

Chapter 13

Ecosystem Modelling in Support of the Conservation of Wild Equids – the Example of the Pryor Mountain Wild Horse Range¹

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13.1 Introduction

It is widely recognised that individual species cannot be conserved without also conserving ecosystems (Samson and Knopf 1996). The concept of ecosystem management embodies this principle, as well as recognising the importance of sustainability, ecological change, spatial and temporal scale, interconnectedness, humans as components of ecosystems, and appropriate ecological models (Christensen *et al.* 1996). The conservation of wild equids, in particular, depends on the principles of ecosystem management. Three of the seven surviving species of equids are threatened with extinction – one is vulnerable, and one is extinct in the wild (IUCN 1996). Their conservation requires careful management to increase remaining populations, and reintroductions into ancestral habitats where viable habitats still exist (Duncan 1992). There is a pressing need for an assessment methodology that explicitly considers the role of horses in ecosystems and the ecological processes necessary for ecosystem viability.

According to an Ecological Society of America report, “ecosystem management should be rooted in the best current models of ecosystem function” (Christensen *et al.* 1996). It has long been recognised that grazing ecosystems function and change as a result of complex interacting processes of plant growth, nutrient cycling, herbivory, and the site water balance (e.g. McNaughton *et al.* 1982; Archer and Smeins 1991; Frank 1998). Simulation models have been constructed to represent these processes and their interactions for nearly three decades. Until relatively recently, however, ecosystem models have been aspatial, representing a mean or aggregate ecosystem response. This has severely limited their application to ecosystems comprised of expansive and heterogeneous landscapes and mobile populations of herbivores – typical characteristics of free-ranging equid ecosystems. Now, however, we have the capability to construct spatially explicit models of ecosystems, which represent many points in space and the movements of organisms among those points (Coughenour 1991). These models can be used to assess the role of equids

in ecosystems, the potential of ecosystems to support equids, and the effects of human-induced changes to ecosystems on the viability of equid populations.

This chapter demonstrates how a spatial ecosystem model can be used to assess a wild horse population and its habitat. Ecosystem modelling has been used to support the management of wild horses (*Equus caballus*) on the Pryor Mountain Wild Horse Range (PMWHR) in southern Montana (Coughenour 1999, 2000). The PMWHR is the first officially designated wild horse range in the US, established in 1968. The Bureau of Land Management (BLM) is responsible for the maintenance of a “thriving ecological balance” on the PMWHR and has deemed it necessary to conduct periodic management removals of wild horses since 1970 to halt and prevent further range degradation (US BLM 1997). The PMWHR horse herd is not an ordinary band of runaways, but is a unique genetic strain with ancestry likely going back to the first Spanish reintroductions (Gregerson 1973; Ryden 1990; Spohnberg 1997). They have probably inhabited the PMWHR for at least a century, and there is historical evidence that they are descendants of horses used by the Crow or Shoshone tribes of Native Americans (Ryden 1990; Brownell 1999).

13.2 Site description

The PMWHR straddles the border between southern Montana and northern Wyoming. It lies approximately 80km due south of Billings, Montana. The range of the Pryor Mountain wild horses includes lands designated as the PMWHR in the 1968 enactment, and lands used by horses under agreement or lease with other government agencies or private landholders (Figure 13.1). The PMWHR lands include portions of the Bighorn Canyon National Recreation Area (BCNRA), administered by the National Park Service, and lands administered by the BLM. Additional lands used under prior agreement include the Lost Water Canyon allotment of the Custer National Forest (US Forest Service [USFS]), and the Mystic allotment comprised of private and BLM lands. The

1. Some of the material contained in this report is taken from (Coughenour 1999, 2000), and is in journal publications. Please contact the author for further information.

