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4 **A BEAVER-WILLOW ECOSYSTEM MODEL**

5 **FINDS STABILITY, OVERCOMPENSATION, AND MUTUALISM**

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20 **ABSTRACT**

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22 Ecologists and land managers need to understand the complex structure and
23 function of beaver-willow ecosystems. We quantified beaver (*Castor canadensis*) and willow
24 (*Salix*) foraging dynamics and developed new models for the SAVANNA ecosystem model

1 to understand and predict the consequences of riparian management. We used the model
2 to test ecological theory regarding ecosystem stability, grazing optimization, and mutualism.
3 The model was initialized using field data from a riparian willow community in Rocky
4 Mountain National Park, Colorado. The model revealed that 4 ha was the minimum area
5 necessary to indefinitely sustain a beaver-willow community with one beaver colony of 2
6 adults, 2 yearlings, and 2 kits. Annual net primary productivity (ANPP) of willow increased
7 across a range of beaver densities until beaver became food limited, which supports the
8 grazing optimization hypothesis. The unique foraging behavior of beaver created a
9 productive and diverse plant architecture dominated by intermediate and large size plants.
10 Browsed and unbrowsed willow sites developed similar stable equilibria 90 years after
11 beaver introduction as selective foraging pressures reshaped plant architecture. Release
12 from beaver herbivory caused willow ANPP and plant architecture to rapidly recover its
13 former state when given suitable growing conditions, which suggests that beaver-willow
14 communities can be highly resilient. The model provides users with a new tool that reveals
15 complex foraging dynamics and explains the ability of beaver and willow to persist
16 indefinitely as mutualists.

17 **INTRODUCTION**

18 The SAVANNA ecosystem model is a management tool designed for large
19 geographic areas with multiple habitat types and species interactions (). The use of
20 SAVANNA to predict the consequences of elk and vegetation management in Rocky
21 Mountain National Park revealed limitations for application to riparian ecosystems
22 dominated by beaver and willow. Specifically, SAVANNA models herbivore foraging
23 dynamics (e.g., ungulates) based on the assumptions that herbivores remove only a portion
24 of current annual growth, herbivores entirely consume removed forage, browsing can occur

1 at frequent time intervals, and response to herbivory can appropriately be measured at the
2 plant level rather than the stem level. These assumptions are not valid for beaver because
3 beaver remove entire stems near ground level, stems need several years to recover
4 suitability so removal occurs at infrequent time intervals, stems are used as both food and
5 construction material, stems may not be fully used, and plants respond to cutting by
6 sprouting new stems from belowground tissues. These limitations prevent the application of
7 SAVANNA to beaver-engineered ecosystems. In this paper we (1) present a new beaver -
8 willow model for SAVANNA that provides users with a tool to understand and predict
9 management consequences in beaver-willow ecosystems, and (2) use the model to test
10 general theory about ecosystem stability, compensatory growth, and mutualism. In a
11 companion paper (Baker et al. companion paper) the model reveals how asymmetrical
12 competition for willow favors elk over beaver.

13 Theoretical and applied ecologists have long sought to understand how plant-animal
14 interactions affect system stability. Mutualisms are positive interactions that benefit both
15 species (Stachowicz 2001) and sometimes can increase system stability (Bruno et al. 2003).
16 The grazing optimization hypothesis suggests plants can overcompensate to the stress of
17 herbivory by increasing their productivity or fitness (McNaughton 1983). Herbivory can also
18 push a community from one stable state to an alternative stable state that resists recovery
19 back to the original state (Beisner et al. 2003). Alternatively, if release from herbivory returns
20 the original state then the community is resilient to herbivory.

21 Beaver are ecosystem engineers that can create positive interactions via physical
22 and biological mechanisms (Jones et al. 1997). Beaver dams, ponds, and canals have
23 important physical effects on ecosystem processes (Johnston and Naiman 1990). Beaver
24 are unique herbivores whose complex foraging behavior most closely resembles the ancient

1 art of coppice forestry, where fast-growing trees are harvested close to the ground to induce
2 basal sprouts. Willows are ubiquitous in Holarctic riparian ecosystems () and have likely
3 coexisted with beaver (*C. canadensis* and *C. fiber*) for millions of years. Willows are highly
4 adapted to disturbed riverine environments and can sprout new stems in proportion to the
5 number cut by beaver (Kindschy 1989). Beaver dams and ponds can improve willow
6 establishment and survival processes and willows can benefit beaver as food and
7 construction material beaver, thus beaver and willow can be mutualists.

8 In this paper we used a simulated beaver-willow model system in Rocky Mountain
9 National Park (RMNP), Colorado, to quantify foraging dynamics and test ecological theory
10 regarding grazing optimization, system stability, and mutualism. We developed a new
11 beaver-willow model to the SAVANNA ecosystem model (Coughenour 1992) and modeled
12 beaver foraging at the level of stems and plants. Foraging dynamics were represented via a
13 nested hierarchy of decision rules based on stem preferences and availability (Ellis et al.
14 1976) relative to a comprehensive simulation model of willow morphology. The model
15 allowed beaver to select stems within plants and tissues within stems, and it considered the
16 seasonal differences in selection and the use of cut stems for fresh food, winter food, or
17 construction material (Doucet et al. 1994). We used the model to determine the minimum
18 area needed to sustain a beaver colony, the annual foraging requirements of the colony,
19 and its energy budget by age class of beaver. Finally, we used modeling experiments to
20 estimate (1) willow productivity and beaver sustainability under a range of beaver densities,
21 (2) the foraging effects of beaver on system stability and plant architecture, and (3) how the
22 initial condition of the willow community affected the ability of selective foraging by beaver to
23 alter the standing crop biomass of willow.

24 METHODS

1 shrub, and tree vegetation. Changes in facet cover are a dynamic outcome of vegetation
2 growth, recruitment, and mortality. Within each facet, the model simulates plant growth and
3 soil water budgets. The spatial structure of the model is defined by vertical soil and plant
4 canopy layers. Plant canopies are organized into strata to compute light intensity using
5 Lambert-Beer's law. Vegetation is represented by the interrelated net primary production
6 and population routines, which predict changes in plant biomass and number of plants,
7 respectively. Herbivory is represented by routines that simulate forage intake, energy
8 balance, population dynamics, and the spatial distributions of animals.

9 SAVANNA was used to simulate the cover area, population structure, and
10 productivity of riparian willow under different elk (*Cervus elaphus*) densities in RMNP
11 (Peinetti 2000). It was parameterized using information from the literature and empirical data
12 from RMNP (Singer and Zeigenfuss 2002). Comparisons of model output (Peinetti 2000)
13 and field data collected inside and outside elk exclosures (Peinetti et al. 2001) showed
14 SAVANNA adequately represented willow aboveground productivity and growth in height.
15 The ability of SAVANNA to estimate willow productivity at larger spatial scales (Zeigenfuss
16 et al. 1999, Zeigenfuss et al. 2002) was verified in RMNP by Coughenour (2001). Thus,
17 SAVANNA was previously calibrated to represent willow populations in RMNP.

18 *Willow population model*

19 SWB includes a willow population model to represent the dynamics of stems and
20 plants appropriate to beaver. SWB includes 6 stem size classes within each of the 6 plant
21 size classes represented by SAVANNA. The numbers of plants or stems promoted to larger
22 size classes is based upon allometric relationships between biomass and size. Each plant
23 size class is described in terms of height, canopy diameter, and aboveground and
24 belowground biomass. Each stem size class is described in terms of biomass. We adapted

1 the configuration of SAVANNA for RMNP willow (Peinetti 2000) to include these specific
2 parameters from the newly developed routines. We used a detailed willow distribution map
3 from Peinetti et al. (2002) to establish the initial condition for SWB, but considered the area
4 to spatially homogeneous because ???_[BB1]. Processes simulated at one level are scaled to
5 the other level. For example, plant carbon fixation is estimated at the plant level in the
6 production routine of SAVANNA based upon total leaf area. The fixed carbon is then
7 allocated to stem size classes in proportion to their contributions to total plant leaf area.
8 Conversely, plant biomass and morphology are derived from the biomass of constituent
9 stem size classes.

10 The distribution of stems within plants is declared at model initialization and
11 subsequently is a dynamic output of the model. A plant in a given size class could be
12 comprised of stems of any size class. To ascribe plants to size classes the following criteria
13 were applied: 1) a plant in a given size class should have a minimum number of stems of a
14 specified size, and 2) if a plant size class is comprised of less than the minimum number of
15 stems required to be in all_[BB2] size classes, the plants in that size class are all demoted to
16 size class one.

17 The number of stems can increase through plant establishment or the development
18 of new stems within an established plant (sprouting). Stem number can decrease due to
19 plant death, death of stems within an established plant, or beaver cutting. Moreover, stems
20 are transferred between size classes based upon net annual biomass accumulation and
21 loss. The net biomass increment of a stem size class depends on stem loss by tissue death
22 or browsing, and stem growth. When a stem size class gains biomass, the proportion of
23 stems promoted to the next larger size class is determined from the quantity of biomass in
24 excess of the biomass expected based on the simulated number of stems in the size class.

1 If biomass per stem in a size class has increased enough to equal the biomass per stem in
2 the next larger size class, then 100% of the stems are transferred. Proportionally fewer
3 stems are transferred when biomass per stem is less than the biomass per stem in the next
4 larger size class. This mechanism maintains a relatively constant size in each class.

5 As with stems, the number of plants in each size class is a dynamic output of the
6 model determined by establishment, mortality, and transfer of individuals between size
7 classes. Establishment increases the number of plants in the smallest size class and death
8 can decrease the number of plants in any size classes. Annual willow establishment is
9 considered proportional to a decreased function of mean water table depth in June, July and
10 August, existing plant density, and woody canopy cover. Plant death is a function of a
11 nominal death rate and growing conditions. Transfer of plants between size classes is
12 calculated at the beginning of the growing season, after the size distribution of stems is
13 updated. The fraction of plants promoted to the next larger size class is equal to the total
14 number of promoted stems divided by the minimum number of stems (*mns*) per plant in the
15 next larger plant size class. Similarly, a fraction of the plants in size classes 2 - 6 are moved
16 to smaller size classes when beaver cutting or old age causes the number of stems to be
17 lower than the minimum number for that size class. Beaver may also remove the entire
18 aboveground biomass of individual willow plants in high use areas. Under adequate growing
19 conditions, willow plants sprout new stems from belowground meristems and rapidly recover
20 lost biomass (Kindschy 1989). The model tracks the number of plants with their entire
21 biomass removed as a variable called "sprouting pool". Only a proportion of plants in the
22 sprouting pool are allowed to sprout during a simulated growing season. The rest of the
23 plants sprout the following simulated growing season. When a plant is allocated to the
24 sprouting pool its root biomass is removed from the population until it sprouts, after which

1 aboveground and belowground biomass is added back into the model as a new plant in size
2 class 1. This mechanism maintains the proper root to shoot ratios of simulated plants. [BB3]

3 We verified t_[BB4]he willow population model by comparing model predictions to field
4 data. Field data were collected during fall 1998 from inside and outside a_[BB5] 30 x 48 m elk
5 exclosure fence that had been constructed in fall 1994 to study browsing effects on willow
6 growth in Endo Valley, RMNP (Peinetti 2000). Plants were placed into the same 6 size
7 classes used in the model (Table 1), thus differences in the size class distribution between
8 fenced and unfenced willow represent differences in willow growth 4 years after release
9 from browsing. The characteristics of unfenced willow were considered as the initial
10 condition for the model. The model was run for 4 years with elk absent and RMNP weather
11 records from 1994 to 1998. We compared the size distribution of fenced willow and model
12 predictions verify that the model accurately represented willow growth.

