

MODEL DESCRIPTION AND DATA INPUTS

Ecosystem Model Structure

SAVANNA is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems. Version 5 of SAVANNA was used here. Versions 1 and 2 were developed to study a nomadic pastoral ecosystem in Kenya (Coughenour 1992). Version 3 was developed for Elk Island National Park in Alberta (Buckley et al. 1995), and Version 4 was applied to the Pryor Mountain Wild Horse Range (Coughenour 2000), northern Colorado (Weisberg et al. 2002), northern Australia (Ludwig et al. 1999), South Africa (Kiker 1998), Tanzania (Boone et al. 2001), and Inner Mongolia (Christensen 2001). SAVANNA simulates processes at landscape through regional spatial scales over annual to decadal time scales. The model is composed of site water balance, plant biomass production, plant population dynamics, litter decomposition and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, and ungulate population dynamics submodels (Figure 17a). The time-step of the model is one week.

Savanna has a hierarchical spatial structure (Figure 17b). It is spatially explicit (i.e., it is sensitive to spatial position) at the landscape scale and it is spatially inexplicit at patch scales. The mosaic of grid-cells covers landscapes or regional-scale ecosystems. Grid-cell size is scaled to the spatial extent of the simulated spatial domain, so as to maintain a sufficient degree of realism in capturing landscape-scale heterogeneity, while also maintaining a computationally feasible total number of grid-cells. Here, the choice was made to use 500m wide grid-cells. At this level of resolution, there were a sufficient number of grid-cells to represent the primary features of the landscape, particularly less common vegetation types such as willow and aspen. While at this resolution not every vegetation patch is represented, the total area of coarse resolution patches is approximately equal to the total area of fine-resolution patches. This is an outcome of the aggregation procedure used in a GIS, which is in this case, the “Contract” procedure in *Idrisi*.

Within each grid-cell the model simulates three vegetation patch types or “facets.” These are defined by the fractional covers of herbaceous plants, shrubs and trees. Since shrub and tree cover are simulated variables, facet cover is a dynamic outcome of vegetation growth and mortality. Facet locations are not modeled, only the fractions of grid-cells that are covered by the facets. Within each facet, the model simulates plant growth and soil water budgets. Variables results are scaled-up to the grid-cell level by multiplying the variables by the fractions of the grid-cell area covered by each facet, and summing the products over all facets.

The area of land within each grid-cell that is covered by trees or shrubs varies in response to changes in tree and shrub numbers and sizes. As a consequence, direct competitive or facilitative interactions among established plants of these three life-forms are limited to patches where established plants are rooted. Trees and herbs, for example, interact directly on tree-dominated patches but do not interact on herbaceous-dominated patches except during the establishment phase. Tree and shrub vegetation covers are defined in terms of rooted area, i.e., the area of ground which corresponds to the exploited soil volume. Cover is defined in terms of

rooted area mainly because 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 soil layer is a zone of potential bare soil evaporation as well as root uptake. The second layer is generally the deepest layer that is exploited by herbaceous roots. The bottom layer is generally occupied only by shrub and tree roots. Plant canopies are organized into herb, shrub and tree strata. In turn, each of these are divided into three substrata to compute light intensity.

Weather

Savanna is driven by monthly weather data. Each month, a regression is performed between precipitation and elevation using data from all weather stations in the study area. If the correlation coefficient (r^2) is >0.2 , the slope of the line (i.e., the rate of increase in precipitation with elevation) and the elevation difference is used to estimate precipitation for the weather station as if it were at the same elevation as the point in question. The elevation-corrected weather station data are then spatially interpolated using inverse distance weighting on the six nearest stations with data. This procedure is followed for each point on the landscape. Temperature for each point on the landscape is similarly estimated from the temperatures at the nearest weather stations by applying adiabatic lapse rates to the station temperatures to estimate temperature at the same elevation as the point in question. The corrected temperature data are spatially interpolated using inverse distance weighting.

Stochastic weather data are created by random sampling of years from the weather files. Each year, a random year of data is drawn from the files, and an additional amount of random variation is added to the data. The sampling and addition of variance are done in such a way that data from all weather stations are affected together, thus preserving the spatial pattern in the original data.

Atmospheric water vapor content is calculated from relative humidity and temperature of the main base station. Relative humidity is calculated from the water vapor concentration, and the temperature at each landscape location. Solar radiation is calculated from monthly cloud cover, latitude, and day of year, correcting for slope and aspect using the methods described by Nikolov and Zeller (1992). Cloud cover is estimated from monthly precipitation and water vapor content.

The weather input file was derived from the weather stations and SNOTEL stations shown in Figure 18. Precipitation was recorded in Estes Park beginning in 1910, and it was recorded in Grand Lake beginning in 1940. Temperature was recorded in Estes Park starting in 1931. Weather stations came on line for the most part beginning in 1949 and into the early 1950s. Older weather stations include Fort Collins (1900-present), and Fraser (1910-present). SNOTEL stations are remote recording devices that recorded precipitation and snow water equivalents beginning in 1981. Temperature data became available from SNOTEL stations in 1990. Weather data since 1948 were obtained from the EarthInfo Inc. NCDC (National Climate Data Center) Summary of the Day CD ROM data bases. Earlier data were obtained from the Colorado Climate

Data Center. SNOTEL data were obtained from USDA NRCS (National Resource Conservation Service) via the internet site of Chris Pacheco of the National Weather and Climate Center, Portland, Oregon.

SAVANNA reconstructs missing weather data while it is running based upon regression equations between data from the primary weather station (Estes Park in this case), and the other weather stations. The parameters from the equations are used in the model to estimate missing data from the main base station data, which are assumed to be complete and continuous. The results are then based on empirical correlations between the main base and the other weather station data. This captures the primary temporal patterns in the region, as well as the main patterns of difference between stations. Although not exact, this provides a realistic representation of climate patterns at the monthly time scale. This procedure was followed for the period 1931-1998. Weather data since 1949 are relatively complete. While data for 1931-1948 were sparse, there were key stations with data, including Estes Park, Grand Lake, and Fraser.

Data for the period 1910-1930 was reconstructed from the deviations from normal observed in the Fraser data. The normals were computed for the period 1949-1998. Then the deviations for 1910-1930 were estimated, in terms of degrees for temperature, and percent of seasonal precipitation. Four seasons were recognized: winter, spring, summer, and fall (months as in tree-ring data below). The deviations were then applied to 1949-1998 normals from other stations to fill in missing values for each of the other stations.

Data for the period 1775-1911 were reconstructed from the tree-ring data base of Fritts (1991a,b). The Fritts data base included reconstructions of temperature for Cheyenne, Wyoming, and precipitation for Fort Collins, Colorado. Data are by season: winter (December-February), spring (March-June), summer (July-August), and fall (September-November). Tree ring data were calibrated against data from weather data from 1901-1963. The method here was to use the reconstructed data of Fritts, along with the actual weather data from Cheyenne and Fort Collins for 1901-1963, to calculate deviations from normal in degrees or percent of normal precipitation, by season. The seasonal deviations were then applied to monthly means from the actual weather station data for 1949-1998, to construct weather data set for 1775-1911.

