species coexistence. Our modeling suggests that willows are highly adapted to herbivory by beaver. Willow communities developed stable states with and without beaver but willow ANPP was 2 times higher and plant size was more heterogeneous with beaver present. The simulated colony removed $1.6\,\text{Mg}\,\text{ha}^{-1}\,\text{year}^{-1}$ of willow biomass as food and construction material, which equaled about 20% of ANPP in the 4-ha site. In contrast, a beaver colony in a riparian aspen community of Minnesota removed $8.4\,\text{Mg}\,\text{ha}^{-1}\,\text{year}^{-1}$, which equaled 100% of the ANNP in a typical aspen forest (Johnston and Naiman, 1990). Large differences in harvested biomass among sites can reflect the amount of waste rather than differences in biomass consumed. Aspen trees typically have more non-food biomass than willow simply because they are much larger in diameter. Plant life history strategy, especially sprouting ability, can also affect beaver persistence. The percentage of ANPP used by beaver also depends on the size and location of the area sampled, as beaver typically cut a higher percentage of stems nearer their central place, such as a food cache, dam, or lodge. Thus, mechanisms that drive the persistence of beaver–willow communities arise from a unique combination of willow life history traits and beaver foraging behavior.

Patch size, territorial behavior, biological and physical site conditions, and competition with other herbivores also influence beaver persistence. We found our simulated beaver family became food limited when the patch size of willow was <4 ha, but was sustained indefinitely when patch size was ≥4 ha. Studies of beaver at Sagehen Creek, California also found willow sustained beaver as they moved upstream or downstream to locate suitable stands of vigorous willow (Hall, 1960). Maximum beaver density can be limited by territorial behaviors, such as scent mounding. Minimum beaver density, including presence, can be influenced by

the distribution of suitable woody vegetation relative to the central place foraging mechanisms of stem size and quality relative to hauling distance and predation risk, which can prevent beaver occupancy in areas of patchy habitat. The availability of alternative forage species can greatly affect the persistence of beaver in willow-dominated landscapes. Beaver and their effects can persist as successional stages of colonization, transient stability, and abandonment at multiple spatial and temporal scales (Gurney and Lawton, 1996). Stream gradients, flow rates, and sedimentation rates can affect the persistence of dams and ponds in fluvial systems. Physical effects can rapidly vanish with beaver abandonment or persist for many decades. Competition for willow can favor livestock or ungulates over beaver in heavily browsed environments, such as many forests and rangelands in the western United States (Baker, 2003; Baker et al., 2005). In these areas, the availability of tall willow suitable for winter food caches is necessary for beaver persistence because other suitable woody vegetation is lacking, but is also where decades of intense browsing by large herbivores has either eliminated willow or created short-hedged plants unsuitable to beaver. Landscape-level effects often appear as a mosaic of past and present beaver activities that as a whole can persist indefinitely in many environments, including riparian willow. Thus, the persistence of beaver and their effects depends on the spatial and temporal scale of beaver-engineered patches, foraging dynamics as modeled in this paper, and other physical and biological characteristics that were not included in our model.

4.5. Beaver willow mutualism

Positive, or facultative, plant–herbivore interactions can be considered mutualisms when both species benefit (Stachowicz, 2001; Bruno et al., 2003). Proximate mutualism occurs when removal of either partner decreases performance of the other partner (de Mazancourt et al., 2005). Evolved dependence occurs when adaptation to a partner is the cause of reduced performance in response to the partner's absence. Plants adapted to herbivory should exhibit mechanisms that create a selective advantage in response to herbivory. Here, we place the beaver–willow model system within the context of this recently developed conceptual framework for mutualism.

Our foraging model quantified how willow can benefit beaver as food and construction material and how beaver foraging can increase the productivity of willow and create a diverse plant architecture. Stem removal by beaver stimulates the plant to rapidly sprout new stems to recover root:shoot ratios. Other studies have shown beaver dams, canals, and ponds can benefit willow establishment and survival processes (Baker and Hill, 2003). Empirical evidence from the headwaters of the Colorado River in RMNP showed willow populations can be entirely dependent on the dams, canals, and ponds built by beaver, which can place water and sediment on high terraces beyond the reach of other fluvial processes (Westbrook, 2005; Westbrook et al., 2006). Beaver and willow likely coexisted in abundance throughout the Holarctic region during several million years of evolution until fur trapping decimated beaver populations, which suggests some beaver and willow populations had ample opportunity for evolved dependence. Alternatively, many willow populations are highly successful in disturbed environments that lack beaver. Thus, some beaver–willow communities may represent examples of proximate mutualism that developed via mechanisms of evolved dependence and may provide ecologists with a model system to develop and apply mutualism theory.