13 *Beaver model.*

14 The beaver model simulates the growth and foraging activities of a single beaver
15 colony. Colony size is constant during the entire run if beaver energy balance is adequate
16 (see below), otherwise colony size is reduced accordingly. The characteristics of individual
17 beaver are based on 3 age classes: kits (< 1 year), yearlings (1 - 2 years), and adults (> 5
18 years)_[BB6]. Subadult ages are excluded from the model because yearling beaver are
19 eliminated from the colony (via dispersal or mortality) after each year of simulation. Each
20 year existing kits are promoted to yearlings and new kits are added to maintain colony
21 number._[BB7]

22 Each age class has an associated body weight equal to the mean body weight of all
23 individuals in the class, and specific parameters associated with energy demands and body
24 growth. Beaver foraging activities are simulated as the harvest of herbaceous material for

1 fresh food and the harvest of woody material for fresh food, the construction of dams and
2 lodges, and the storage and consumption of a winter food cache. Biomass removed
3 depends on beaver food preferences and biomass availability. Beaver preferences are
4 represented by input indices specific for each foraging activity. Each preference index is
5 multiplied by the available biomass and normalized to a 0 – 1 scale (Appendix 1). Fresh
6 food selection for willow includes two levels of decision; a selection for stem size and a
7 selection for stem tissues (bark, leaves, and current annual growth). In all foraging activities,
8 the amount of biomass removed depends on the intake rate of beaver. Intake of food (Kg of
9 plant biomass) is calculated first by Kg of beaver body weight per day and then scaled to
10 the colony by considering the total body weight of the beaver in the colony and the weekly
11 time step of the model. The representation of dam construction is slightly different from
12 other foraging activities. We assume that dam construction occurs during the first year a
13 colony is established and dam maintenance occurs during the following years. The willow
14 biomass used to construct and maintain dams is an input parameter of the model, and
15 beaver cut willow stems until all required biomass is collected. As in the other foraging
16 activities, stems selected for harvest are determined using preference indices and stem
17 availability. Preferences for dams are constrained to include fixed proportions of small (class
18 2), medium (classes 3 and 4) and large stems (classes 5 and 6); class 1 stems are
19 unsuitable as they are too small for dam construction (Barnes and Mallik, 1996). Stem
20 preference indices are applied within each size class.^[BB8]

21 Biomass consumed by beaver is transformed to metabolizable energy intake is^[BB9]
22 the product of total biomass consumed, the dry matter digestibility of each tissue, the gross
23 energy content of plant tissues, and the ability to metabolize digested forage.

1 Colony energy balance is determined by comparing the energy acquired via foraging^[BB10]
2 and metabolic energy required by the activity of beaver in the colony. Energy deficits and
3 surpluses are translated into changes in body weight. A positive energy balance produces
4 an increase in the mean body weight of the colony, while a negative energy balance has the
5 opposite result. Total metabolic energy required is calculated as:

$$6 \quad \text{MER} = [\text{BMR} + \text{AR} + \text{ERC}] * \text{md} \quad (\text{Eq. 1})$$

7
8 where BMR is the basal metabolic requirement, AR is the activity requirement, ERC is the
9 energy required for construction of dams and a winter food cache, and md represents
10 metabolic depression during winter (scaled 0 – 1). BMR is estimated from the following
11 allometric equation of energy and body size (W) (Novakoswski 1967, Belovsky 1984).

$$12 \quad \text{BMR} = 70 * W^{0.75} \quad (\text{Eq. 2})$$

13
14 BMR is increased by 12% for kits (McArthur 1989). BAR is estimated by multiplying BMR by
15 1.5 for kits and by 2 for yearlings and adults. The energetic cost associated with cutting and
16 moving stems of different sizes (ERC) is estimated following an approach similar to one
17 used by Belovsky (1984). Periods of low metabolic rate coincide with the time that adult and
18 yearling beaver use food from their winter food cache (November - April); periods of high
19 metabolic rate apply to beaver of all age classes for the remainder of the year and for kits
20 during winter. Weight gain only occurs if food metabolic energy (FME) is higher than
21 metabolic energy required (MER). The increase in body weight of the mean individual in the
22 colony in each time step is calculated as:

$$23 \quad \Delta \text{BW} = (\text{FME} - \text{MER}) * \text{BW}_E \quad (\text{Eq. 3})$$

24

1 where $BWE_{[BB11]}$ is the energy to body weight conversion factor.
2 Animal condition is evaluated by a 0 – 1 index that varies from minimum (0) to maximum (1)
3 body weight. The condition index is calculated by comparing the actual body weight of
4 individuals in each age class ($BW(i)$) with the expected maximum and minimum body
5 weight for that size class.

$$6 \quad CI(j) = \frac{BW(i) - MnBW(i)}{ExBW(i) - MnBW(i)} \quad (Eq. 13)$$

8
9 At each weekly time step, the expected maximum body weights are updated by adding a
10 nominal body growth weight to the expected maximum weight for each age class and time
11 of the year. The expected minimum body weight is calculated as a fraction of the maximum
12 expected weight. Expected maximum and minimum weights are reset to initial values once
13 each year when individuals are aged. The increase in body weight in each time step (BW_i)
14 depends upon the following conditions: a) yearlings and adults can increase their body
15 weight only during the period of high metabolic rate but kits can grow throughout the year
16 (albeit at a different rate), because we assume that kits are less affected by metabolic
17 depression than other age classes; b) during periods with high energy inputs the actual
18 growth rate could be slightly above the nominal body growth rate, which allows recovery of
19 weight lost after a food shortage period; and c) when the energy gained is not sufficient to
20 support the nominal body growth rate, the realized growth is partitioned between age
21 classes. Conversely, body weight is reduced when there is a negative energy balance, for
22 example when beaver live in poor quality habitat. The energy lost ($MER - FME$) is
23 transformed to mass units using the efficiency of conversion of energy to body $_{[BB12]}$. Rate of
24 weight gain and loss are limited to maximum values. $_{[BB13]}$

Model application

We simulated a beaver colony comprised of 6 individuals (2 adults, 2 yearlings, and 2 kits) in a riparian willow community of RMNP. Habitats characteristics were based on the biomass, density, and size distribution of willow stems and plants. We initialized the model using field data collected in 1998 from Endo Valley from a site that had likely received a low level of elk and beaver use for many decades, although historical use data were unavailable (Table 1). Peinetti (2000) found that willows had a woody biomass of 610 g m^{-2} , a density of 3,200 plants ha^{-1} , and the frequency distribution of size classes 1 – 6 was 0.210, 0.409, 0.175, 0.122, 0.064, and 0.020. The simulated 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 the stochastic weather routine in *Savanna* (Coughenour 1993) and local records from weather stations and SNOTEL sites in and near RMNP, which represented a mid-elevation (2,500 m) montane ecosystem. We removed past herbivore effects on initial condition by running the model with elk and beaver absent until willow ANPP stabilized, which occurred after 50 years. We estimated the minimum area needed to sustain a complete beaver colony for 150 years by introducing adults, yearlings, and kits (in that order) into 1 – 4 ha of the willow community. 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 colony of 2 adults, 2 yearlings, and 2 kits.

We used the 4-ha minimum area to run the following 5 experiments. First, we estimated the annual foraging requirements of a beaver colony in terms of the number and size distribution of willow stems cut for use as fresh food (consumed without storage), a winter food cache, and woody material to build and maintain a beaver dam. Second, we used the same experimental conditions to develop an annual energy budget for the colony

1 in terms of energy balance and growth by age class. Third, we used the same experimental
2 conditions to investigate willow response to beaver herbivory by comparing willow
3 productivity under a range of beaver densities. Productivity metrics included biomass
4 removed (offtake) and biomass remaining (standing crop). Fourth, we investigated likely
5 underlying mechanisms that explain willow response to beaver herbivory. In this experiment
6 we compared the response variables willow ANPP and frequency distribution of stem size
7 classes for model runs with beaver present and beaver absent. In addition, we compared
8 belowground net primary productivity (BNPP) with beaver present and beaver absent. Fifth,
9 we investigated how the initial condition of the willow community (browsed vs. unbrowsed)
10 affected the ability of beaver herbivory to drive community structure and system stability. We
11 defined the response variable as willow standing crop and defined the *browsed condition* as
12 the condition represented by the original Endo Valley field data and the *unbrowsed*
13 *condition* as the simulated conditions at the same site with elk and beaver absent for 50
14 years. In these simulations, the number of willow plants remained similar but the size of
15 stems and plants differed at initial condition.

16 **RESULTS**

17 *Willow model verification*

18 We verified the ability of the model to accurately predict willow growth rates by
19 comparing model output and field data for the response variable plant density by size class
20 (Fig. 1). The initial condition for the simulation was an unfenced willow site where elk
21 browsing had suppressed plant growth. Class 1 plants (height < 5 m) dominated this site
22 with a density of 3,400 plants ha⁻¹. In contrast, after 4 years of protection from elk browsing
23 the paired fenced site was dominated by class 2 and class 3 plants. The density of plants in
24 size classes 4 – 6 was similar in the fenced and unfenced sites, perhaps because 4 growing

1 seasons was not enough time for plants to reach the larger size classes (Baker et al. 2005).
2 We found simulated data were consistent with observed data model, which suggests the
3 model accurately predicted plant growth during the 4 years following initial condition. We
4 were unable to verify the model's ability to predict long-term growth rates for willow because
5 long-term field data were unavailable. Thus, simulations verified model predictions of willow
6 growth rates during a 4-year period.