Water Submodels and Soil Properties

The water budget submodel simulates soil moisture dynamics and use on each patch type on each grid-cell. A soil map is used in conjunction with soil properties for each soil type, to determine soil water holding capacities of each subarea on each grid-cell. Water is routed to three soil layers using a simple "tipping bucket" approach that drains water in excess of field capacity to subsequently deeper layers. The water budget includes terms for precipitation, interception, runoff, runoff, infiltration, deep drainage, bare soil evaporation, and transpiration.

The runoff curve number method of the U.S. Soil Conservation Service is used to calculate runoff (Wight and Skiles 1987). Runoff depends on daily rainfall, the quantity and distribution of water in the soil relative to water holding capacity, and the condition curve number for the soil. Runoff curve numbers are based on range site classifications and range

condition such that runoff increases under low plant and litter cover. The curve number for good condition is given in Table 1, A higher runoff curve number is specified for fair range condition. Bare soil evaporation is simulated using the Ritchie (1972) model (Wight and Skiles 1987). Evaporation also increases under low plant and litter cover.

A soils map and soil survey data did not exist for RMNP, nor for the area outside of the park in Larimer County. Instead, the vegetation/cover map was used as a surrogate for soil types, assuming that vegetation/cover types were correlated to soil types. Soil properties for each vegetation type were derived from available sources describing soils in the relevant vegetation types. Baron (1992) was a source of soil texture data for tundra and subalpine forests. Stohlgren (1999) and Binkley et al. (2002) reported soil texture, %N, and %C in soils of grazing exclosures on the elk winter range. Leader (1995) reported soil texture, %N, and %C in soils from montane forests, meadows, and transition areas on the elk winter range. Menezes (2000) reported values of soil texture, %N, and %C in riparian willow communities on the elk winter range. Soil data from other vegetation types was derived from the Larimer County Soil Survey (Moreland 1980). Texture data (percent sand, silt, clay) were the bases for calculating field capacity and wilting points. The resultant soil parameters are shown in Table 1.

The snow submodel adds water to the snowpack if temperature is below freezing. Melting during night and day are modeled individually. The rate of snowmelt is proportional to the difference in temperature above 0° C at night and -1° C in the day. The fraction of melt due to short vs. longwave radiation is calculated based on incoming short and longwave radiation and emissivities of the surface. The fraction is used to correct snow melt rate for differences in incoming shortwave radiation due to slope and aspect. Water may also be lost from the snowpack through sublimation.

Precipitation is redistributed on the landscape using a topographic similarity index (TSI) (Beven and Kirkby 1979, Band et al. 1993, Hartman 1999). Grid-cells in topographic positions with large contributing areas above them are more likely to receive water through runoff, baseflow, or wind redistribution of snow. For each grid-cell, the TSI is calculated as the log of the contributing area above the cell divided by the tangent of the slope. The contributing area map is calculated using the FLOWACCUM procedure in ARC/INFO. The ratio of the TSI at a point to the average TSI for a watershed gives a basis for redistribution of precipitation. A map is calculated that is the ratio of net water input to the water input from precipitation (Figure 19). The map is computed in such a way as to ensure that the total water input to watersheds, or 1 km blocks, equals actual precipitation. The map is contracted to a 500 m resolution by averaging of contiguous cells. During a model run, the map value is multiplied by the precipitation value to compute net precipitation input to a cell.

A simple hydrology model simulates streamflow in a watershed. A watershed map is read into the model. For each watershed, the model tracks the amount of water in a baseflow pool, which is derived from deep drainage (the amount of water draining from the bottom soil layer when it is in excess of field capacity). The baseflow water flows into the stream at a rate calibrated to match general streamflow patterns. Surface runoff, computed as described above, also flows into the stream. The output is total streamflow volume for that watershed over time.

Watersheds for the streams flowing into Moraine Park and Horseshoe Park (Figure 6) were used in model runs, in order to affect riparian zone water tables on the winter range. A map for the entire Big Thompson watershed was used in separate runs to compare model output to streamflow data.

Water table depth is specified by either month for each soil type, or it is tied to streamflow in the watershed using an empirical function. In this application, water table depth is tied to streamflow in two watersheds on the elk winter range - the Moraine Park watershed and the Horseshoe Park watershed. Thus, water table depth in riparian willow habitats in those two parks are affected by streamflow. A summary of the data for water table depths in short and tall willow communities at these two locations is shown in Figure 20. These data are from the recent study of Singer et al. (Singer et al. 1999, 2001a, 2002; Zeigenfuss et.al. 2002). Artificial dams were constructed in some treatments, to examine potential effects of beaver. In Moraine Park, water tables were deepest in tall willow, followed by shallower depths in short willow with dammed streams, and short willow with undammed streams. In Horseshoe Park, the reverse pattern was observed, with deepest water tables in short willow.

In riparian willow and subirrigated vegetation elsewhere, water table depth is specified by month of year, with shallower depths occurring during times of spring runoff. There is a relatively shallow water table in willow and subirrigated habitats on the vegetation map. For “other low elevation willow,” I use the mean monthly water table depths observed in Horseshoe Park tall willow (Figure 20b). For “heavily subirrigated” I use the depths observed in Moraine Park short willow (Figure 20a). “Partly subirrigated” water tables are 1 m deep in August-February, decreasing to 0.3-0.5 m deep in spring. Water tables in aspen are assumed to be 1.1 m deep in September-February, decreasing to 0.65 m deep in the spring. Cottonwood water tables decrease from 0.6 m in fall-winter to 0.4 m in spring. In all other vegetation types, the water table is assumed to be too deep to be of any use to plants.

Microclimate and Light

The microclimate submodel simulates windspeed profiles and aerodynamic resistances to water vapor diffusion. These depend upon canopy height, and reference height windspeed. Potential evapotranspiration (PET) and transpiration are calculated using the Penman-Monteith formula (Monteith 1973). PET is derived using Penman-Monteith with zero stomatal conductance. Transpiration is calculated from canopy-scale stomatal conductance. PET and transpiration are affected by radiation, temperature, humidity, and windspeed.

The light submodel simulates shading within and among plant canopies. On tree-covered facets, incident radiation first passes through the tree canopy, then the shrub understory and finally the herbaceous understory. Light extinction follows an exponential decay function (Beer's Law) which is dependent on leaf area index and a light extinction coefficient. The model tracks the relative heights of woody plants in different size/age classes, so for example small or young shrubs and trees will be more shaded than large or old shrubs and trees.

Plant Biomass Production

The net primary production (NPP) submodel simulates plant biomass flows and dynamics. Plant biomass production is affected by light, water, temperature, nitrogen and herbivory. The NPP submodel is explicitly linked to the water budget submodel through transpiration and plant water use. Herbaceous biomass is allocated to leaves, stems and roots. Woody plants allocate to leaves, fine branch, coarse branch, fine root, and coarse root. Allocation between fine roots and leaves in both herbaceous and woody plants is influenced by nutrient and water availability, with slightly more allocation to roots when soil resources are limiting. The allocation to various tissues in woody plants depends on plant size. Allometric relationships of allocation versus size are embedded in the biomasses of leaves, fine and coarse stems, and fine and coarse roots, per plant for each of six plant age/size classes. Plant tissues die due to water or temperature stress or phenological stage, and they turn over at a nominal rate that reflects their maximal longevities. Simulated plants maintain a pool of labile carbon, largely consisting of carbohydrates. Early regrowth in the spring or following grazing is supported by this pool, until needs can be met by photosynthesis.