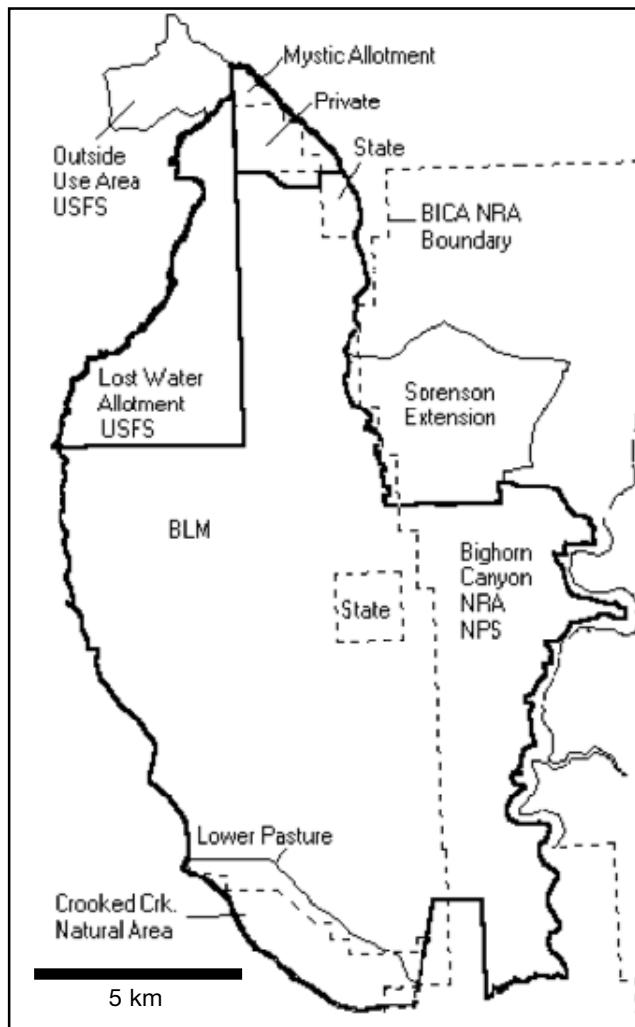


Figure 13.1. Lands used by horses under agreement or lease with other government agencies or private landholders.

Sorenson Extension of the BCNRA has been used by horses in the past under agreement. Additional lands are leased from the state of Montana. The Crooked Creek Natural Area is a Federal protective withdrawal area (BLM), and is not available to horses.

The climate of the PMWHR is temperate continental, with cold winters and warm summers. Mean annual precipitation at Lovell, Wyoming, from 1948 to 1996 was 170mm, with a standard deviation of 37mm. The PMWHR landscape is topographically diverse. Elevations range from 1,200–2,400m. A prominent feature of the landscape is the steep-walled escarpment that runs north and south, rising dramatically above the lower elevation plains and bajadas below. The landscape is characterised by deep, steep-walled canyons, isolated plateaus, and foothill slopes.

The vegetation of the PMWHR is diverse, due to the large elevation and associated climatic gradient, but also due to the wide variety of soils and substrates, and patterns

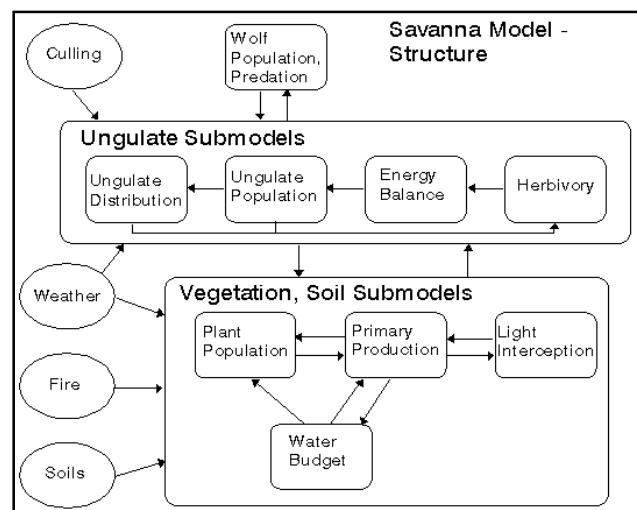
of water redistribution on the landscape. Vegetation types include desert shrublands at lowest elevations, sagebrush grasslands, several grassland types spanning all elevations, juniper and curl-leaf mountain mahogany woodlands at low to mid elevations, and coniferous forests at the higher elevations.