7 *Beaver foraging requirements*

8 We compared the use and availability of forage in a 4-ha riparian willow site by a
9 single beaver colony (2 adults, 2 yearlings, and 2 kits) in a steady state condition. Willow
10 availability in the 4 ha site averaged 401,000 live stems during the last 50 years of the
11 model run (Table 2). Willow had 65.3 Mg of aboveground woody biomass with a mean
12 ANPP of 21 Mg year⁻¹ with beaver present. Beaver cut 5.5% of available woody biomass
13 each year for use as fresh food and a winter food cache, which was 18% of willow ANPP.
14 Grasses comprised < 1% of the diet. Beaver used 2.0 Mg of woody biomass to construct a
15 single dam during their first year of occupancy and 0.4 Mg year⁻¹ to maintain the dam.
16 Combined use of woody biomass totaled 28% of willow ANPP in the first year and 20% in
17 remaining years. Relatively large differences between the amounts of woody biomass
18 removed and consumed as fresh and winter food (Table 2) reflects the value of bark and
19 small twigs as food and the remaining biomass as waste. The model did not consider the
20 use of peeled stems as construction material for dams and lodges, which often occurs in
21 natural beaver populations. The size and number of willow stems cut by beaver depended
22 on beaver preference indices and current stem availability, which affected future stem
23 availability via regrowth patterns. Thus, selective foraging by beaver created a dynamic

1 feedback mechanism in the model that reflected how beaver used willow and how willow
2 responded to beaver in the 4-ha simulated beaver-willow community.

3 The size distribution of stems used by beaver in the 4-ha site reflected beaver
4 preferences, stem availability, and stem use as fresh food, winter food, or construction
5 material (Fig. 1). The colony used more stems for fresh food than for the winter food cache
6 (Table 2), and stems for fresh food represented a more diverse size structure (Fig. 1a). Most
7 stems cut for the winter food cache were from the largest size class (Fig. 1b). Size
8 differences of stems used for fresh food and the food cache reflect the models
9 representation of the central place foraging behavior of beaver. Stems cut for the cache
10 must be returned the pond for storage but stems cut as fresh food can be consumed in the
11 nearest safe place. Large stems contain much more food than small stems in moderate size
12 willow species, and they are still small enough to be easily cut and transported by beaver.
13 The parameters built into the model reflected these preferences, as did model output.
14 Similarly, stems used for dam construction reflected both beaver preferences and willow
15 availability. The largest stems (class 6) dominated dam construction material, although all
16 other size classes except class 1 (stems < 1 m tall) were also used (Fig. 1c). Thus, the
17 interaction of beaver preference indices with dynamic stem availability creates the
18 consequence of beaver foraging effects on willow, which is reflected as the number and size
19 of stems used for fresh food, winter food, and dam construction.

20 *Beaver energy budgets*

21 Energy gained by the colony in the 4-ha site increased in proportion to increase in
22 body size of individual beaver (mostly yearlings and kits) during May – October when they
23 were most active and food availability was high (Fig. 2 a and b). The food metabolic energy
24 (FME) gained was greater than metabolic energy required (MER; without growth costs)

1 during most of the year, with the greatest differences in May – October when kit and
2 yearling growth rates were highest. This demonstrates the simulated 4-ha area was capable
3 of supporting the complete annual needs of the colony, as the model was tuned to have an
4 energy balance close to demand (MER plus growth costs). The condition index (simulated
5 weight minus expected weight) was higher for adults and yearlings than for kits. The
6 condition index of kits averaged near bellow 1.0 for the entire year and was the lowest near
7 the end of April (Fig. 2), which was after ice-out but before spring green-up when high-
8 energy food was scarce and demands of growth increased as beaver became more active.

9 *Willow response to beaver foraging*

10 We tested the effects of beaver foraging on willow productivity by varying beaver
11 density within the simulated 4-ha willow site and observing change in willow ANPP. The
12 response pattern showed ANPP increased as herbivore pressure increased until density
13 was about 1.5 beaver ha^{-1} , or 1 colony in 4 ha (Fig. 3). Beaver persisted at these densities
14 for the entire 100-year model run, and ANPP reached a stable state which suggests
15 indefinite sustainability. Simulations with higher beaver densities caused ANPP trends to
16 decrease until beaver were excluded by food limitation when density reached 2.0 beaver
17 ha^{-1} . Thus, willow productivity was higher under all levels of sustainable beaver herbivory,
18 which is consistent with the grazing optimization hypothesis.

19 How did beaver foraging affect willow productivity and structure? We compared
20 ANPP and plant architecture during model runs with beaver absent and beaver present in a
21 simulate 4 ha willow (Fig. 4). The initial condition of the browsed willow community had an
22 ANPP of about 3.2 Mg ha^{-1} and was dominated by shorter plants (Fig. 4a). Release from elk
23 and beaver herbivory caused ANPP to increase from 3.2 to over 5.0 Mg ha^{-1} during the first
24 12 years as plants were promoted from smaller to larger sizes and the system became

1 dominated by intermediate size plants (Fig. 4b). ANPP declined rapidly for 12 more years
2 and then more slowly for about 26 more years as intermediate size plants were promoted to
3 larger size classes. A stable equilibrium occurred during years 50 – 250 when ANPP had
4 stabilized near 2.5 Mg ha^{-1} and 80 % of plants were $\geq 2.0 \text{ m}$ tall (Fig. 4c). We repeated the
5 simulation and introduced a beaver colony at year 50 when the system had recovered from
6 previous herbivory and was relatively stable. At this point ANPP was about 3.0 Mg ha^{-1} and
7 willow $\geq 2.0 \text{ m}$ tall comprised 40% of the population (Fig. 4d). We found ANPP increased
8 from 3.0 to over 5.0 Mg ha^{-1} during the first 20 years after beaver introduction. Beaver
9 annually removed about 20% ($1.0 \text{ Mg ha}^{-1} \text{ year}^{-1}$) of available ANPP from the 4-ha site
10 during this time. Beaver created a more balanced distribution of plants that was dominated
11 by intermediate sizes but also included many large plants (compare Fig. 4 c and e). Beaver
12 and willow persisted in this stable equilibrium until beaver were removed at year 150. ANPP
13 rapidly decreased after beaver removal until it stabilized near the level with beaver absent,
14 and the path of ANPP decrease with beaver removed mirrored the path of increase with
15 beaver introduced. We also modeled the effect of beaver on belowground productivity
16 (BNPP) because critics of grazing optimization theory suggested browsing usually
17 decreases BNPP (Belsky 1986). We found BNPP developed stable equilibria both with and
18 without beaver, but values stabilized at slightly higher levels with beaver present (6.0 Mg
19 ha^{-1}) than with beaver absent (5.0 Mg ha^{-1}). Thus, willow developed a more diverse plant
20 architecture and increased productivity in response to beaver herbivory.

21 *Beaver effects on system stability*

22 How do beaver affect system stability given different initial habitat conditions? We
23 created two different initial conditions from the original Endo Valley field data (Fig. 5). The
24 browsed initial condition (see Fig. 4a) represented the original field data and the unbrowsed

1 initial condition (see Fig. 4d) represented the same area after a 50-year model run with
2 beaver and elk absent to remove the effects of past herbivory. We compared willow
3 standing crop (woody biomass) during two 200-year simulations with beaver present and
4 found both conditions developed similar stable equilibria and biomass levels after 90 years
5 (Fig. 5). Woody biomass increased from 6.4 to 16.4 Mg ha⁻¹ for the browsed initial condition
6 and decreased from 27.0 to 16.4 Mg ha⁻¹ for the unbrowsed initial condition. The
7 combination of use, availability, and beaver foraging preferences likely explains the rapid
8 convergence of willow biomass from different initial conditions. Stem use depended on
9 availability, with large stems more preferred. More large stems were available in the
10 unbrowsed condition than in browsed condition when the simulation started, thus more large
11 stems were used. Removal of large stems increased the proportion of small stems as plants
12 recovered root:shoot ratios. Also, large stems contain a lower proportion of biomass from
13 bark and small twigs (Baker and Cade 1985), thus more non-food biomass is discarded
14 from large stems. In contrast the browsed treatment had fewer large stems available at time
15 zero, which reduced their use as food and reduced the amount of biomass cut for food
16 because smaller stems had less waste than larger stems. In addition, standing crop
17 increased as suppressed stems increased in size after release from browsing and were
18 promoted to the larger size classes (Baker et al . 2005). Thus, the selective foraging
19 pressures of beaver created similar stable equilibria from two willow communities with vastly
20 different initial conditions.

21 **DISCUSSION**

22 We developed beaver and willow models to the Savanna ecological model and
23 investigated foraging dynamics in a simulated beaver-willow community in Rocky Mountain
24 National Park, Colorado. We predicted the size class distribution and number of willow

1 stems required by a beaver colony (2 adults, 2 yearlings, and 2 kits) for fresh food, stored
2 winter food, and dam construction (Fig. 1), and modeled energy balance and growth in the
3 beaver colony (Fig. 2). We found the beaver colony required a minimum of 4 ha to achieve
4 long-term stability, when the rates of willow removal and regrowth remained near
5 equilibrium. Beaver foraging increased willow productivity across a range of beaver
6 densities until food limitation excluded beaver (Fig. 3). The unique foraging behavior of
7 beaver strongly shaped the size distribution of willow plants and created a diverse plant
8 architecture dominated by intermediate and large size plants (Fig. 4). Release from beaver
9 herbivory caused willow ANPP and plant architecture to rapidly recover its undisturbed
10 state. Browsed and unbrowsed willow sites developed similar stable equilibria 90 years after
11 beaver introduction, as selective foraging pressure reshaped plant architecture (Fig. 5).
12 Thus, modeling experiments revealed foraging interactions that help explain the intrinsic
13 ability of beaver and willow to persist indefinitely as mutualists in some riparian
14 communities.

15 *Model performance*

16 *Beaver model.*— The model estimated a beaver colony in RMNP cut about 70 willow
17 stems per day during its first year of occupancy, when one dam and one winter food cache
18 were constructed. Beaver foraging requirements vary in response to biological and physical
19 site characteristics. For example, a beaver colony in boreal forest at Isle Royale, Michigan,
20 cut about 30 plants per day from a mixed community that included *Alnus*, *Acer*, and *Betula*
21 (Belovsky 1984). Beaver annually used 4% of available willow stems at our Rocky Mountain
22 study site (Table 2), whereas Eurasian beaver (*C. fiber*) used 1 – 5% of available willow (*S.*
23 *alba*) standing crop in the Netherlands (Nolet et al. 1994). Beaver energetic needs can differ
24 for wild and captive populations. Our model predicted higher energy demands for wild

1 beaver than found in studies of captive beaver, which typically lack estimates for energy
2 expended to obtain and transport stems, construct and maintain dams and lodges, and
3 store winter food (Pearson 1960, Woodward 1994). Captive beaver consumed 30 – 40 %
4 less biomass than predicted by our model (Aleksiuk and Cowan 1969, Woodward 1994).
5 Construction needs can substantially increase minimum area requirements but are difficult
6 to predict because the number and size of dams and lodges built by beaver depends on
7 local geomorphology, hydrology, and other site-specific conditions (Doucet et. al 1994).
8 Beaver used 2.5 Mg of willow to build and maintain a dam in our Rocky Mountain study. Site
9 sustainability can be increased and area needs decreased if beaver dams contain a high
10 proportion of stems from non-food species, peeled stems, dead stems, woody debris, or
11 rocks and other non-plant materials (Doucet et al 1994, Barnes and Mallik 1996). Our model
12 assumed the beaver dam consisted entirely of intact willow stems, as no information was
13 available to quantify other construction material. Also, beaver likely use fewer stems in sites
14 where they do not build and maintain dams, such as in lakes or large rivers, or when they
15 use abandoned dams that require maintenance only (Johnston and Naiman 1990). Thus,
16 beaver are highly adaptable to local environmental conditions and modeling assumptions
17 that reflect site-specific needs will yield better predictions.