Potential net photosynthesis is calculated as

$$P_{sl} = PAR / \sqrt{1 + (\alpha \times PAR / P_{smx})^2}$$

$$P_s = P_{sl} \times E_{fwp}(A_{wpet}) \times E_{ftp}(T_{day}) \times E_{fnp}(P_{nb})$$

where P_{smx} is maximal net photosynthesis rate, PAR is photosynthetically active radiation, α is the initial slope of the light response curve, and P_{sl} is light-limited photosynthetic rate. The initial slope α is also equal to the light use efficiency, and the light response asymptotes at saturating light intensities. The 0-1 function E_{fnp} describes how P_s decreases as plant nitrogen concentration (P_{nb}) decreases. The 0-1 function E_{fwp} reduces P_s due to water stress. A_{wpet} is the ratio of available water (mm d^{-1}) to potential evapotranspiration (mm d^{-1}). E_{ftp} is a bell-shaped temperature effect, generated from optimum, minimum, and maximum temperatures for photosynthesis.

After potential photosynthesis is calculated, stomatal conductance is calculated based upon the equation of Ball et al. (1997), in which stomates open wider as photosynthesis (P_s) and humidity (H) increase, and as atmospheric CO_2 (C) decreases.

$$g_s = e_0 + e_1 \times (P_s \times H / C)$$

From stomatal conductance, atmospheric water vapor pressure deficit, windspeed, and radiation, the model uses the Penman-Monteith approach to calculate transpiration. From transpiration and net photosynthesis, the model calculates water use efficiency.

Root water uptake to supply transpiration demand is allocated among soil layers in proportion to the products of available water and root biomass in each layer. The water demands for competing plants are summed, and if total demand exceeds supply, water is allocated among species in proportion to demands. Photosynthesis is then recalculated from water use using the water use efficiency calculated above. Thus, plants rooted in the same soil layer compete for

water, but when water is limiting, it is allocated among species in proportion to their demands. The demand for water in a layer depends on transpiration rate, and the proportion of roots and water in that layer

Parameters affecting photosynthesis and stomatal conductance are shown in Table 2. Some parameters were based upon previous modeling of N. American temperate grasses (Coughenour and Chen 1997). Values are set with reference to the generic values for plant functional groups in Woodward and Smith (1994). Shrub ecophysiology was parameterized largely based upon information for sagebrush (Doeschler et al. 1990, DeLucia and Heckathorn 1989, DeLucia and Schlesinger 1991, Branson et al. 1976, Fetcher 1981). Conifer parameter values were based upon Fahey et al. (1985), Pearson et al. (1987), Day et al. (1989), Prescott et al. (1989), DeLucia and Schlesinger (1991), Levernz (1995), and Ryan et al (1996). Peinetti (2000) and Peinetti and Coughenour (2001) used ecophysiological data of Alstad et al. (1999), Peinetti (2000) and other sources to parameterize willow. Weisberg (2000) parameterized aspen based on Bartos and Johnson (1974), Bonan (1993), and Kubiske et al. (1997).

Photosynthate is allocated between roots and shoots to preserve a functional balance in herbaceous plants, and allometric relationships in woody plants. Phenology and water affect shoot:root partitioning, with an increased fraction being diverted to roots in later phenophases, and under higher water stress. In woody plants, allocation is more complex due to differences in allometry (ratios among tissue types) among size classes. Allocation varies to preserve the proper allometric relationships. Allometry data for willow were developed by Peinetti (2000), based on original data, and data of Zeigenfuss et al. (1999, 2002), and Cannell (1987). Allometry parameters for upland shrubs were based upon sagebrush data reported by Sturges and Trlica (1978), Branson et al. (1976), and Fetcher (1981). Aspen allometry was parameterized by Weisberg (2000). Coniferous tree allometries were parameterized from information in Brown (1978), Keane et al. (1989), Kerr and Smith (1955), Dale et al. (1986), Knight (1991), Kaufman et al. (1982), and Vogt (1991). Allometry parameters for one size class of woody functional groups are shown in Table 3.

Respiration is separated into growth and maintenance components. Maintenance respiration depends upon nitrogen concentration (Ryan 1991), and temperature. Due to high biomass, maintenance respiration in woody plants can outstrip carbon supply, so must be limited to 50% of available photosynthate.

Plant tissues senesce at rates affected by water stress, temperature, and phenology. Shoot tissues (leaves and stems of herbs and shrubs, leaves of trees) are transferred to "standing dead" upon senescence. Then the standing dead falls to "litter" on the soil surface. Dying roots are transferred directly to belowground "litter". Plant tissue senescence rates, and transfer rates from standing dead to litter are calibrated to match observed biomass dynamics, and ratios of live to dead shoot tissues. Root turnover rates are based on previous modeling experience (Coughenour and Chen 1997, Parton et al. 1997, 1993), which are in turn based on data from comparable species.

Plant Populations

Plant population submodels simulate plant establishment, size, and mortality. The woody plant population model represents six age/size classes of plants. Plants are promoted to subsequent age/size classes if they reach a certain age, and they are of a certain size. Woody plant establishment and mortality can both be set to zero to effectively turn off this section of the model, leaving plant densities fixed. For purposes here, only willow and aspen population dynamics were simulated. Population sizes of upland shrubs, pine, and other conifers were assumed to be constant. Establishment rate is affected by water and temperature, and woody cover. As cover increases, establishment rate declines to reflect effects of shading and competition for space and soil resources. Woody establishment is also affected by herbaceous biomass, to represent competition between seedlings and herbaceous plants. Because woody establishment only occurs on the herbaceous (non-woody) facet, when a closed forest is simulated, establishment will only occur in gaps, or openings resulting from tree death. Parameters affecting woody plant population dynamics are shown in Table 4.

In the case of herbaceous plants, the model represents an index of basal cover measured in units of potential shoot biomass. This index of basal cover increases if simulated root biomass becomes large relative to the value expected for the current basal cover. The basal cover index decreases when root biomass is at low values relative to the root mass expected for the current basal cover. Shoot production in a given year cannot exceed the amount expected for the current basal cover. In this way, the model simulates degradation, or a loss of potential production, due to overgrazing or climatic stress. Likewise, it simulates a gradual recovery of potential production under good growing conditions. Values for this function are given in Table 5 (vegetative growth rate vs. shoot:root ratio).

A micro-scale disturbance regime is imposed on herbaceous plants. Plants are killed at a specified rate (fraction of plant cover per year) to simulate disturbances due to other herbivores (e.g., small mammals, insects), or humans. Disturbance rates were set to 0.05 yr^{-1} for managed grasslands, $0.075\text{-}0.1 \text{ yr}^{-1}$ for native communities, and 0.15 yr^{-1} for disturbed lands. An exogenous seed rain replenishes herbaceous plant populations (basal area). The composition of the seed rain is assumed to be invariant, and is usually assumed to have the same composition as initial conditions. The seed rain is expressed in the same units as basal cover, in grams of shoot biomass. These values of g m^{-2} shoot biomass are then multiplied by the exogenous seed-based reproduction rates in Table 5. An endogenous seed-based reproductive rate is also modeled in which the reproduction rate is multiplied by potential shoot biomass.