4.6. Conclusions

Our modeling suggests that a single beaver family can persist indefinitely in 4 ha of riparian willow without becoming food lim-

ited. We estimate beaver used about 4% of available stems each year for fresh food, stored winter food, and dam maintenance. Selective foraging by beaver increased willow productivity and created a diverse plant architecture that was dominated by medium to large size plants. These outcomes resulted from a unique feedback mechanism generated by dynamic stem selection by beaver relative to the dynamic structure of the willow community. Conditions that generated long-term stability were relatively robust to differences in stem preferences by beaver and in the initial condition of the willow community. Thus, the model suggests long-term beaver herbivory may increase productivity, decrease biomass, and increase structural heterogeneity in a willow community, all of which are interesting ecological hypotheses that could be tested with empirical data.

References

Agricultural Research Council Working Party, 1980. The Nutrient Requirements of Ruminant Livestock, CAB, England.
Aleksiuk, M., 1970. The seasonal food regime of arctic beavers. Ecology 51, 264–270.
Aleksiuk, M., Cowan, I.Mc.T., 1969a. Aspects of seasonal energy expenditure in the beaver (*Castor canadensis* Kulh) at the northern limit of its distribution. Can. J. Zool. 47, 471–481.
Aleksiuk, M., Cowan, I.Mc.T., 1969b. The winter metabolic depression in Artic beavers (*Castor canadensis* Kulh) with comparisons to California beavers. Can. J. Zool. 47, 965–979.
Baker, B.W., 2003. Beaver (*Castor canadensis*) in heavily browsed environments. Lutra 46, 173–181.
Baker, B.W., Cade, B.S., 1995. Predicting biomass of beaver food from willow stem diameters. J. Range Manage. 48, 322–326.
Baker, B.W., Hill, E.P., 2003. Beaver (*Castor canadensis*). In: Feldhamer, G.A., Thompson, B.C., Chapman, J.A. (Eds.), Wild Mammals of North America: Biology, Management, and Conservation. The Johns Hopkins University Press, Baltimore and London, pp. 288–310.
Baker, B.W., Ducharme, H.C., Mitchell, D.C.S., Stanley, T.R., Peinetti, H.R., 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. Ecol. Appl. 15, 110–118.
Barnes, D.M., Mallik, A.U., 1996. Use of woody plants in construction of beaver dams in northern Ontario. Can. J. Zool. 74, 1781–1786.
Belovsky, G.E., 1984. Summer diet optimization by beaver. Am. Midl. Nat. 111, 209–222.
Belsky, A.J., 1986. Does herbivory benefit plants? A review of the evidence. Am. Nat. 127, 870–892.
Brenner, F.J., 1962. Foods consumed by beavers in Crawford County, Pennsylvania. J. Wildl. Manage. 26, 104–107.
Briske, D.D., 1993. Grazing optimization: a plea for a balanced perspective. Ecol. Appl. 3, 24–26.
Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18, 119–125.
Cannell, M.G.R., Milne, R., Sheppard, L.J., Unsworth, M.H., 1987. Radiation interception and productivity of willow. J. Appl. Ecol. 24, 261–278.
Coppock, D.L., Swift, D.M., Ellis, J.E., Galvin, K., 1986. Seasonal patterns of energy allocation to basal metabolism, activity, and production for livestock in a nomadic pastoral ecosystem. J. Agric. Sci. 107, 357–365.
Cottrell, T., 1995. Willow colonization of Rocky Mountain mires. Can. J. For. Res. 25, 215–222.
Coughenour, M.B., 1992. Spatial modeling and landscape characterization of an African pastoral ecosystem: a prototype model and its potential use for monitoring drought. In: McKenzie, D., Hyatt, D., McDonald, V. (Eds.), Ecological Indicators. Elsevier Applied Science, London & New York, pp. 787–810.
Coughenour, M.B., 1994. The SAVANNA landscape model—Documentation and Users Guide. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO.
Coughenour, M.B., 2001. Executive summary of model-based assessment of elk in the Rocky Mountain National Park ecosystem. In: Singer, F.J., Zeigenfuss, L.C. (Eds.), Ecological evaluation of the abundance and effects of elk herbivory in Rocky Mountain National Park, Colorado, 1994–1999, U.S. Geological Survey, Fort Collins, Colorado, pp. 251–266 (Open file report 02-208).
Coughenour, M.B., 2002. Elk in the Rocky Mountain National Park Ecosystem—A Model-Based Assessment. Final Report to USGS Biological Resources Division, Ft. Collins, Colorado and U.S. National Park Service, Rocky Mtn. Nat. Park, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado, pp. 225.

Currier, A.A., Kitts, W.D., Cowan, I.M.cT., 1960. Cellulose digestion in the beaver (*Castor canadensis*). Can. J. Zool. 38, 1109–1111.

de Mazancourt, C., Loreau, M., Dieckmann, U., 2005. Understanding mutualism when there is adaptation to the partner. J. Ecol. 93, 305–314.

DeByle, N.V., 1985. Animal impacts. In: DeByle, N.V., Winokur, R.P. (Eds.), Aspen: Ecology and Management in the Western United States, USDA Forest Service, General Technical Report RM-119, pp. 115–123.