18 Is our beaver foraging model realistic? We found a single beaver colony required a
19 minimum of 4 ha to persist indefinitely (≥ 150 years) in a site where all willow stems were
20 equally available. Assuming a 4-ha riparian willow zone is 50 m wide by 800 m long and a
21 suitable physical environment, then it seems likely it could indefinitely sustain a single
22 colony that was free to move dams, lodges, and foraging areas upstream or downstream as
23 needed. We were unable to verify these predictions with quantitative field data, but
24 qualitative data from a beaver telemetry study in RMNP suggests predictions are realistic for

1 sites (e.g., Wild Basin) subjected to minimal additional herbivory (B. W. Baker unpublished
2 data). Our model represented foraging dynamics at the stem level, which is consistent with
3 recommendations by other beaver-willow studies at Sagehen Creek, Nevada (Woodard
4 1994). Our model assumes a spatially uniform environment and excludes the effects of
5 beaver on willow establishment and survival processes. The model also assumes a similar
6 plant density and number of stems per plant with and without beaver. The assumptions
7 likely fail to capture the true complexity of beaver-willow interactions. For example, stem
8 removal can increase the number of stems per plants and affect plant density. Cut stems
9 can sprout adventitious roots and became established as new individuals (Cottrell 1995).
10 Beaver dams can create bare moist sediment and raise the water table, which can affect
11 growth and survival of willow (Baker and Hill 2003). Beaver are central place foragers that
12 can select stem size based on hauling distance. As distance increases selection favors the
13 smaller trunks of larger trees, such as aspen, and larger stems of smaller shrubs, such as
14 willow (Woodard 1994). The foraging and dam building activities of beaver create
15 heterogeneous plant communities and succession patterns that occur as complex patches
16 in the landscape (Sturtevant 1998, Westbrook 2005). Therefore, beaver can structure a
17 willow community into a much more complex state than predicted by our relatively simple
18 foraging dynamics model.

19 *Plant response to beaver foraging*

20 *Patterns.*— We found that willow ANPP was higher under all sustainable levels of
21 beaver herbivory (Fig. 3). The trend showed ANPP increased until beaver densities reached
22 $0.25 \text{ colonies ha}^{-1}$ and decreased with higher densities until food limitation excluded beaver
23 at densities of $\geq 0.33 \text{ colonies ha}^{-1}$. BNPP was slightly higher with all sustainable beaver
24 densities. Beaver herbivory altered plant architecture by creating a more balanced and

1 diverse size structure that included a large proportion of plants in the intermediate and tall
2 sizes (Fig. 4e). The absence of beaver allowed plants to continue to grow in size as they
3 aged, and unlimited growth developed a homogeneous community of larger willow that was
4 only half as productive as the more heterogeneous beaver-willow community (Fig. 4c).
5 Simulations showed the standing crop of woody biomass was 27.0 Mg ha^{-1} without beaver
6 and 16.4 Mg ha^{-1} with beaver (Fig. 5, Unbrowsed Initial Condition, Time = 0 years and 90
7 years). These patterns were largely the dynamic consequence of stem availability, beaver
8 size preferences for food and construction material, increased stem turnover rate, and
9 sprouting following stem removal. Thus, beaver herbivory increased productivity, decreased
10 biomass, and increased structural heterogeneity in the willow community.

11 Response to beaver foraging depends on plant life history traits. Beaver typically cut
12 stems near the ground level, which can stimulate the growth of vigorous new shoots from
13 the root collar or remaining stem segment. Red willow (*S. lasiandra*) in Oregon increased
14 stem production in proportion to the number of stems cut per plant, with a stem elongation
15 rate of 3.3 cm day^{-1} on cut plants and 0.4 cm day^{-1} on controls (Kindschy 1985, 1989).
16 Mountain willow (*S. monticola*) plants in RMNP recovered 148.4% of their pre-cut stem
17 number during the first growing season after all stems were removed to simulate beaver
18 herbivory (Baker et al. 2005). Cottonwood trees (*Populus fremontii*) subjected to repeated
19 beaver cutting developed a shrub-like growth form that had 3 times more basal branches
20 and were only 25% as tall as uncut trees (McGinley and Whitman 1985). Beaver cutting
21 usually stimulates vigorous suckering in clonal species such as aspen (*Populus*
22 *tremuloides*) and coyote willow (*Salix exigua*) (DeByle 1985). Disturbance can stimulate
23 seedling establishment in non-sprouting woody plants, such as some *Nothofagus* species in
24 Tierra del Fuego, Argentina (Veblen et al. 1996). Thus, plant response to beaver foraging

1 varies by growth form (tree vs. shrub) and reproductive strategy (sprouting vs. seed, clonal
2 vs. non-clonal).

3 *Mechanisms.*— Beaver herbivory is similar to the ancient art of coppice forestry, as
4 both disturbances can produce a sustainable supply of small diameter stems for fuel and
5 construction. Willows are often selected for short rotation coppice systems designed to
6 produce renewable energy sources. Coppiced systems are clear-cut at the plant and patch
7 levels whereas beaver are more selective, but some compensatory growth mechanisms
8 likely apply to both systems. Our results showed selective foraging by beaver increased
9 structural heterogeneity in willow. A diverse canopy structure can increase productivity,
10 especially if it includes more and younger stems. Light intercepted by green woody stems is
11 used for photosynthesis, particularly in the re-fixation of respiratory CO₂. A large proportion
12 of solar radiation is intercepted by the stems and branches of woody plants, which is greatly
13 affected by their spacing (Cannell et al. 1987). Productivity is higher in leaves than in stems
14 and the leaf area index is higher when leaves are distributed throughout both the horizontal
15 and vertical planes of the canopy, which increases the efficiency of intercepting solar
16 radiation. Small stems have a low leaf area index and large stems have a high proportion of
17 non-photosynthetic tissues, so optimum productivity often occurs in intermediate size stems.
18 Beaver foraging thins out some larger stems and creates a more balanced size structure,
19 which increases the ratio of photosynthetic to non-photosynthetic tissue. Thus, mechanisms
20 that result from vigorous sprouting and a diverse plant architecture partially explain how
21 beaver herbivory increases willow productivity.

22 *Overcompensation.*— The grazing optimization hypothesis suggests plants can
23 overcompensate in response to herbivory (McNaughton 1983). The debate created by this
24 hypothesis has formed its own 3-decade body of evidence, but not consensus (Belsky 1986,

1 Briske 1993). Our beaver-willow model provides some insights for a unique herbivore in an
2 optimum and controlled riparian environment. We found the response of willow ANPP to
3 beaver cutting closely mirrored the classic theoretical pattern expected for
4 overcompensation (McNaughton 1983). Belsky (1986) suggested root productivity should
5 decline in response to herbivory, however we found willow BNPP slightly increased in
6 response to beaver. Aboveground woody biomass declined as younger and smaller stems
7 replaced mature stems cut by beaver. Thus, beaver foraging increased productivity but
8 decreased biomass.

9 Does increased willow productivity in response to beaver infer a fitness benefit to
10 willow? Asexual reproduction via spouting or suckering is an important evolutionary and life
11 history strategy in willows. Most willow species evolved in highly disturbed riverine
12 environments (Karrenberg et al. 2002) and are well adapted to beaver disturbance. Cut
13 stem sections can sprout new roots and shoots, which perpetuates individual genomes.
14 Willows are long-lived plants (100+ years) and beaver-cut plants can sprout vigorously from
15 the root collar or the stem below the cut; however, it's unknown how repeated but
16 intermittent stem removal typical in beaver systems affects plant lifespan. Intermittent
17 cutting can allow the time needed for new shoots to mature and produce seed, but it's
18 unknown how stem removal and regrowth affects the lifetime reproductive success of
19 plants. The dams, ponds, and canals built by beaver can benefit the physical environment of
20 willow and can place water and sediment in locations that floods cannot reach (Westbrook
21 2005, Westbrook et al. *In press*). If beaver foraging optimizes willow productivity and beaver
22 construction optimizes willow establishment and survival processes, then beaver likely
23 improve the fitness of some willow populations.

24 *Stability, persistence, and mutualism*

1 *Stability.*— Simulated willow communities both with and without beaver developed
2 stable equilibria, but willow ANPP was two times higher and plant size was more
3 heterogeneous with beaver present (Fig. 4 c and e). When beaver were removed from the
4 simulation, ANPP decreased in a trajectory similar to its path of increase, and eventually
5 productivity and plant size structure became similar to the undisturbed state (Fig. 4 f and g).
6 Ecological theory suggests an alternative stable state exists if ceasing a disturbance does
7 not return the community back to its initial condition, and hysteresis is revealed if the return
8 trajectory of the equilibrium point differs from the outbound path (Beisner et al. 2003, Suding
9 et al. 2004). Our model showed a beaver-willow community existing in a stable equilibrium
10 was highly resilient after release from herbivory, thus it did not exhibit the characteristics of
11 an alternative stable state or hysteresis. This interpretation is consistent with empirical
12 evidence from RMNP that showed willow can rapidly recover biomass and size if regrowth
13 remains undisturbed after beaver herbivory (Baker et al. 2005). Willow plants recovered
14 151% of their pre-cut stem number and 93% of their pre-cut stem biomass in only 3 years
15 after complete stem removal. Thus, willow are resilient and highly adapted to beaver
16 herbivory and can exist in a stable equilibrium either with beaver in suitable environments.

17 *Persistence.*— We found a beaver-willow community persisted as a productive and
18 stable equilibrium in a 4-ha riparian area. The simulated colony removed $1.6 \text{ Mg ha}^{-1} \text{ year}^{-1}$
19 of willow biomass as food and construction material, which equaled about 20% of ANPP in
20 the 4-ha site. In contrast, a beaver colony in a riparian aspen community of Minnesota
21 removed $8.4 \text{ Mg ha}^{-1} \text{ year}^{-1}$, which equaled 100% of the ANPP in a typical aspen forest
22 (Johnston and Naiman 1990). Large differences in harvested biomass among sites can
23 reflect the amount of waste rather than differences in biomass consumed. Aspen trees
24 typically have more non-food biomass than willow simply because they are much larger in

1 diameter. Plant life history strategy, especially sprouting ability, can also affect beaver
2 persistence. The riparian forest ecology in Tierra del Fuego, South America, was
3 dramatically altered after 50 beaver (25 mated pairs) were introduced in the 1940s to start a
4 fur industry. Beaver found southern beech trees (*Nothofagus* spp.) suitable as food and
5 construction material and the population rapidly expanded to over 100,000 individuals
6 (Lizzaralde 1993). Vegetative reproduction is weak or lacking in preferred *Nothofagus*
7 species. Poor sprouting and abundant unoccupied habitat favor short beaver persistence
8 times as beaver seek virgin riparian forage along stream corridors rather than upland forage
9 located further from water at established sites. Thus, beaver foraging behavior and the life
10 history strategy, size, and composition of plant communities influence the spatial and
11 temporal persistence of beaver.