Vegetation Management

Some vegetation types outside the national park are managed through the addition of water, fertilizer, and mowing. These types include golf courses, lawns, and improved pastures. For these, a rate of water input is specified in mm month^{-1} , a rate of fertilizer N input is specified in $\text{gN m}^{-2} \text{ month}^{-1}$, and a cutting regime is specified as a biomass density to cut to. When grass is cut, phenology is reset to a juvenile stage, which in turn maintains a high leaf nitrogen concentration in the green regrowth, to the extent that it regrows. Golf course grass is assumed to

be fertilized with $20 \text{ g N m}^{-2} \text{ yr}^{-1}$ and irrigated with $1400 \text{ mm water yr}^{-1}$. Other domestic lawns are assumed to be irrigated with $90 \text{ mm water yr}^{-1}$. Golf courses are assumed to be mowed to 150 g m^{-2} year around.

Litter Decomposition, N Cycling, and Soil Organic Matter Dynamics

A decomposition and N cycling submodel simulates the breakdown of dead plant materials and animal feces and urine, and the formation and turnover of soil organic matter (SOM). The decomposition submodel is based upon the CENTURY model (Parton et al. 1987, 1993). Dying plant tissues are divided into fast (metabolic) and slowly (structural) decomposing litter, as well as fine and coarse branches and roots. The fractionation between metabolic and structural litter depends upon the ratio of lignin to nitrogen in the dying tissues. As lignin increases and nitrogen decreases, the fraction partitioned to structural litter increases. The two litter fractions are decomposed at rates that depend upon soil moisture and temperature, with faster decomposition rates under warm, wet conditions (Parton et al. 1987). A fraction of the decomposed carbon is respired by microbes. Nitrogen is released during decomposition to mineral forms that can be taken up by the plants or incorporated into the active SOM pool. Three SOM pools having different turnover rates are simulated. Decomposing metabolic litter flows to active SOM and respiration, while decomposing structural litter flows to the active and resistant pools and respiration. Decomposing active SOM flows to the intermediate and slow turnover SOM pools. Decomposing intermediate SOM flows to active and slow SOM pools, and respiration. Decomposing slow pool SOM flows to the active pool, and respiration. Inorganic nitrogen (ammonium and nitrate) is released upon decomposition if substrate nitrogen concentration is higher than the N concentration of microbial biomass. Mineral N is taken up from the soil if substrate nitrogen concentration is lower than microbial N concentration. Parameters for the decomposition model are taken from Parton et al. (1987, 1993).

Nitrogen consumed by herbivores is recycled as either urine or feces. It is assumed that 50% of N flows to feces and 50 % to urine. The undigestible fraction of carbon intake flows to feces. Fecal C and N are partitioned to structural and metabolic litter. Urine N flows to inorganic N (ammonium).

Nitrogen enters the system through atmospheric wet and dry deposition and biotic fixation, and it leaves the system through denitrification and the volatilization of ammonia from urine. Denitrification losses are simulated as a 5% fraction of N gross mineralization, as in Parton et al. (1987, 1993). Nitrogen lost to urine volatilization is assumed to be 20% of urine N. N deposition from precipitation and the atmosphere is based on data from the National Atmospheric Deposition Program data from their Beaver Meadows site (data obtained from NADP web site). There are 0.21 gN m^{-2} input irrespective of precipitation, and an added $0.0033 \text{ g N per mm precipitation}$. Biotic fixation is modeled as a function of annual precipitation, as in Parton et al. (1987, 1993).

An added amount of N input to riparian and water subsidized communities was necessary to support observed levels of plant growth. This N likely is transported into the system as N dissolved in ground or stream water. The N could originate from precipitation, and leachate

from upstream soils. The additional N requirement is consistent with findings of Menezes (2000) who showed N inputs from stream water to willow based on ^{15}N stable isotope concentrations in plants, soil, and stream water. An amount of $0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ was necessary for willow and heavily subirrigated vegetation, $0.35 \text{ g N m}^{-2} \text{ yr}^{-1}$ was needed for aspen, and $0.25 \text{ g N m}^{-2} \text{ yr}^{-1}$ was needed for partly subirrigated sites.

Plant nitrogen uptake is represented using an equation that specifies a maximal uptake rate per gram of root tissue. The uptake rate is reduced at low soil N concentrations using a Michaelis-Menton function. Only mineral N is taken up, i.e., the N released during decomposition of litter and soil organic matter, and assumed to be ammonium and nitrate. Competition for soil N is calculated when the total plant demand exceeds supply. As with water, uptake is then allocated among competitors in proportion to demands.

Plant nitrogen is regulated within bounds by curtailing uptake as plant N concentration increases to the maximum value. Nitrogen in green leaves is calculated based on phenology. In most plants, young leaves have a higher N concentration than old leaves. N in dying plant tissues is transferred to litter based on a specified N concentration of dying tissues. Because the N concentration of dying tissues is usually lower than that of the live plant, N is effectively conserved through retranslocation when tissues die.

Parameters for plant N concentrations are given in Table 2. Values for live and dead leaf N concentrations for herbs and upland shrubs are taken from Hobbs (1979), Singer et al. (2001a, 2002), and Zeigenfuss et al. (1999, 2002). Values for willow N were parameterized by Peinetti (2000), from original data, Menezes (2000), and Thilenius (1990). Values are consistent with those of Zeigenfuss et al. (2002). Aspen tissue N concentrations were parameterized by Weisberg (2000) from multiple sources. Conifer N concentrations were based on Fahey et al. (1983), Pearson et al. (1987), Prescott (1989), Doescher et al. (1990), and Ryan (1996).

Herbivore Forage Intake

Herbivore forage intake is determined by diet selection, forage quantity and quality, and snow cover. Forage intake rate responds to forage biomass according to a functional response (Holling 1959, Caughley and Lawton 1975). As forage biomass increases, forage intake rate increases, with intake rate eventually reaching a maximal value. Here, the functional response is approximated as a linear function (Table 6). Forage intake rate is also affected by snow depth. Above a certain depth, intake rate declines linearly with increasing depth, until it reaches zero. The effect of snow depth is only applied to that fraction of the plant that is covered by snow. Thus, for that portion of the woody plants extruding above the snow, snow depth has no effect.

Animals choose among available plant types and tissues to achieve a preferred diet composition. Diet composition is determined by using preference weightings, similar to Ellis et al. (1976). In this approach, diet composition is affected by the relative availabilities of different forage types as well as by herbivore preferences. This ensures that diet flexibly responds to temporal and spatial changes in the mixture of available forage. Preference indices in the dietary selection model were calibrated so that the diets of elk were similar to those reported by Riorden

(1948, cited in Stevens 1980), Baker and Hobbs (1982), Hobbs et al. (1981), Stevens (1980), and Singer et al. (2002). Deer diet selection was calibrated to attain diets similar to those observed by Stevens (1980).