13.3 The ecosystem model

An ecosystem simulation model called SAVANNA (Coughenour 1992, 1993) was used to represent ecosystem dynamics and interactions on the PMWHR landscape. The model is comprised of submodels 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 (Figure 13.2). Ecosystem simulation models consist of mathematical equations that describe changes and interactions within the ecosystem, while maintaining consistency with fundamental principles such as the conservation of matter and energy and fundamental biological attributes of organisms and populations. The SAVANNA model is capable of simulating grassland, shrubland, savanna, and forested ecosystems. It simulates landscape processes through regional spatial scales over annual to decadal time scales. Typically, the landscape is divided into 5,000–10,000 square grid-cells (Figure 13.3). A grid-cell size of 500×500m was used in the PMWHR simulations. The model simulates ecosystem processes on each of these grid-cells, including water and nutrient balances, plant growth, and herbivory.

SAVANNA uses monthly weather station data as basic input to its hydrological submodel. Precipitation data from the weather stations are spatially interpolated

Figure 13.2. The SAVANNA ecosystem simulation model.



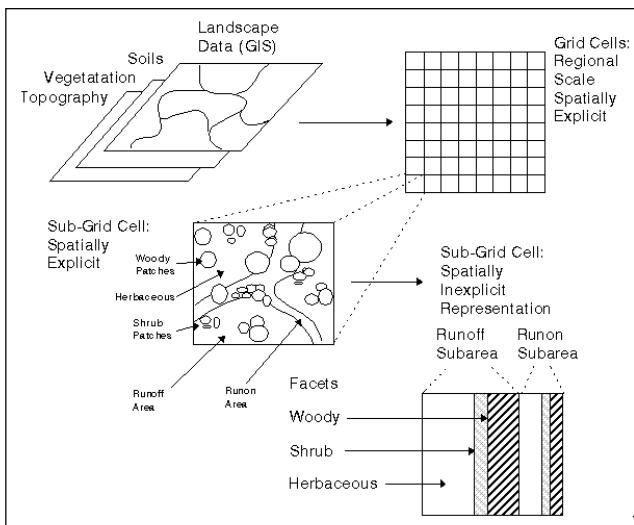


Figure 13.3. In SAVANNA the landscape is divided into 5,000–10,000 square grid-cells.

to create monthly precipitation maps. The interpolation scheme corrects for elevation differences between the weather stations and the grid-cells. The water balance submodel then simulates soil moisture dynamics and use on each grid-cell. A soils map is read into the model upon initialisation. By knowing the water holding capacity of each soil type, the model can use the map to determine soil water-holding capacities of each grid-cell. The water budget for each grid-cell includes terms for precipitation, interception by leaves and detritus, runoff, runon, infiltration to subsurface layers, deep drainage losses, bare soil evaporation, root water uptake, and transpiration losses from leaves.

The net primary production (NPP) submodel simulates plant biomass production and dynamics. Plant biomass production is affected by light, water, temperature, nitrogen, and herbivory. This submodel is explicitly linked to the water budget submodel through transpiration and plant water use. Plants must transpire water in order to manufacture biomass through photosynthesis. The newly produced biomass is allocated to leaves, stems, and roots. Plant tissues die at nominal rates that reflect their maximal longevities, but death rates may be accelerated due to water or temperature stress, or phenological stage.

Nitrogen enters the system dissolved in rainfall or snow. Certain atmospheric forms can be deposited directly on soil and leaf surfaces. Nitrogen gas is also incorporated by symbiotic or free-living nitrogen-fixing microorganisms. A litter decomposition and nitrogen cycling submodel simulates the breakdown of dead plant materials and animal faeces. Nitrogen is released during decomposition to mineral forms that can be taken up by plants. Nitrogen taken up by plants is either transferred to soil detritus due to tissue mortality, or it is lost to herbivory, and recycled from herbivores to soil as urine or faeces. Nitrogen leaves

the system through conversion to gaseous forms during detritus decomposition, or through volatilisation of ammonia from the urea in herbivore urine.

Forage intake by herbivores is influenced by diet selection, forage abundance, forage quality, and snow cover. Animals choose among available plant types and tissues to achieve a preferred diet composition. Diet composition is affected by the relative availability of different forage types as well as preferences or avoidances. As forage biomass increases from zero to a specified level, forage intake rate increases. Forage intake rate is increasingly inhibited by deeper snow.