12 Patch size, territorial behavior, and physical site conditions also influence beaver
13 persistence. We found a beaver colony became food limited when patch size was < 4 ha.
14 Maximum beaver density can also be limited by territorial behaviors, such as scent-
15 mounding. Minimum beaver density, including presence, can be influenced by the
16 distribution of suitable woody vegetation relative to the central place foraging mechanisms
17 of stem size and quality relative to hauling distance and predation risk, which can prevent
18 beaver occupancy in areas of patchy habitat. Beaver and their effects can persist as
19 successional stages of colonization, transient stability, and abandonment at multiple spatial
20 and temporal scales (Gurney and Lawton 1996). Stream gradients, flow rates, and
21 sedimentation rates can affect the persistence of dams and ponds in fluvial systems.
22 Physical effects can rapidly vanish with beaver abandonment or persist for many decades.
23 Landscape-level effects often appear as a mosaic of past and present beaver activities that
24 as a whole can persist indefinitely in many environments, including riparian willow. Thus, the

1 persistence of beaver and their effects depends on the spatial and temporal scale of
2 beaver-engineered patches, foraging dynamics as modeled in this paper, and the many
3 physical and biological characteristics that were not included in our model.

4 *Beaver-willow mutualism.*— Facultative, or positive, interactions between species can
5 be considered mutualisms when both species benefit (Stachowicz 2001). Our foraging
6 model quantified how willow can benefit beaver as food and construction material and how
7 beaver foraging can benefit the productivity of willow and create a more diverse plant
8 architecture. Other studies have shown beaver dams, canals, and ponds can benefit willow
9 establishment and survival processes (Baker and Hill 2003). Thus, beaver can benefit
10 willow, willow can benefit beaver, and these positive interactions can be considered
11 facultative mutualism.

12 Mutualism is widespread in nature and important and controversial to many
13 ecologists. Proximate mutualism occurs when removal of either partner decreases
14 performance of the other partner (Mazancourt et al . 2005). Evolved dependence occurs
15 when adaptation to a partner is the cause of reduced performance in response to the
16 partner's absence. Plants adapted to herbivory should exhibit mechanisms that create a
17 selective advantage in response to herbivory. Here, we place the beaver-willow model
18 system within the context of this recently developed conceptual framework for mutualism.

19 We found removal of beaver decreased willow productivity and suitable willow was
20 necessary to sustain beaver. Beaver cutting stimulated vigorous sprouting in willow and
21 beaver and willow persisted indefinitely in a stable equilibrium, but the effects of beaver on
22 lifetime reproductive success of willow was unknown. Empirical evidence from the
23 headwaters of the Colorado River in RMNP showed willow populations can be entirely
24 dependent on the dams, canals, and ponds built by beaver, which can place water and

1 sediment on high terraces beyond the reach of other fluvial processes (Westbrook 2005,
2 Westbrook et al. *In press*). Beaver and willow likely coexisted in abundance throughout the
3 Holarctic region during several million years of evolution until fur trapping decimated beaver
4 populations, which suggests some beaver and willow populations had ample opportunity for
5 evolved dependence. Alternatively, many willow populations are highly successful in
6 disturbed environments that lack beaver. Thus, some beaver-willow ecosystems may
7 represent examples of proximate mutualism that developed via mechanisms of evolved
8 dependence and may provide ecologists with a model system to develop and apply
9 mutualism theory.

10 *Management Implications*

11 Beaver folklore is a rich and colorful tapestry of fact, fiction, and myth. For example, it
12 is widely believed that without proper management beaver will invariably “eat themselves
13 out of house and home.” We found a single beaver colony persisted indefinitely in ≥ 4 ha of
14 riparian willow without becoming food limited. The colony annually used 16,550 of 400,100
15 available stems in the 4 ha site for fresh food, winter food, and dam maintenance. Stem
16 regrowth rate equaled stem replacement rate, but selective foraging created more diverse
17 plant architecture. The cumulative foraging impact could appear substantial if 4% of stems
18 were cut annually and if beaver-cut stumps were easily visible and took many years to rot
19 and disappear. Thus, obvious but sustainable foraging effects in beaver-willow communities
20 could mislead managers into thinking beaver populations were too high and required
21 increased harvest.

22 Beaver can be useful as restoration agents in riparian ecosystems degraded by
23 erosion or excessive herbivory by livestock or ungulates (Apple et al. 1985, Baker and Hill
24 2003). They can be transplanted into degraded montane or sagebrush-steppe streams to

1 encourage willow establishment and survival after the cause of degradation has been
2 managed. In some cases (sink populations) beaver may persist only long enough to build
3 dams and ponds from sagebrush or other material to create the desired riparian response
4 for willow. Sink populations can be supplemented with willow to improve overwinter survival
5 until local willow growth increases reproductive success and creates a source beaver
6 population (Baker and Hill 2003). Our model estimates the amount of willow needed to
7 overwinter a beaver colony and create a source population of dispersing yearlings. We
8 found a beaver colony annually used 1,450 stems (1.4 Mg of biomass) to construct a food
9 cache that indefinitely sustained the colony during winter and helped create a source
10 population that produced 2 dispersing yearlings (Table 2). This estimate gives managers a
11 good starting point for the inevitable trial and error that drives most beaver restoration
12 projects. Also, we found the presence the beaver for ≥ 90 years developed stable equilibria
13 and similar standing crop biomass from very different initial willow conditions. Thus, our
14 model quantifies the biomass needed for sustainable beaver restoration and shows similar
15 riparian restoration endpoints can be obtained from vastly different initial willow conditions.

16 **LITERATURE CITED**

- 17 Aleksasuk, M., and I. Cowan. 1969. Aspects of seasonal energy expenditure in the beaver
18 (*Castor canadensis*). Canadian Journal of Zoology 47:471–481.
- 19 Apple, L. L., B. H. Smith, J. D. Dunder, and B. W. Baker. 1985. The use of beavers for
20 riparian/aquatic habitat restoration of cold desert, gully-cut stream systems in
21 southwestern Wyoming. Pages 123–130 in G. Pilleri, editor. Investigations on
22 beavers, Volume 4, Brain Anatomy Institute, Berne, Switzerland.
- 23 ARC. 1980. The nutrient requirements of ruminant livestock. Slough: Commonwealth
24 Agricultural Bureau.

- 1 Baker, B. W., and B. S. Cade. 1995. Predicting biomass of beaver food from willow stem
2 diameters. *Journal of Range Management* 48:322–326.
- 3 Baker, B. W., and E. P. Hill. 2003. Beaver (*Castor canadensis*). Pages 288–310 in G. A.
4 Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild Mammals of North*
5 *America: Biology, Management, and Conservation*. Second Edition. The Johns
6 Hopkins University Press, Baltimore and London.
- 7 Baker, B. W., H. C. Ducharme, D. C. S. Mitchell, T. R. Stanley, and H. R. Peinetti. 2005.
8 Interaction of beaver and elk herbivory reduces standing crop of willow. *Ecological*
9 *Applications* 15:110–118.
- 10 Barnes, D. M., and A. U. Mallik. 1996. Use of woody plants in construction of beaver dams
11 in northern Ontario. *Canadian Journal of Zoology* 74:1781–1786.
- 12 Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology.
13 *Frontiers in Ecology and the Environment* 1:376–382.
- 14 Belovsky, G. E. 1984. Summer diet optimization by beaver. *American Midland Naturalist*
15 111:209–222.
- 16 Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. *American*
17 *Naturalist* 127:870–892.
- 18 Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into
19 ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- 20 Cannell, M. G. R., R. Milne, L. J. Sheppard, and M. H. Unsworth. 1987. Radiation
21 interception and productivity of willow. *Journal of Applied Ecology* 24:261–278.
- 22 Coppock, D., D. Swift, J. Ellis, and K. Galvin. 1986. Seasonal patterns of energy allocation
23 to basal metabolism, activity and production for livestock in a nomadic pastoral
24 ecosystems. *J. Agric. Sci. Camb.* 107:357–365.

- 1 Cottrell, T. 1995. Willow colonization of Rocky Mountain mires. *Canadian Journal of Forest*
2 *Research* 25:215–222.
- 3 Coughenour, M. B. 1992. Spatial modeling and landscape characterization of an African
4 pastoral ecosystem: a prototype model and its potential use for monitoring drought. in
5 D. McKenzie, D. Hyatt, and V. McDonald, editors. *Ecological Indicators*. Elsevier
6 Applied Science, London & New York.
- 7 Coughenour, M. B. 1993. The SAVANNA landscape model - Documentation and Users
8 Guide. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins
9 Colorado.
- 10 Coughenour, M. B. 2001. Executive summary of model-based assessment of elk in the
11 Rocky Mountain National Park ecosystem. Pages 251 – 266 *in* Singer, F. J., and L.
12 C. Zeigenfuss, compilers. *Ecological evaluation of the abundance and effects of elk*
13 *herbivory in Rocky Mountain National Park, Colorado, 1994–1999*. U.S. Geological
14 Survey, Fort Collins, Colorado. Open file report 02-208.
- 15 DeByle, N. V. 1985. Animal impacts. Pages 115 –123 *in* N. V. DeByle and R. P. Winokur,
16 editors. *Aspen: Ecology and Management in the Western United States*. USDA
17 Forest Service, General Technical Report RM-119.
- 18 Doucet, C. M., I. T. Adams, and J. M. Fryxell. 1994. Beaver dam and cache composition:
19 are woody species used differently? *Ecoscience* 1:268–270.
- 20 Ellis, J., J. Wiens, C. Rodell, and J. Anway. 1976. A conceptual model of diet selection as
21 an ecosystem process. *Journal of Theoretic Biology* 60:93–108.
- 22 Gurney, W. C. S., and J. H. Lawton. 1996. The population dynamics of ecosystem
23 engineers. *Oikos* 76:273–283.