When herbivores consume plant tissues plants may also die. Death of plants is distinct from death of tissues. Thus, while aboveground tissues may be eaten, the plant may still be alive due to uneaten above- and belowground tissues. Plant mortality is expressed as a function of the fraction of the shoot biomass that is eaten. Seedlings of woody plants are more susceptible to browsing than established individuals.

The distribution of browsing over woody size classes is determined from plant height and animal reach height. Plants with canopy bottoms above the reach heights of the herbivore are unavailable. The fraction of plant biomass buried by snow varies with plant type. Browsing is apportioned among size classes in proportion to available biomass.

Beaver impacts on woody plants are treated differently than ungulate impacts due to the fact that they cut stems at the base. Beaver herbivory on leaves, current annual growth twigs and fine branches is calculated in the same way that ungulate herbivory is calculated. However, a significant amount of biomass, especially coarse branch, is wasted, i.e., not eaten. The amount wasted is derived from the allometry of tissue types on each size class of plant that is eaten. For example, if a certain amount of leaf is eaten from a willow size class, then an allometric matching quantity of coarse branch is felled, and transferred to coarse wood litter. The plant, or fraction of plant, is not necessarily killed, but may resprout. Resprouts are added back to the youngest age/size class, and the allometric root biomass for the youngest size class is protected from death. The remainder of the root biomass is transferred to belowground litter.

Maximum intake rates for elk are based on Watkins et al. (1991). They found an $0.027 \text{ kg kg}^{-1} \text{ d}^{-1}$ intake rate for a 200 kg elk, and a $0.031 \text{ kg kg}^{-1} \text{ d}^{-1}$ intake rate for a 150 kg elk. These values must be adjusted upwards to compensate for the reducing effect of forage digestibility in the model. The functional response for elk was based on Wickstrom et al. (1984) and Hudson and Watkins (1986), but their values for the forage biomass at half-saturation proved to be too low to be workable in RMNP. Consequently, this value was calibrated, but to a value that is still biologically reasonable. The effects of snow depth on forage intake are poorly studied, but a synthesis of data suggest that intake declines above 20 cm, and become severely constrained by 75 cm (Cassier and Able 1990, Coughenour 1994). Maximum forage intake rate of deer was set on the high side of observed values, to offset the simulated reduction due to digestibility and the suboptimal forage biomass in field trials. Walmo et al. (1977) found $1.7\text{-}2.1 \text{ kg kg}^{-1} \text{ d}^{-1}$. Hobbs (1989) used $1.7 \text{ kg kg}^{-1} \text{ d}^{-1}$ based on data from Alldredge et al. (1974), who in turn found a range of $1.5\text{-}2.3 \text{ kg kg}^{-1} \text{ d}^{-1}$. Based on 2.22 g min^{-1} and 16 hr feeding (Hobbs 1989, Wickstrom et al. 1984), a value of $3.2 \text{ kg kg}^{-1} \text{ d}^{-1}$ is derived. The functional response for deer is variable in the literature, ranging from a half saturation at 2 g m^{-2} (Wickstrom et al. 1984) to a value of 15 g m^{-2} , derived from a scaling relationship between body size and maximal forage intake (Kshatryia 1999). A median value was used. The maximum forage intake of Beaver was set based on data in Aleksasuk and Cowan (1969a,b), adjusted upwards slightly to account for less than optimal

conditions for foraging in their experiment. The value describing the functional response was based on body size and maximal forage intake rate (Kshatryia 1999).

Herbivore Energy Balance

The herbivore energy balance submodel simulates body weight of the mean animal of each herd or subpopulation, based on differences between energy intake and energy expenditure. Energy intake depends on forage biomass intake and forage digestibility. Expenditures depend on body weight and travel patterns. The body weight of the mean animal is used to derive an animal condition index, which affects ungulate population dynamics. Metabolizable energy intake from forage consumption is the product of kg total forage intake per animal per day, the mean digestibility of the forage, the gross energy content of digestible plant matter, and its metabolizability.

The energy balance model is partly based upon the models of Coppock et al. (1986) and Hobbs (1989). Energy requirements consist of a "base cost" metabolic energy demand per unit body weight per day and added energetic costs of activity, growth, thermoregulation, gestation, and lactation. A minimum and maximum energy requirement is specified, with the minimum corresponding to a resting metabolic rate. The maximum includes energy for activities. The model lets energy use vary between the minimum and maximum in relationship to condition index. If the condition index is high, animals use more energy on activity. If condition index is low, animals conserve energy by reducing activity. If energy intake exceeds requirements, then the animals convert the excess energy to fat. If energy intake is less than requirements, the deficit is drawn from fat reserves.

Animal condition index is a number that varies between 0.0 and 1.1, and is calculated as the ratio of kg's below maximum body weight to the difference between maximum and minimum body weights (kg). At condition index 0.0, animals are at the minimum weight while at condition index of 1.0, animals are at maximum weight. Condition index can increase slightly above 1.0 to allow forage intake to continue above maximum body weight. However, above 100% of maximum body weight, forage intake rate is reduced due to satiation.

Metabolic energy costs for elk were based on prior analyses of Hobbs (1982) and Watkins et al. (1991). Hobbs' calculations result in approximately $0.19 \text{ MJ kg}^{-1} \text{ d}^{-1}$, including all activity costs. Watkins' data suggest $0.12\text{-}0.16 \text{ MJ kg}^{-1} \text{ d}^{-1}$ for resting and standing animals. Since activity costs of traveling are calculated separately, I used a range of $0.12\text{-}0.16 \text{ MJ kg}^{-1} \text{ d}^{-1}$. Thermoregulatory costs are based on lower critical temperature and thermal conductance values given by Parker and Robbins (1985). Gestation costs are based on the equation of Robbins (1984), and also used by Hobbs (1985), where the cost is a function of body size and stage of gestation. Travel costs per unit distance are based on the function of body weight of Parker and Robbins (1984). Distance traveled is computed from time budget and speed of movement while traveling and feeding at 50 m s^{-1} and 1.5 m s^{-1} respectively. Hours per day spent traveling are from Craighead et al. (1973), while hours spent eating are from Green and Bear (1990). Energy budgets of deer are more simply modeled, as costs of traveling, and thermoregulation are not distinguished. A total energy cost is estimated based on numerous sources. The Hobbs (1989)

model for white-tailed deer gives $74 \text{ kcal kg}^{0.75}$, which is $0.12 \text{ MJ kg}^{-1} \text{ d}^{-1}$ for a 60 kg deer in severe winter, and $0.098 \text{ MJ kg}^{-1} \text{ d}^{-1}$ for just a lying cost. A range of values of $82\text{-}140 \text{ kcal kg}^{0.75}$ is reported by Mautz and Fair (1980). The upper limit corresponds to a maximum of $0.21 \text{ MJ kg}^{-1} \text{ d}^{-1}$ for a 65 kg deer.