The animal energy balance submodel simulates average body weight of each population or herd based upon rates of energy intake and energy expenditure. Energy intake rate is derived from forage biomass intake rate and the concentration of digestible energy in the forage. Expenditures depend on body weight, stage of gestation, lactation, activity, and travel patterns. As energy intake increases, animals gain weight. When energy use exceeds intake, animals use energy stored as fat, and thus lose weight. A body condition index is calculated from body weight, with heavier animals being considered to be in better condition. In this way, herbivore body condition declines during times of food shortage. Since food shortage can be brought about by competition with other herbivores, the likelihood of food shortage increases as the number of herbivores increases.

The herbivore population dynamics submodel represents changes in the number of animals in each age class, for each sex. Birth and death rates are affected by animal condition indices. This is the way the model represents population responses to factors affecting forage availability, including plant growth rates, snow depth, and competition for forage by other animals.

The herbivore spatial distribution submodel simulates animal distributions over the landscape or region. Animals are redistributed in relationship to the distribution of a habitat suitability index. The habitat suitability index is affected by slope, temperature, forage biomass, forage intake rate, snow depth, distance to water, and tree cover. Since some of these variables change on a seasonal basis, animal distribution also changes seasonally. Animals can also be forced to occupy a certain area, or be excluded from certain areas by reading maps of these areas into the model.

13.4 Model parameterisation

Six groups of plants were simulated: grasses, forbs, shrubs, mountain mahogany, juniper, and coniferous trees. These groups were chosen to meet the objectives of this modelling analysis, without making the model overly complex. Many of the plant model parameters were taken from the literature, for example, from data on photosynthesis,

biomass allocation, tissue nitrogen concentrations, and plant allometry. Data from Detling and Gerhardt (1996), Gerhardt and Detling (1998), Fahnestock (1998), and Peterson (1999) were used to parameterise the plant growth model, and test its predictions. The objective was to maximise the model's skill in providing realistic simulations by making maximal use of information contained in the field data and literature.

A vegetation map existed for BCNRA (Knight *et al.* 1987), but none existed for the remainder of the PMWHR. A vegetation map for the PMWHR was developed by merging the BCNRA vegetation map with a modelled vegetation map for the remaining area. The modelled vegetation map was based on a map of forest cover from USGS quad sheets, the soils map, and qualitative relationships between major vegetation types, elevation, and soils observed on the Knight *et al.* (1987) map.

There are three relatively distinct herds of horses in the PMWHR, occupying habitats that are separated by distinct topographic barriers (Hall 1972; US BLM 1984, 1997; Singer *et al.* 2000). Each of the three herds was modelled separately and distributions were limited to their respective range areas. Seasonal movements were modelled as dynamic responses to changing forage and snow conditions, with a seasonal avoidance of areas below 1,500m in summer.

The locations of known horse watering points within the horse range were digitised from information provided by BLM personnel (L. Padden, BLM, pers. comm.). A map of distance to water was calculated using GIS. Bighorn sheep were kept within the seasonal ranges observed by Irby *et al.* (1994). Within these ranges, the model redistributed animals in relation to forage biomass and forage energy intake rate. Mule deer winter on the PMWHR, but during summer, most migrate to ranges north of the PMWHR (Irby *et al.* 1994). The model was parameterised so that the entire deer herd was on the PMWHR during December–April, and 10% were on the PMWHR during June–October.

Some model runs used observed animal population data as input, rather than simulating animal population dynamics. In such simulations, the summarised horse population data from USDI/BLM (1997) were used, based on data from Taylor (1990 memo) and Garrott and Taylor (1990). Sheep population data were obtained from Coates and Schemnitz (1989) and Kissell (1996). Mule deer population sizes were based upon information from Kissell (1996).

In model runs where the animal populations were simulated, they were normally culled or hunted at observed rates. Horse culling data from the USDI/BLM (1997) were used in simulations using observed culling data. Deer were culled to maintain the population between 500 and 700. Bighorn sheep have never been culled or hunted.

Population model parameters for horses were obtained from Garrott and Taylor (1990) and Singer *et al.* (1997,

2000), while population model parameters for bighorn sheep were derived from Leslie and Douglas (1986), Kissel (1996), Singer *et al.* (1997, 2000), and Coates and Schemnitz (1989).

Based on information in Lewis (1995), Pilliner (1992), National Research Council (1973, 1978), and others, maintenance and basic activity energy requirements were derived. Gestation and lactation costs were added using the multipliers given in Lewis (1995).