- 1 Johnston, C. A., and R. J. Naiman. 1990. Aquatic patch creation in relation to beaver
2 population trends. *Ecology* 71:1617–1621.
- 3 Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of
4 organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.
- 5 Karrenberg, S., P. J. Edwards, and J. Kollmann. 2002. The life history of Salicaceae living in
6 the active zone of floodplains. *Freshwater Biology* 47:733–748.
- 7 Kindschy, R. R. 1985. Response of red willow to beaver use in southeastern Oregon.
8 *Journal of Wildlife Management* 49:26–28.
- 9 Kindschy, R. R. 1989. Regrowth of willow following simulated beaver cutting. *Wildlife*
10 *Society Bulletin* 17:290–294.
- 11 Lizarralde, M. S. 1993. Current status of the introduced beaver (*Castor canadensis*)
12 population in Tierra del Fuego, Argentina. *Ambio* 22:351–358.
- 13 Mazancourt, C. de, M. Loreau, and U. Dieckmann. 2005. Understanding mutualism when
14 there is adaptation to the partner. *Journal of Ecology* 93:305–314.
- 15 McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. *Oikos*
16 40:329–336.
- 17 McArthur, R. 1989. Energy metabolism and thermoregulation of beaver (*Castor*
18 *canadensis*). *Canadian Journal of Botany* 67:651–657.
- 19 McGinley, M. A., and T. G. Whitman. 1985. Central place foraging by beavers (*Castor*
20 *canadensis*): a test of foraging predictions and the impact of selective feeding on the
21 growth form of cottonwoods (*Populus fremontii*). *Oecologia* 66:558–562.
- 22 Nolet, B. A., A. Hoekstra, and M. M. Ottenheim. 1994. Selective foraging on woody species
23 by the beaver *Castor fiber*, and its impact on a riparian willow forest. *Biological*
24 *Conservation* 70:117–128.

- 1 Novakowski, N. 1967. The winter bionergetics of a beaver population in northern latitudes.
2 Canadian Journal of Zoology 45:1107–1118.
- 3 Parton, W., D. Schimel, C. Cole, and D. Ojima. 1987. Analysis of factors controlling soil
4 organic matter levels in Great Plains Grasslands. Soil Science Society of America
5 Journal 511:1173–1179.
- 6 Pearson, A. 1960. A study of the growth and reproduction of the beaver (*Castor canadensis*
7 Kulh) correlated with the quality and quantity of some habitat factors. M.S. thesis.
8 University of British Columbia, Vancouver.
- 9 Peinetti, H. R. 2000. Riparian willow dynamics and their interaction with environmental and
10 biological factors in the elk winter range of Rocky Mountain National Park (Colorado)
11 - A multi-scale analysis. Ph.D. dissertation. Colorado State University, Fort Collins,
12 Colorado, USA.
- 13 Peinetti, H.R., M. A. Kalkhan, and M. B. Coughenour. 2002. Long-term changes in willow
14 spatial distribution on the elk winter range of Rocky Mountain National Park (USA).
15 Landscape Ecology 17:341–354.
- 16 Peinetti, H. R., R. S. C. Menezes, and M. B. Coughenour. 2001. Changes induced by elk
17 browsing in the aboveground biomass production and distribution of willow (*Salix*
18 *monticola* Bebb): their relationships with plant water, carbon, and nitrogen dynamics.
19 Oecologia 127:334–342.
- 20 Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities.
21 Bioscience 51:235–246.
- 22 Sturtevant, B. R. 1998. A model of wetland vegetation dynamics in simulated beaver
23 impoundments. Ecological Modeling 112:195–225.

- 1 Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive
2 feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19:46–53.
- 3 Veblin, T. T., C. Donoso, T. Kitzberger, and A. J. Rebertus (1996). Ecology of Southern
4 Chilean and Argentinean *Nothofagus* forests. Pages 293 –353 in T. T. Veblen, R. S.
5 Hill, and J. Read, editors. *The Ecology and Biogeography of Nothofagus Forests*.
6 Yale University Press, New Haven, Connecticut.
- 7 Westbrook, C. J., D. J. Cooper, and B. W. Baker. 2005. Beaver dams and overbank floods
8 influence groundwater-surface water interactions of a Rocky Mountain riparian area.
9 *Water Resources Research* 42, W06404, doi:10.1029/2005WR004560.
- 10 Woodard, E. L. 1994. Behavior, activity patterns, and foraging strategies of beaver (*Castor*
11 *canadensis*) on Sagehen Creek, California. Ph.D. Dissertation. University of
12 California, Berkeley, California. 286 pp.
- 13

1 Table 1. Morphological characteristics used to initialize the willow population model. Values
 2 are based on field measurements taken in Endo Valley, Rocky

a. Plant size class						
	1	2	3	4	5	6
Height (m)	0.5	1.2	2.4	2.9	3.4	3.8
Canopy bottom (m)	0.0	0.0	0.0	0.3	0.5	0.7
Canopy area (m ²)	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)	120	240	900	2,500	6,500	14,500

3 Mountain National Park, Colorado, USA, 1998.

4

1 (*)

	b. Stem size class					
	1	2	3	4	5	6
Height (m)	0.5	1.2	2.4	2.9	3.4	3.8
Woody biomass (g) (*)	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	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

37 Total stem biomass excluding leaves.

38

1 Table 2. Foraging effects of a beaver colony (2 adults, 2 yearlings, and 2 kits) in a simulated
 2 willow community in Rocky Mountain National Park, Colorado, USA. Values are means of
 3 the last 50 simulated years⁽¹⁾ and indicate totals for the 4 ha site during stable equilibrium.

		Biomass (Mg)				Number of stems
		Leaves ⁽²⁾	CAG ⁽³⁾	Woody (4)	Total ⁽⁵⁾	
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
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1

2

3 ⁽¹⁾ The model run was IC + 50 years NB NE + 100 years B NE; where IC=field data, B =
4 beaver, NB = no beaver, NE = no elk.

5

6 ⁽²⁾ Leaves at peak biomass.

7

8 ⁽³⁾ Current annual growth (CAG) biomass at the end of the growing season.

9

10 ⁽⁴⁾ Stem biomass at the end of the growing season (excluding leaves but including CAG).

11

12 ⁽⁵⁾ Total does not equal the sum of leaves, CAG, and woody because leaves are reported at
13 peak biomass, which occurred before the end of the growing season, and thereafter leaf
14 biomass was allocated to CAG and older woody tissues.

15

Figure Legend

1
2 Figure 1.^[BB14] The willow population model for SAVANNA-WILLOW-BEAVER (SWB) was
3 verified using field data collected in 1998^[BB15] from Endo Valley, Rocky Mountain National
4 Park, Colorado. The model was initialized using the size class distribution (plants ha⁻¹) of
5 willow plants in an^[BB16] unfenced site (30 × 46 m) where elk browsing had suppressed plant
6 growth for many decades. We compared model output after 4 years of simulated time with
7 elk absent and field data collected 4 years after the site^[BB17] was fenced to exclude elk. We
8 found the simulated data were consistent with field data, which suggests the model
9 accurately predicted willow growth rates during the 4-year time period.

10
11 Figure 2. The number of willow stems predicted to be cut by a beaver colony (2 adults, 2
12 yearlings, and 2 kits) when foraging for fresh food, a winter food cache, and construction of
13 a single beaver dam. Values represent the consequence of stem availability and beaver
14 preference indices for stem sizes. Stem availability changed during the 150-year model run
15 to adjust for stem removal by beaver, stem regrowth, and promotion of smaller stems to
16 larger size classes. Values for (a) and (b) are means of the last 50 simulated years (error
17 bars are standard deviations). Values for (c) represent only the first year with beaver (year
18 51), when 2.0 Mg of willow biomass was used to build a beaver dam; error bars are lacking
19 because n = 1 year.

20 *Run configuration = IC + 50 years NB NE + 100 B NE*

21 *where; IC = initial condition (RMNP field data), B = beaver, NB = no beaver, NE = no elk.*

22 *Beaver density = 1 colony in 4 ha.*

23

1 Figure 3. Energy balance (a) and growth (b) of beaver when foraging in a stable equilibrium.
2 Food metabolic energy (FME) was based on the availability of willow suitable as beaver
3 food. Metabolic energy required (MER) was based on beaver body size and activity without
4 considering the cost of growth. The difference between energy gained and energy required
5 (FME – MER) was the cost of growth. The figures shows that the configuration of the model
6 in terms of food intake was appropriate relative to maintenance of good body condition.
7 Values represent a mean of the last 50 simulated years.

8

9 *Run configuration = IC + 50 years NB NE + 100 B NE*

10 *where; IC = initial condition (RMNP field data), B = beaver, NB = no beaver, NE = no elk.*

11 *Beaver density = 1 colony in 4 ha.*

12

13 Figure 4. Change in aboveground willow productivity (ANPP) due to beaver cutting shows
14 willow overcompensated for herbivore pressure across a range of beaver densities and was
15 highest (5.3 Mg ha^{-1}) at moderate densities of $1.5 \text{ beaver ha}^{-1}$, or 1 colony of 6 beaver (2
16 adults, 2 yearlings, and 2 kits) in 4 ha. Values represent a mean of the last 50 simulated
17 years after the model had reached a steady state, except when density was 2.0 beaver
18 ha^{-1} and the system was unsustainable.

19

20 *Run configuration = IC + 50 years NB NE + 100 B NE*

21 *where; IC = initial condition (RMNP field data), B = beaver, NB = no beaver, NE = no elk.*

22 *Beaver density varied among the eight runs, but was constant within runs.*

23

1 Figure 5. Comparison of willow productivity (ANPP) and plant size distribution (proportion
2 in 6 classes) with beaver present and beaver absent. Release from light elk browsing
3 resulted in a rapid increase in ANPP during the first 12 years and then a rapid decrease
4 during the next 12 years. The introduction of beaver at year 50 resulted in a rapid increase
5 in ANPP, which stabilized near 5.0 Mg ha^{-1} with beaver present and near 2.0 Mg ha^{-1} with
6 beaver absent. Willow size class distributions (box “c” versus box “e”) shows beaver
7 increased the proportion of willow plants in the intermediate size classes, likely a result of
8 increased stem turnover rate and foraging preferences for larger willow. Beaver removal at
9 year 150 determines a decrease in ANPP and changes in plant size distribution until
10 stabilization to similar characteristics as with beaver absent.

11

12 *Run configuration:*

13 *Beaver absent = IC + 250 years NB NE*

14 *Beaver present = IC + 50 years NB NE + 100 years B NE + 100 years NB NE*

15 *where; IC = initial condition (RMNP field data), B = beaver, NB = no beaver, NE = no elk.*

16 *Beaver density = 1 colony in 4 ha. Slight differences between runs during the first 50 years*
17 *were due to differences in simulated weather patterns during each model run.*

18

19 Figure 6. This 200-year simulation shows that two 4-ha beaver-willow communities
20 developed similar stable state conditions regardless of willow biomass availability when a
21 beaver colony (2 adults, 2 yearlings, and 2 kits) was introduced (Time = 0). The *Browsed*
22 *Initial Condition* represents the introduction of beaver into a browsing suppressed system
23 (original Endo Valley field data, Rocky Mountain National Park) where the woody biomass of
24 willow at time zero was 6.4 Mg ha^{-1} . The *Unbrowsed Initial Condition* represents the

1 introduction of beaver into a unbrowsed system (same area 50 years after release from light
2 browsing) where the woody biomass of willow at time zero was 27.0 Mg ha^{-1} . Woody
3 biomass represents the standing crop of live stem material after leaf fall. Plant size
4 distribution for Time = 0 years is the same as Fig. 4a for the *Browsed Initial Condition* and
5 Fig. 4b. for the *Unbrowsed Initial Condition*; at Time = 200 years it is similar to Fig. 4e for
6 both conditions.