Herbivore Population Dynamics

The herbivore population dynamics submodel is an age-sex class model with one age class for each year, for each sex. Recruitment rates and death rates are affected by animal condition indices. Recruitment rather than birth is simulated, because very early calf/fawn survival rate is not distinguished. As condition index increases, recruitment rates increase and death rates decline. The effect of condition index on recruitment rate is multiplicative. For example, a condition index of 0.2 might reduce recruitment rate to 35% of the maximum. The effect of condition on death rate supercedes the nominal death rate if it is larger. The effects of condition index represent population responses to ecological conditions governing forage availability (e.g., forage production, snow depth) and intra- and interspecific competition. As competing animals can reduce forage supply, forage intake rate, and thus body condition, they can consequently reduce population growth rate of the species in question. The equation for recruitment is

$$\text{Recruit} = \sum \text{Female}_i \times \text{Birthrt}_i * F(\text{CI}_{\text{gest}})$$

where Recruit is number of surviving newborns in the season, Female_i is the number of females in age class i , Birthrt_i is the maximum birth rate by age class (Table 7), and CI_{gest} is the condition index averaged over the period of gestation. The functions of CI_{gest} are shown in Figure 21. The equation for deaths is

$$\text{Deaths}_i = \text{Animals}_i * \max[\text{Deathrt}_{\text{Nom}}, \text{Deathrt}_{\text{CI}}]$$

where Deaths_i is the number of animals dying in age class i , Animals_i is number of animals in age class i , $\text{Deathrt}_{\text{Nom}}$ is the nominal death rate (Table 7), and $\text{Deathrt}_{\text{CI}}$ is the death rate as a function of body condition (Figure 21).

Animals can be removed in a rule-based manner. A removal will occur at a specified “trigger” population size, to reduce the population to a specified “target” number. Removals can also be prescribed with an observed number of animals per year, or an observed fraction of animals per year. This latter option was used to simulate observed population dynamics. Elk reduction data for the park elk herd and mule deer population for 1939-1978 were obtained from Stevens (1980). Data for hunter harvest in Game Management Unit (GMU) 20 for 1983-1996 were obtained from Colorado Division of Wildlife. Unfortunately, it is unknown what fractions of the deer and elk harvested by sport hunters in GMU 20 are derived from the populations which winter in the park or town elk ranges. There were many elk and deer wintering outside the park/town range, largely in the National Forest, throughout this period, and this is where the hunting occurred. GMU 20 is very large, extending from the continental divide, to the eastern boundaries of the towns of Loveland and Fort Collins, and from the northern boundary of the

park to the southern boundary of the town of Longmont. The large number of deer and elk that were harvested could not have entirely come from the herds which winter inside the park or in the town of Estes Park. For example, there were many years where the reported deer harvest exceeded the number of deer estimated to be on the park winter range. There were very few elk wintering in town in the 1970s, yet Stevens (1980) reports sport harvests from GMU 20 of an average of 203 per year from 1969/70 through 1978/79. Furthermore, it appeared that “hunting, although significant along the park boundary, probably affects the overall herd, but would not appear to have much effect on the numbers wintering within the park” (Stevens 1980). Model results to be presented below support this statement. It, therefore, seems most likely that hunter harvests prior to the time when elk began to winter in the town in significant numbers were primarily from herd segments which neither wintered in the park, nor in the town, but elsewhere in Roosevelt National Forest. For this reason, I did not apply the harvest data reported by Stevens for 1939-1978 to the park herd segment. I only applied the number taken out by direct management reductions (e.g., 340 removed from within the park in 1949-1950). It was assumed that no animals wintered in town prior to 1968 (see below), so the harvest data prior to that time were simply not used. Given the fact that the town herd was probably very small through the 1970s, the uncertainty of how many of the sport harvested animals would have come from that small herd, and the strong likelihood that this fraction probably varied during that time, I made the following simplifying assumptions. Between 1988-1999, when count data for the town herd are available, the annual sport hunt from GMU 20 was on average 20% of the size of the town herd. I assumed this value of 20% could be used to calculate a recalled sport harvest for 1969-1987, which is the size of the sport harvest adjusted for the growth of the town herd over that time. Thus, I assumed that the recalled harvest was 20% of the number of animals simulated in the town herd. For the years 1988-1998, I used the actual rate, i.e., the actual harvest divided by the size of the town herd. As explained above, rates rather than actual numbers were used in the model. The model used the rates to calculate the size of the harvests from GMU 20. Finally, only a fraction of the GMU harvest was likely to have come from the town herd, and it was assumed that none of it came from the park herd. The fraction that comes from the town herd could only be derived by model fitting. Lubow et al. (2001) used this procedure to estimate that 35% of the harvest was from the town herd. I found this estimate to be too high, given the other values of the elk model parameters that fit the park herd dynamics. Through model fitting, I found that only 16% of the GMU 20 harvest could be supported by the town herd. To put this in context, the average annual harvest 1988-1998 was 269. Thus, the difference between 35% and 16% is 51 elk per year compared to a mean herd size of 1,572.

Emigration rate can be specified in terms of a certain fraction of the population per month. Emigrators from a source population can be directed into another simulated population, or they can be removed from the herd and not put into any other herd, thereby representing their dispersal out of the simulated study area. For the purposes of this study, elk from the park herd were assumed to disperse to the town herd, while animals from the town herd were only assumed to disperse out of the simulated study area. There was assumed to be no flow of animals from the town herd back to the park herd. The emigration was assumed to begin in 1968, at the time of cessation of reductions within the park. Monthly emigration rates of 0.0055 and 0.01 for yearling females and males were found by fitting the model to the park and town herd population data. Other age/sex classes were assumed to not be involved in emigration.

Survival and births rates are shown in Table 7. Survival rates are used to calculate the nominal death rates ($Deathrt_{Nom}$). Survivorships in the younger age classes for elk are based on Lubow et al. (2001), while survivorships in the older age classes are taken from Houston (1982). Maximum birth rate (i.e., pregnancy rate) for elk is based on information obtained by the CDOW (1966). The effects of condition on recruitment were calibrated so that the model predicted observed values of calf:cow ratios, as reported by Lubow et al. (2001) and Stevens (1980) over a wide range of elk densities. The condition-dependent death rate function ($Deathrt_{Cl}$) was calibrated to fit observed population data for the park elk herd. Deer population parameters (Table 7) were largely based on Bartholow (1988). Effect of condition on recruitment was calibrated to achieve observed fawn:doe ratios (Stevens 1980). Effect of condition on death is set to a biologically reasonable value, since a good data set for deer population dynamics was lacking.

Herbivore Spatial Distribution

The herbivore spatial distribution submodel dynamically simulates animal distributions over the simulated landscape or region. The habitat suitability index (HSI) of a grid-cell is affected by 0-1 effects of preference-weighted forage biomass, forage intake rate, green and dead herbaceous biomass, snow depth, slope, tree cover, and a prescribed “force”.

$$HSI = F(Pforage) \times F(\text{energy intake rate}) \times F(\text{green herb}) \times F(\text{dead herb}) \times F(\text{snow}) \times \min[F(\text{slope}), F(\text{cover})] \times F(\text{force}) \times \text{Noise}$$

The preference-weighted forage biomass ($Pforage$) is the sum of dietary preference indices times forage biomass over all dietary items in the grid-cell. Multiplicative effects are used so that each effect always has an impact on HSI, irrespective of the values of other effects. $Pforage$ represents an effect of dietary selection. The intake rate effect implicitly includes the digestibility of the forage. The effect of green herb biomass represents selection for green leaf, while the effect of dead herb biomass represents a negative preference for dead leaf and a interference effect of dead leaf on selectivity for green leaf. The minimum of the slope and cover effects is taken, hypothesizing that either one or the other will govern selection for the grid-cell, eg. if the slope is too steep it doesn't matter what the cover is, and if cover is unsuitable it doesn't matter what the slope is. “Noise” is a uniform random variate (0.8-1.0) that prevents animals from attaining an ideal free (ie. perfect) distribution.