Maximum forage intake rates were based on values reported in the scientific literature. Conventional wisdom is that a horse will eat about 2.5% of body weight per day, although lactating mares and growing foals may eat more (Pilliner 1992). Duncan (1992) argued that breeding or growing equids are capable of much higher intake rates than typically reported in standard feeding trials. Five wild species, studied by Foose (1982), had intake rates that were markedly lower than intake rates of productive domestic animals. However, zebras that had been caught in the wild and that had been recently tamed had very high intake rates – corresponding to 4% per day (Gakahu 1982).

The spatial distribution model was parameterised based upon known habitat preferences. There are three relatively distinct herds of horses in the PMWHR, occupying habitats that are separated by distinct topographic barriers (Hall 1972; US BLM 1984, 1997; Singer *et al.* 2000). Each herd was modelled separately, and each was restricted in the model to their respective range. The Dryhead herd in the east spends the entire year at low elevations below the Sykes Ridge escarpment. The Sykes Ridge herd in the middle moves up and down Sykes Ridge, to high elevations in summer, and low elevations in winter. The Burnt Timber Ridge herd to the west moves similarly up and down a separate ridge. The summer ranges of the herds from Sykes Ridge and Burnt Timber Ridge overlap at the top of the mountain. Sykes Ridge and Burnt Timber Ridge ranges are separated by a steep, deep canyon (Big Coulee). Each of the three herds was modelled separately and limited to their distinct ranges. A small rate of inter-herd exchange was simulated, in accordance with existing data. Seasonal movements were modelled as dynamic responses to changing forage and snow conditions, with a seasonal avoidance of areas below 1,500m in summer.

13.5 Model application

The model performed well in simulating herbaceous plant growth with and without grazing, and it successfully simulated herbaceous biomass dynamics across a wide range of sites and weather years. The biomass dynamics data collected by James Detling and his colleagues proved to be critically important, particularly since they were collected at monthly intervals, over a wide variety of site types. The proportions of grasses and forbs, the rates of

transfers from live to dead, and the rates of transfers of dead tissues to soil all proved to be adequately simulated. More subtly, this suite of tests indicated that the model correctly represented biomass production, as opposed to simple biomass amounts. This is a subtle but important distinction. Biomass amount is usually lower than biomass production because biomass is always being transferred to detritus and herbivores. So, biomass amount is likely to be an underestimate of the actual amount of forage that is being produced.

Without horse grazing, above ground grass biomass varied nearly two-fold inter-annually. Grass biomass generally increased over time. Forb biomass increased less, so the proportion of forbs in total herbaceous biomass decreased. Grass biomass varied two-fold with the observed levels of horse grazing, and forb biomass was similar to grass biomass, whilst the ratio of grass to forbs was similar throughout. With no horse culling, biomass of grasses decreased over time.

The model simulated reasonable population dynamics and distributions of horses, bighorn sheep, and mule deer. These distributions were comparable to the best information available at the time. The rates of forage

offtake per animal, and the compositions of the herbivore's diets, also proved to be realistic, and consistent with the best available data.

Forage intake rate by horses varied seasonally from <0.5% of body weight per day to the maximum of 3.5% per day. Minimum values varied more among years than maximum values, with especially low minimal intake rates being predicted for 1978 and 1979. Generally, the most stressful years for forage intake were also years with deeper snow depths. Maximum intake rates for the Dryhead herd were consistently lower than for the other two herds, as a result of the lower forage biomass on the Dryhead summer range. Intake rates were markedly reduced when horse herds were not culled. Maxima and minima were both reduced at higher horse densities, as a consequence of intraspecific competition for forage.

Horse condition indices varied primarily between 0.5 and 1.0, indicating that body weight varied from 50% to 100% of its maximum. Years with high minimum forage intake rates were years with high minimum condition indices. Condition indices on the Sykes Ridge and Burnt Timber Ridge ranges often reached lower minimum values than on the Dryhead range, most likely a result of deeper

Figure 13.4. Herbaceous ANPP (annual net primary production) in Pryor Mountain Wild Horse Range.