7

8 *Run configuration:*

9 *Browsed Initial Condition = IC + 200 years B NE*

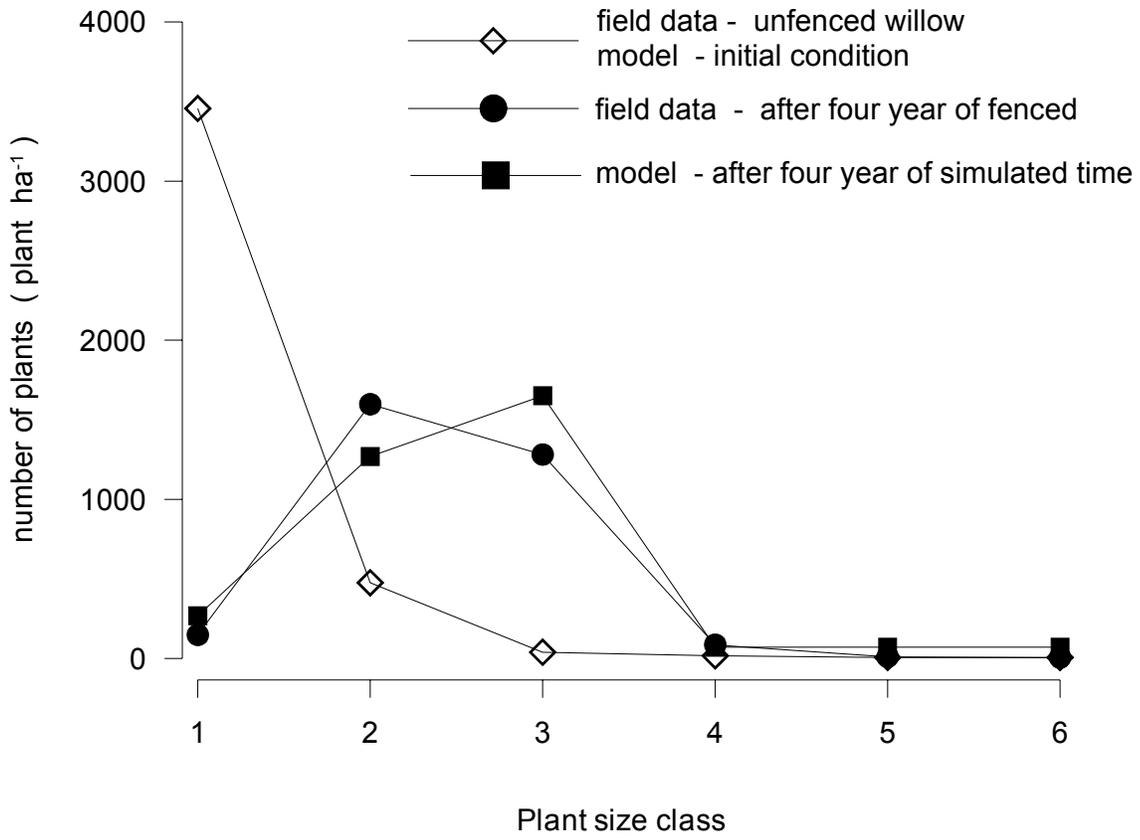
10 *Unbrowsed Initial Condition¹ = IC + 50 years NB NE + 200 years B NE*

11 *where; IC = initial condition (RMNP field data), B = beaver, NB = no beaver, NE = no elk.*

12 *Beaver density = 1 colony in 4 ha.*

13 ¹*Only the last 200 years are shown because the first 50-year period was used to simulate*
14 *an unbrowsed willow community that lacked the effects of elk and beaver herbivory at time*
15 *zero.*

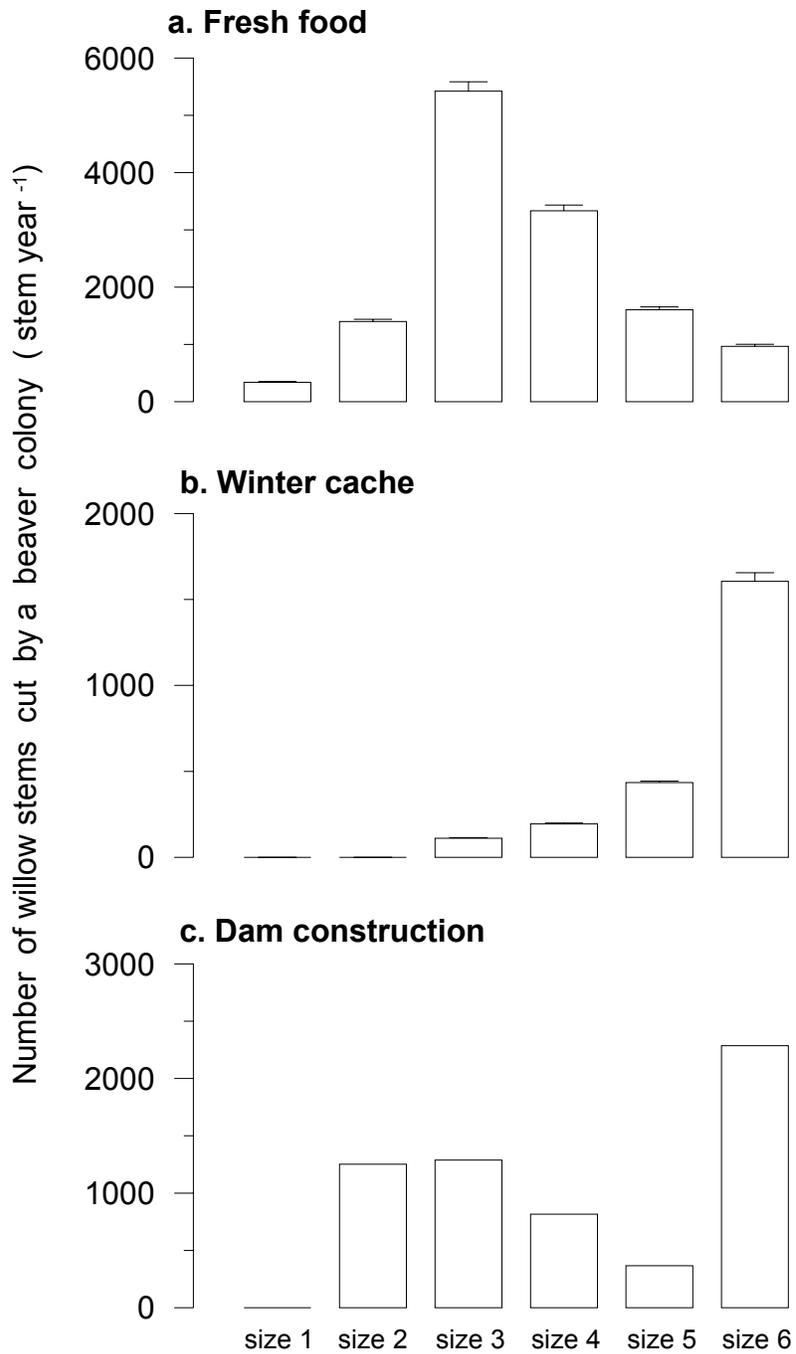
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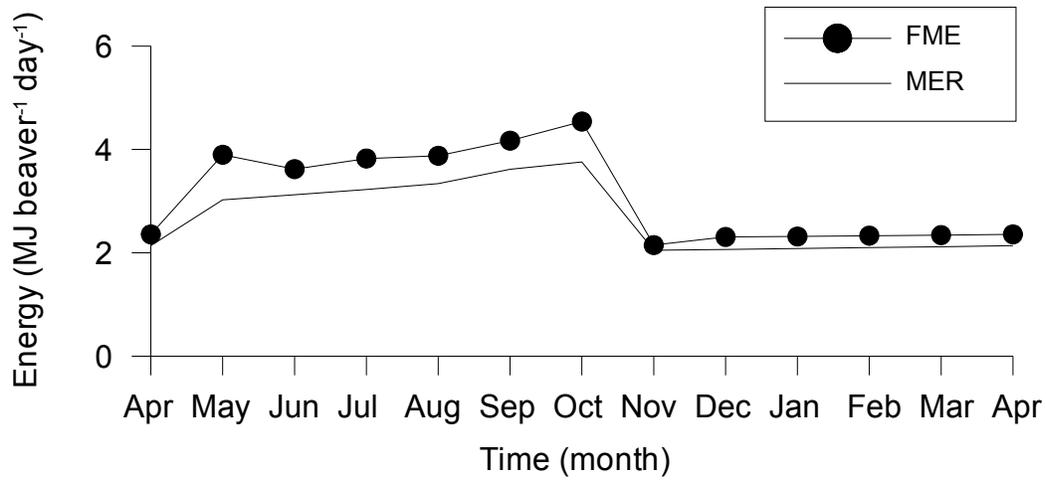
Figure 1_[BB18]