Doucet, C.M., Adams, I.T., Fryxell, J.M., 1994. Beaver dam and cache composition: are woody species used differently? Ecoscience 1, 268–270.

Ellis, J.E., Wiens, J.A., Rodell, C.F., Anway, J.C., 1976. A conceptual model of diet selection as an ecosystem process. J. Theor. Biol. 60, 93–108.

Gurney, W.C.S., Lawton, J.H., 1996. The population dynamics of ecosystem engineers. Oikos 76, 273–283.

Hall, J.G., 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology 41, 484–494.

Hoover, W.H., Clarke, S.D., 1972. Fiber digestion in the beaver. J. Nutr. 102, 9–16.

Johnston, C.A., Naiman, R.J., 1990. Aquatic patch creation in relation to beaver population trends. Ecology 71, 1617–1621.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Karrenberg, S., Edwards, P.J., Kollmann, J., 2002. The life history of Salicaceae living in the active zone of floodplains. Freshwater Biol. 47, 733–748.

Kindschy, R.R., 1985. Response of red willow to beaver use in southeastern Oregon. J. Wildl. Manage. 49, 26–28.

Kindschy, R.R., 1989. Regrowth of willow following simulated beaver cutting. Wildl. Soc. Bull. 17, 290–294.

MacArthur, R.A., 1989. Energy metabolism and thermoregulation of beaver (*Castor canadensis*). Can. J. Zool. 67, 651–657.

McDonald, P., Edwards, R.A., Greenhalgh, J.F.D., 1988. Animal Nutrition. Longman, London and New York, 543 pp.

McGinley, M.A., Whitman, T.G., 1985. Central place foraging by beavers (*Castor canadensis*): a test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). Oecologia 66, 558–562.

McNaughton, S.J., 1983. Compensatory plant growth as a response to herbivory. Oikos 40, 329–336.

Muller-Schwarze, D., Sun, L., 2003. The Beaver: Natural History of a Wetlands Engineer. Cornell University Press, Ithaca, New York, 190 pp.

Nolet, B.A., Hoekstra, A., Ottenheim, M.M., 1994. Selective foraging on woody species by the beaver, *Castor fiber*, and its impact on a riparian willow forest. Biol. Conserv. 70, 117–128.

Novakowski, N.S., 1967. The winter bioenergetics of a beaver population in northern latitudes. Can. J. Zool. 45, 1107–1118.

Parton, W., Schimel, D., Cole, C., Ojima, D., 1987. Analysis of factors controlling soil organic matter levels in Great Plains Grasslands. J. Am. Soc. Soil Sci. 511, 1173–1179.

Pearson, A., 1960. A study of the growth and reproduction of the beaver (*Castor canadensis* Kulh) correlated with the quality and quantity of some habitat factors. M.S. Thesis. University of British Columbia, Vancouver.

Peinetti, H.R., 2000. Riparian Willow Dynamics and Their Interaction with Environmental and Biological Factors in the Elk Winter Range of Rocky Mountain National Park (Colorado)—A Multi-scale Analysis. Ph.D. Dissertation. Colorado State University, Fort Collins, Colorado, USA.

Peinetti, H.R., Kalkhan, M.A., Coughenour, M.B., 2002. Long-term changes in willow spatial distribution on the elk winter range of Rocky Mountain National Park (USA). Landsc. Ecol. 17, 341–354.

Peinetti, H.R., Menezes, R.S.C., Coughenour, M.B., 2001. Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola* Bebb): their relationships with plant water, carbon, and nitrogen dynamics. Oecologia 127, 334–342.

Schmidt-Nielsen, K., 1972. Locomotion: energy cost of swimming, flying, and running. Science 177, 222–228.

Stachowicz, J.J., 2001. Mutualism, facilitation, and the structure of ecological communities. Bioscience 51, 235–246.

Sturtevant, B.R., 1998. A model of wetland vegetation dynamics in simulated beaver impoundments. Ecol. Model. 112, 195–225.

Westbrook, C.J., 2005. Beaver as Drivers of Hydrogeomorphic and Ecological Processes in a Mountain Valley. Ph.D. Dissertation. Colorado State University, Fort Collins, Colorado.

Westbrook, C.J., Cooper, D.J., Baker, B.W., 2006. Beaver dams and overbank floods influence groundwater–surface water interactions of a Rocky Mountain riparian area. Water Resour. Res. 42, W06404, doi:10.1029/2005WR004560.

Woodard, E.L., 1994. Behavior, activity patterns, and foraging strategies of beaver (*Castor canadensis*) on Sagehen Creek, California. Ph.D. Dissertation. University of California, Berkeley, California, 286 pp.

Zeigenfuss, L.C., Singer, F.J., Williams, S.A., Johnson, T.L., 2002. Influences of herbivory and water on willow in elk winter range. J. Wildl. Manage. 66, 788795.