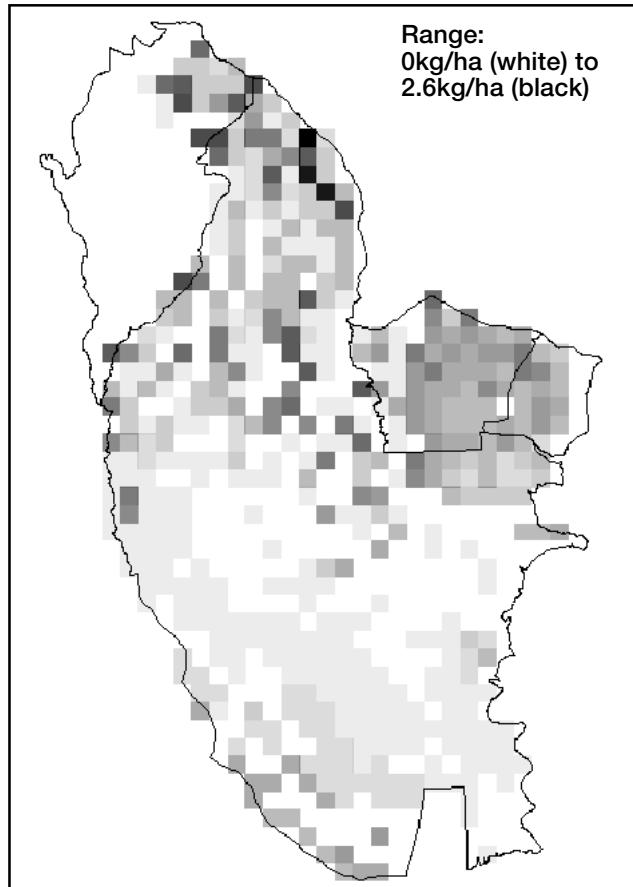
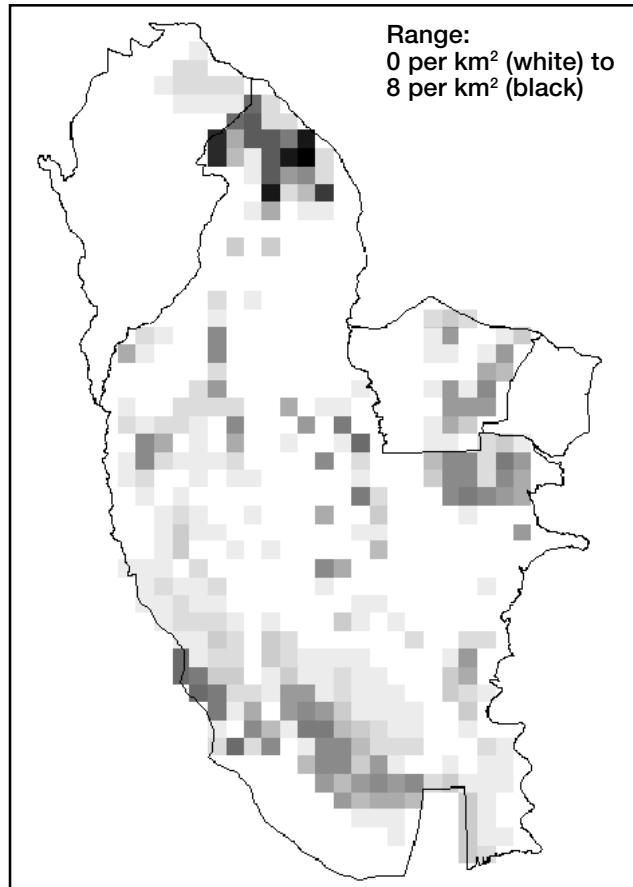


Figure 13.5. Horse densities (year-long) in Pryor Mountain Wild Horse Range.



snow cover at the higher elevations. When horse herds were not culled, horse condition indices decreased. Both maximal and minimal values decreased on the Dryhead range, while on the higher elevation ranges, only the minimum values decreased.

Gradients of herbaceous ANPP (annual net primary production) across the landscape were partly due to precipitation gradients and partly due to soil differences (Figure 13.4). Lands within the Sorenson Extension, and just south of it were more productive for a similar amount of precipitation than areas further south on the Dryhead horse range. The difference was clearly related to the distribution of deeper and shallower soils, and their associated water-holding capacities.

Horse densities were heterogeneously distributed on the landscape (Figure 13.5). With observed horse numbers, highest use areas at low elevations were 2–5 head per km² year-long. Heavy use areas at the top of the mountain were higher, reaching 6–8 head per km² year-long.