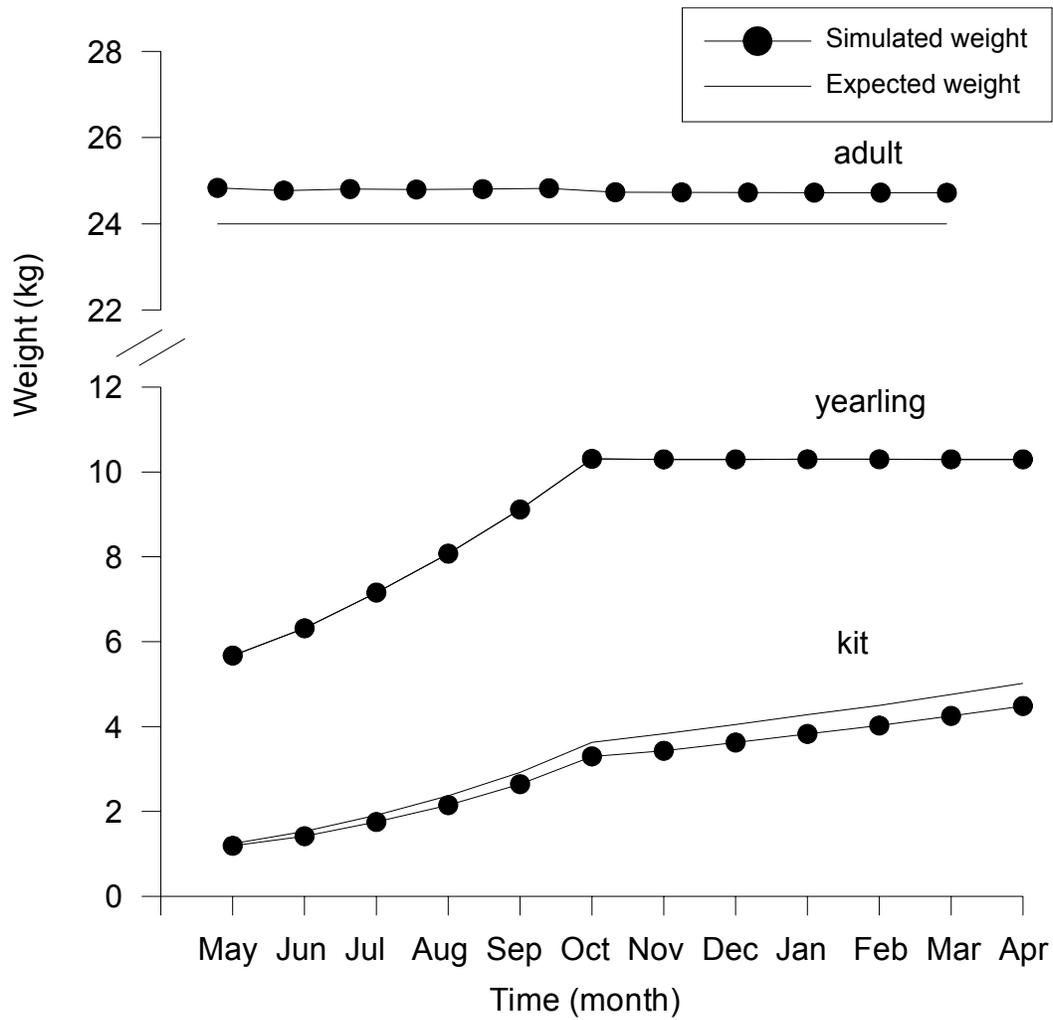
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Figure 2

a. ENERGY BALANCE



b. GROWTH

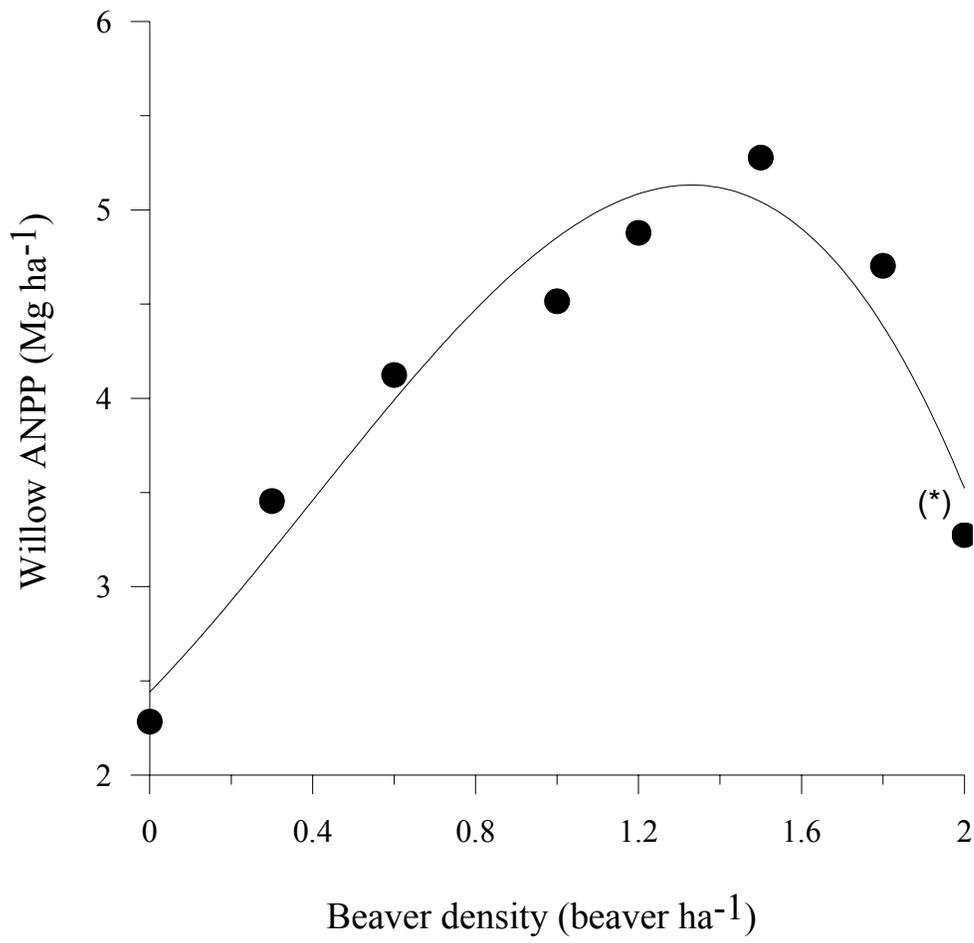


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Figure 3

1



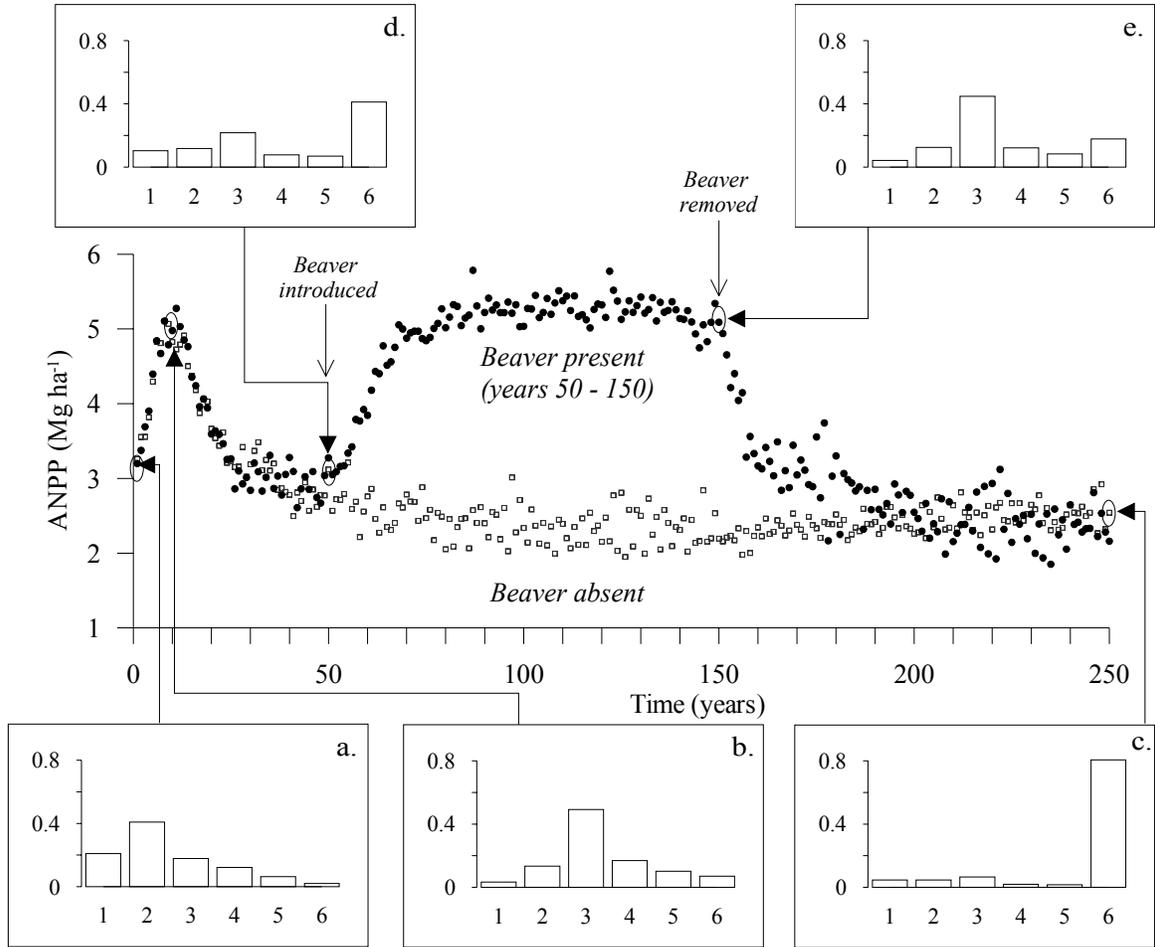
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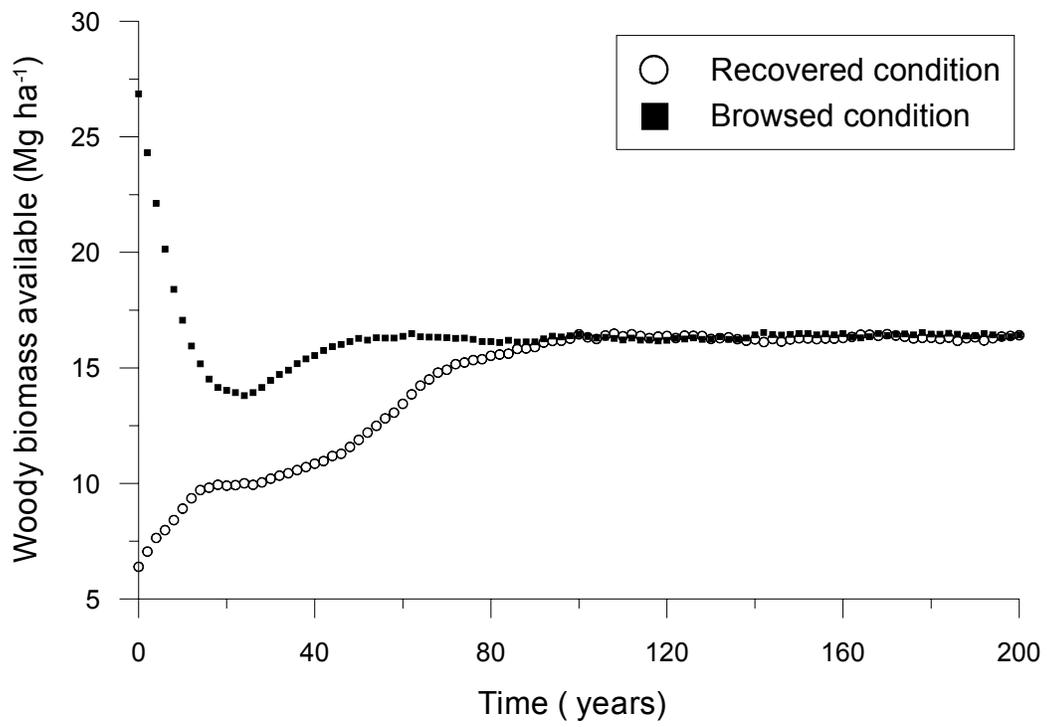
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Figure 4



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Figure 5



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Figure 6