“Force” maps are read into the model that define the a population's range at different times of the year. A range is defined as the total area available to the population. The spatial distribution model calculates how the population is distributed within its range. The value of $F(\text{force})$ will be 1 inside the range, and 0 outside the range. In the case of elk and deer, summer and winter range maps are read in, with the winter range map being used during November through April. The summer range map was used in June through September. A transition range map, which includes all of the summer and winter ranges, was used in May and November, giving the animals freedom to move in response to snow cover during those months. Range maps used in the model are shown in Figure 22. Singer et al. (2002) delimited three subherd winter ranges based upon Larkins' (1997) radiolocation data. I combined their range maps for the

Moraine Park and Horseshoe Park subherds to represent the range for my park subherd. I similarly delimited the combined summer range myself by circumscribing the majority of Larkins radiolocation data (Larkins 1997). I used a map of the area covered by in-town ground counts (T. Johnson, R. Monello, pers. comm.) to represent the town herd winter range. For lack of other data, deer ranges were assumed to be the same as elk ranges. Beaver habitats were defined by the distribution of willow and aspen on the vegetation map within the area where beaver have been historically observed (Packard 1947b, Stevens and Christiansen 1980, Hickman 1964, Zeigenfuss et.al. 2002). Only the habitats on the elk winter range were included in these modeling analyses, although beaver do occur at low elevations on the western slope. The total area for beaver on the 500 km resolution maps was 425 ha. Thus, if 450 beaver are simulated, this is a density of 1.06 beaver per ha, or 106 per km². If colony size is 6 animals per colony, this is 5.67 ha per colony.

Once the HSIs are computed for every grid-cell in the animal's range, they are summed, and normalized (so that they sum to 0.0). Then the animals in the population are distributed across their range in proportion to the distribution of the normalized habitat suitability indices among grid-cells. The redistribution occurs on a weekly basis.

Parameters which determine animal spatial distributions are shown in Table 8. The effect of energy intake rate was scaled to observed ranges of energy requirements for the animals. The effect of slope on elk was estimated from the distribution of radio locations of Larkins (1997). The effect of slope for deer was set so they use steeper slopes than elk. Beaver are assumed to only use flat terrain. The effect of snow depth for elk was set based on previous modeling experience and literature review (Coughenour 1994, Coughenour and Singer 1996). The effect of snow depth for deer was scaled to that of elk, based on difference in body size, particularly brisket height. The effect of green herbaceous biomass was set to span a range of values typical of upland herbaceous communities in RMNP. Although the foraging functional response saturates at lower values, the function here is intended to affect animal density rather than individual animal responses. The maximum density for elk was set based upon aerial survey data (Lubow et al. 2002). The minimum density for beaver was set to prevent unreasonably low concentrations at low simulated population sizes. Assuming there are 6 beaver per colony (Packard 1947b), a value of 40 beaver km⁻² would give 15 ha per colony.

Wolf Population Dynamics and Predation

The wolf submodel simulates wolf predation on ungulates and resultant wolf population dynamics. It is derived from a model that was used to assess wolf reintroduction into Yellowstone National Park (Boyce and Gaillard 1991, Boyce 1993).

Population Dynamics

Wolf population dynamics are modeled with the logistic equation for population growth, in which the value of the population finite rate of increase (R) is dependent on the number of

prey killed per wolf per year and the maximum number or carrying capacity of wolves in the system. R is defined in

$$\text{Wolf}_{t+1} = R \times \text{Wolf}_t$$

where Wolf_t is wolf numbers at time t . The conversion of prey killed into rate of population increase is scaled so that the maximum possible increase rate is achieved at the maximum predation rate,

$$R = R_{\max} \sum \text{Prkill}_i / \text{Fmax}_i$$

where R_{\max} is maximum finite rate of increase, Prkill is actual predation rate on each species, and Fmax is maximum predation rate on a species. Thus, R declines linearly as predation rate declines. Values for R_{\max} are found in Table 9. The value for R_{\max} was selected based on the maximum value observed in Yellowstone. In 1996, there were 40 wolves while in 1997, the population had increased to 86, giving a finite rate of increase of 2.1. Boyce used a value of 1.8, although he noted Ballard et al. (1987) observed a value of 2.4 in Alaska.

When the number of wolves reaches a maximum value, R is capped at a value of 1.0 (i.e., no further increase is allowed). The maximum number of wolves is specified based on the size of the range being simulated. Territory size is assumed to decrease with increasing prey density, using the data of Walters et al. (1983). Although these calculations could be based on pack size, and maximum density expressed in terms of packs per km^2 , this adds little to the final result unless the mechanisms governing pack size are simulated. Since pack size is not a modeled variable, I simply express wolf density in terms of numbers of animals per km^2 .

Walters et al. (1983) summarize empirical data by plotting territory size against prey biomass density. I converted their data to form an equivalent plot of wolf density versus prey biomass density (Figure 23). Pack size has varied from 3-16 animals in recent reintroductions in North America (USFWS 1999). In Montana, the mean pack size in 1999 was 6.7, while in Yellowstone, it was 7.5. However, these included young packs and non-breeding packs with 2-5 animals. On the Yellowstone elk winter range, the 5 established packs averaged 11.4 animals, while in Montana, with a probable lower prey density, the mean breeding pack size was 8.6. Accordingly, I assumed a typical pack size of 10 to convert territory size (area per pack) in Walters et al. (1983) to area per wolf. The inverse of the latter gives maximum number of wolves per area. (i.e. carrying capacity). In addition to the data given in Walters et al. (1983), I estimated maximal density of 0.05-0.075 wolves km^{-2} . Peterson (1976) reported 0.084 wolves km^{-2} was observed in Isle Royal, probably the highest ever observed. Mech (1966) observed 0.038-0.056 km^{-2} on Isle Royal. In comparison, densities in northern Minnesota have varied from 0.023-0.039 km^{-2} , while in Alaska densities have ranged 0.006-0.002 km^{-2} , and in Canada 0.003-0.007 km^{-2} (Ballard et al. 1987). The resulting plot (Figure 23) can be interpreted as describing a range of values bounded by the upper and lower extreme data points, with a median-value function lying in between. I used the median-value function in most of the model runs presented here.

The wolf densities in Figure 23 can be converted to pack territory sizes as follows. At the

maximum density of 0.08 km⁻², and a pack size of 10, the pack territory would be 125 km². At a density of 0.05 km⁻², territory size would be 200 km². At a mid-range density of 0.02 km⁻², territory size would be 500 km², and at a low density of 0.01 km⁻², territory size would be 1,000 km². In comparison, pack home ranges in NW Montana averaged 480 km², with a minimum of 63 km² and maximum of 1,190 km². In Yellowstone, home ranges varied from 88-2,419 with a mean of 890 km². On the northern winter range, mean home range was 465 km² (USFS 1999).