Between 1970 and 1996, 40–70% of the landscape experienced light herbivory of grasses (using observed horse numbers). However, 5–20% of the landscape received >80% herbivory and 5–15% experienced herbivory in the 50–80% range. The fraction of the landscape receiving >80% herbivory varied markedly from year to year.

The effects of grazing on ANPP can be displayed as a map of the differences between ANPP with and without horses. There were smaller decreases in ANPP on portions of the landscape, and there were no differences, or even increases in ANPP in some areas due to herbivory. Grass ANPP was diminished by herbivory more than forb ANPP, most likely due to higher dietary preferences for grasses. With observed horse numbers, grass ANPP was 60–80% lower in some areas than without horses. With no horse culling, there were areas where grass ANPP was reduced by 80–90% and forb ANPP was reduced by 50–70%.

As horse numbers increased, herbaceous ANPP on the primary horse range decreased by 10–13% for each additional 50 horses. There was approximately 75% as much herbaceous production with 200 horses as with 50 horses. With 350 horses, ANPP was about 60% of that with 50 horses.

Mean horse condition index declined with increases in horse numbers, indicating increased competition for food. Indeed, forage intake rate declined with increasing horse number.

In addition to the results just described, the model also produced the following results that are relevant to ecosystem management:

1. Grazers generally decreased above-ground herbaceous plant biomass, with potential implications for site water balance, and habitats for other species.
2. As herbivory pressure increased, forbs increase in relative abundance compared to grasses. An increase

in the ratio of forbs to grasses is often taken as a sign of decreased range condition.

3. Basal cover and root biomass decreased under increased herbivory due to decreases in above and below-ground primary production relative to root turnover.
4. The percentage of the landscape where grasses were grazed in excess of 80% increased from 16% at 125 horses to 25% at 225 horses. This level of grazing is negatively perceived by most. Importantly, the response was a smooth transition, rather than a discontinuous threshold response to increasing horse numbers.
5. The mean proportion of herbaceous plant growth consumed on the entire landscape varied from a mean of 15% at 125 horses to a mean of 23% at 225 horses. Thus, the mean offtake level on the landscape was well below the 50% level often used by range managers, despite the fact that much of the landscape was grazed quite heavily.
6. Horses had little effect on bighorn sheep populations due to a high degree of spatial segregation, dietary separation, and the fact that sheep are strongly influenced by their own density within their own range.
7. Horses increased to over 300 in many weather scenarios, and even to over 450, if they were not culled. This could be regarded as the ecological or food-limited carrying capacity of the population. However at ecological carrying capacity, plant biomass and horse condition would be unacceptably low, and horse mortality would be unacceptably high.

13.6 Using ecosystem models for the management of wild equids

The feasibility of using modelling to assess equid-ecosystem interactions was demonstrated. The model performed in a realistic way to soil properties, climate, grazing pressure, and their interactions. Predictions of plant biomass dynamics were consistent with data over a wide range of soils and climatic conditions. Plant production and biomass generally declined under increasing levels of herbivory, as expected. Horse distributions were generally consistent with available data, as were herbivore forage intake rates and energy use rates. Animal condition varied in response to the balance between forage intake and energy expenditure, as expected. Simulated and observed horse population dynamics were in general agreement over a 27-year period.

Horse grazing affected plants and soils as expected. Above and below-ground biomass declined as horse number increased, as did litter, plant cover, and total net primary production. The significant point here is that these plant and soil responses could be quantified, and embodied into a dynamic model that could be used to explain observed responses, and furthermore, predict

responses to alternative scenarios of climate, land use, and herd management.

The approach taken here for assessing carrying capacity was to construct a process-based ecosystem model, run it under different management and climate scenarios, and judge which scenario among a full spectrum of possibilities is most desirable. This approach is not as ‘cut and dried’ as traditional approaches, but the benefits are as follows: 1) It shows the range of possible outcomes. Responses may be continuous, taking the form of many shades of grey, rather than discreet categories that can more easily be deemed to be good or bad. 2) It does not make simplifying assumptions about ecosystem processes (e.g. that plant-herbivore systems come into an equilibrium, that if herbivores consume more than 50% of plant production the plants will die, that the herbivores are food or predator limited, or that herbivory is uniformly distributed over space and time). 3) It does not make implicit assumptions about what is acceptable or proper. Instead, that decision is deferred until the alternative results are presented and explained. This forces scientists and decision-makers to tackle the judgement of appropriateness head-on, rather than relying on an aprior criteria that may or may not be relevant to the situation at hand.

The ecosystem approach unifies the formerly disparate, nutrition-based and population-based methods for estimating carrying capacity without making simplifying assumptions characteristic of each one alone. The nutritional approach, which calculates how many animals can be supported by the forage base, operates under the assumption that herbivores are food-limited, and that population growth rate will decline to zero when food becomes limiting. On the other hand, the population response is not simulated – the population approach operates under the assumption that if population growth has declined to zero, the population must be at nutritional carrying capacity. Instead of making such assumptions, the ecosystem modelling approach represents the actual linkage between forage abundance and population growth rate.

The responses of plants and soils to herbivory are modelled explicitly, by modelling plant growth responses to the loss of photosynthetic tissue, reallocation of carbon by the plant, and the recycling of nutrients from the herbivore to the soil. Since plant growth responds to moisture and temperature, the model can be used to examine changes in the plant-herbivore system and carrying capacity that might occur under climatic change. This is particularly useful since responses to potential global warming are becoming an increasingly prevalent concern. In the shorter term, this feature of the model is useful for looking at the range of variability in forage supply and herbivore responses among different weather years, and sequences of weather years such as droughts.

The spatial component of the model proved to be essential for several reasons. First, forage biomass and

vegetation types varied considerably over the landscape due to large elevation, precipitation, and soil differences. Second, horse distributions were not at all uniform, resulting in uneven distribution of grazing intensity. Third, it was critical to distinguish the spatial habitats of horses and bighorn sheep in order to accurately portray the interaction between these two populations. The uneven distribution of grazing pressure precluded the use of a single proper use factor when estimating the appropriate numbers of horses. Instead, a proper use factor must be two-tiered, specifying both the spatial stratification of grazing intensity, and the acceptable grazing pressure within strata. An example of this would be to state that no more than X% of the landscape should experience a utilisation level of greater Y%.

The PMWHR case is interesting because the designated horse range involves multiple land use agencies – the BLM, the National Park Service, the US Forest Service, and private landowners. Additionally, there are several important groups of stakeholders with often conflicting points of view, ranging from wild horse enthusiasts, to wildlife protectionists, to recreational users. This is probably not an uncommon situation, and is likely to become even more common as human populations expand and human land use intensifies. The utility of an objective, or neutral model as an object of discussion becomes evident in situations involving multiple use, since it provides a statement of the way things are, or would be, under different management scenarios. It is also an instrument that can be used to find alternative solutions, which are palpable to multiple stakeholders. This is the idea behind our current efforts to incorporate the model into an Integrated Modelling and Assessment System (IMAS) in order to assess interactions between wildlife and livestock in East Africa (using funding from the USAID Global Livestock Collaborative Research Support Program).

Ecosystem model-based assessments could be very useful for projecting potential successes of wild horse reintroductions, and in guiding management after initial reintroductions have been made. Laudably, efforts are being made to assess carrying capacities of potential reintroduction sites. However, the efforts are often based on the traditional approaches. There is a need, and a capability to conduct even more thorough assessments that address the importances of temporal and spatial heterogeneities.

To conclude, the ecosystem model provides a broader and more explanatory foundation upon which to base management decisions than traditional approaches to habitat carrying capacity or population viability, including assessments of threatened and endangered species. The ecosystem modelling approach, while more difficult to implement, has greater explanatory and predictive power than the traditional methodologies. Ecosystem modelling is a critical component of ecosystem management (Christensen *et al.* 1997). As part of an adaptive

management process, an ecosystem model should be revisited periodically, to check the consistency of its predictions with actual results. Ecosystem monitoring should be established to corroborate or refute key model predictions. The model should then be revised, based upon the new information, and a new assessment should be carried out. In this way, resource management and the basis for it, can be improved over the long term.

The opportunity to conduct an ecosystem modelling assessment of a wild horse range appears to be unprecedented. The Pryor Mountain horses have remarkable historical and ecological attributes that merit special attention. The approach of combining ecological field studies and ecosystem modelling, as has been carried out in the PMWHR, should prove equally useful for the scientific management and conservation of wild equids worldwide.

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