It is important to put prey biomass densities in the context of other observed values, since prey biomass density affects predator number as in Figure 23. If there are 2,000 elk and 300 deer on the total wolf/elk range (388 km²), the prey biomass density is 1,134 kg km⁻² elk plus 42 kg km² of deer, using body weights of 220 kg and 55 kg for each. The total of 1,176 kg km⁻² is near the saturating value of 1,300 kg km⁻² used in Figure 23. With half as many elk, the biomass density is 610 kg km⁻². In comparison, in 1998-1999 about 11,700 elk were counted on the Yellowstone northern range, which could feasibly correspond to 14,000 animals after correcting for sightability. The total size of the wolf home ranges is 2,326 km², giving a prey biomass density of 1,324 kg km⁻².

Predation

The number of prey animals killed depends on the relative densities of prey and wolves. A multispecies disk equation, modified to incorporate a Type III functional response is used (Holling 1959, Abrams and Allison 1982). This version of the equation assumes prey overlap on the same range. The equation is

$$Prkill_i = (Attack_i \times Prden_i \times Tprden) / (1 + Attack_i \times Handtm_i \times Tprden^2)$$

where Prkill is the number of prey of type i killed per predator per year, Prden is prey density (number per km² in the prey's range, size of prey range given in Table 9), and Tprden is the sum of Prden over all prey species. The size of the prey range is used here rather than the size of the predator range, because the predation process is presumably affected by the prey density in the area where the predation is occurring. Attack is the attack rate, computed as

$$Attack_i = 1 / (W_{0i}^2 \times Handtm_i)$$

where W₀ is the prey density (number per km²) at the inflection point of the functional response. This equation is derived from knowing that

$$W_0 = \sqrt{[1 / (Attack \times Handtm)]}$$

Handtm is handling time, computed as

$$Handtm_i = 1 / Fmax_i$$

where Fmax is the maximum predation rate on prey type i.

It can be shown algebraically from the set of equations above that

$$\text{Prkill}_i = (\text{Fmax} \times \text{Prden}_i \times \text{Tprden}) / (\text{W}_0^2 + \text{Tprden}^2)$$

which is another form of the functional response equation.

Total predation (number of prey per year) is calculated as the product of per-predator kill rate and total number of predators in the range of the prey.

$$\text{Tkill}_i = \text{Prkill}_i \times \text{Wolf}$$

The total number of predators in the range of the prey is affected by predator and prey relative migration patterns. For example, if prey move out of the range of the predators on a seasonal basis, then in effect, there are that many fewer predators preying on the prey. Conversely, predators may migrate along with prey. Alternatively, a portion of the predators may have territories in one seasonal prey range, while another portion of predators may have their territories in another seasonal prey range. For example, in Yellowstone, certain wolf packs have established territories on elk winter range while others have territories on elk summer range. This complexity is not represented explicitly in the model. Instead, the user specifies an estimate of the fraction of prey that are in range of all of the predators for each month. These fractions must be derived by creating a conceptual scenario of the seasonal overlaps between predator and prey ranges. The scenario which I chose was that two wolf packs would be likely to occur over the total range. I estimated two packs based on typical pack sizes, the typical range of wolf densities (or conversely of pack territory sizes), and the size of the combined elk summer plus winter ranges. I surmised that one pack would be based on the west slope and the other on the east slope of the continental divide. The pack territory on the east slope would cover the winter range, and portions of the summer range. The pack territory on the west slope would cover the remainder of the summer range. In this scenario, half of the predators would overlap with elk in the six winter months (November-April). All of the predators would overlap with elk in the six transition and summer months (May-October). Thus, the fraction of predator-prey overlap on a year-long basis is $[(6 \times 0.5) + (6 \times 1.0)] / 12 = 0.75$.

The multi-species form of the equation represents shifting of predation from one species to another as their relative densities change. Predation is distributed among sex and age classes of prey using a prey vulnerability index. This is used to make very young animals, and older animals more vulnerable than prime aged animals. Predation can either be additive, compensatory, or some mixture of both. Additive mortality due to predation is assumed to be additional to the normal prey mortality rate due to age and nutrition. Compensatory mortality is subtracted from the normal prey mortality, with the idea being that wolves are killing animals that are most likely to be dying due to other causes.

Predation is distributed among age and sex classes within a species using a vulnerability index. It is commonly observed that predators focus on weaker or otherwise more vulnerable animals. For example, in Yellowstone, 56% of predator mortalities on elk were calves, 22% were prime-aged (1-9yrs) and 22% were old (>9yrs) (Kerry Murphy, pers. comm.). This represents a

disproportionate mortality of calves. Vulnerability indices are weighting factors, to indicate relative vulnerabilities among age/sex classes. The product of vulnerability (V) times the number of animals (N) is normalized to the total to give the fraction of predation on each age/sex class k.

$$\text{PrAgeSex}_k = (V_k \times N_k) / (\sum V_k \times N_k)$$

The maximum predation rate for elk is set at the value used by Boyce (25 elk wolf⁻¹ yr⁻¹, Table 9). Recent kill rates in Yellowstone have been about 1 kill per 2.5 days per pack in early winter and 1 kill per 1.5 days in late winter (K. Murphy pers. comm.). Assuming there are on average 10 wolves per pack, this converts to 18-24 elk wolf⁻¹ year⁻¹. Boyce calculated from the data of Carbyn (1983) that wolves kill 0.21 kg prey per kg wolf per day. If wolves are on average 40 kg and elk are 220 kg, this would be equivalent to 14 elk wolf⁻¹ yr⁻¹. Boyce used a higher value than typically observed to account for surplus killing when elk are highly abundant, i.e., when elk density is high enough for wolves to actually achieve the maximum predation rate. Another reason to use a value on the high side of the observed range in Yellowstone is that predation rates observed in Yellowstone thus far are unlikely to be maximal. For deer, I used Boyce's value of 110 deer wolf⁻¹ year⁻¹, based on the assumption that deer are 1.3 times as preferred as elk after Cowan (1947, cited in Boyce 1993), and the difference in body sizes between deer and elk.

The characteristic shape of the functional response is shown in Figure 24a. Although this is a Type III response, the S-shape is minimal. When densities are converted to numbers based on winter prey range size (Figure 23b), it can be seen that there is a continuous increase in predation rate between 0 and 1,000 elk, and that above 1,500 elk, the predation rate is saturated. Saturation for deer does not occur until a much larger population size of over 3,000. The sensitivity of the equation to the parameter W_0 is demonstrated in Figure 24c.

Compensatory mortality is potentially an important modifier of predator impact on prey populations, but is still little understood. Compensatory mortality is defined as the fraction of prey killed by predators that would have died anyway due to disease, malnutrition, or other causes. This fraction of predation would therefore have no impact on prey population dynamics. It would be expected that the fraction of compensatory mortality would increase with the degree of selectivity of predators for weak or old prey animals. Additive mortality is the mortality that predators exert in addition to the other causes of prey mortality, so it is this fraction which would cause predators to affect prey populations. Compensatory and additive mortalities are distinguished by simply specifying the proportion of prey killed that is compensatory. The remainder is additive. The fraction of predation that is compensatory is not removed from the prey population, but does count towards increasing the predators population growth rate.