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Ungulates in western coniferous forests: habitat relationships, population dynamics, and ecosystem processes

Introduction

Wild ungulates play important roles in coniferous forest throughout western North America. Their biology is well known compared with that of other species of wildlife. They have sufficiently large home ranges to integrate spatial patterns across landscapes. Finally, they are often migratory (Wallmo 1981, Nicholson et al. 1997). Their life-history characteristics require consideration of entire landscapes rather than isolated patches of habitat for purposes of conservation and management (Hanley 1996, Kie et al. 2002). Ungulates require temporally and spatially diverse habitat components such as food and cover. These mammals can have significant effects on vegetation composition and basic ecosystem processes such as nutrient cycling, thereby acting as keystone species (Molvar et al. 1993, Wallis de Vries 1995, Hanley 1996, Hobbs 1996, Nicholson et al. 1997, Simberloff 1998, Kie et al. 2002).

Ungulates have economic value to society as well. Most species provide recreational hunting opportunities and also can have non-consumptive, aesthetic values (Loomis et al. 1989). Conversely, ungulates can cause damage to gardens and other landscaping (Conover 1997), to agricultural crops, (Austin and Urness 1993), and to new tree seedlings (Bandy and Taber 1974). Damage from deer–vehicle collisions also can be substantial (Romin and Bissonette 1996).

Four species of ungulates, all members of the family Cervidae, commonly occur in coniferous forests in western North America: elk (*Cervus elaphus*), moose (*Alces alces*), mule and black-tailed deer (*Odocoileus*

hemionus), and white-tailed deer (*Odocoileus virginianus*). North American elk, or wapiti, are conspecific with European red deer, and are widespread throughout western North America. Rocky Mountain elk (*C. elaphus nelsoni*) occur in forests from southern Arizona and New Mexico northward to British Columbia and Alberta. Roosevelt elk (*C. elaphus roosevelti*) are associated with coastal forests of redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga douglasii*), and Sitka spruce (*Picea sitchensis*) in northern California, Oregon, Washington, and British Columbia, and have been translocated to Afognak, Raspberry, and Kodiak Islands in Alaska (Bryant and Maser 1982, Wisdom and Cook 2000).

Moose, conspecific with European elk, range from Utah and Colorado to Alaska. Shira's moose (*A. alces shirasi*) occurs in Utah, Colorado, Wyoming, Idaho, Montana, Washington, and southern British Columbia (Franzmann 2000). Northwestern moose (*A. alces andersoni*) occur primarily in British Columbia, Alberta, and other Canadian provinces. Alaskan moose (*A. alces gigas*) occur in boreal forests throughout Alaska and in the western Yukon Territory (Franzmann 2000).

Mule deer of various subspecies are nearly ubiquitous in western North America and often are associated with forested habitats (Kie and Czech 2000). Columbian black-tailed deer (*O. hemionus columbianus*) occur in coastal forests in northern California, Oregon, Washington, and southern British Columbia. This subspecies also has been transplanted to the island of Kauai in Hawaii. Sitka black-tailed deer (*O. hemionus sitkensis*) occur in spruce forests in northern British Columbia and southeastern Alaska (Kie and Czech 2000).

White-tailed deer inhabit coniferous forests in the northwestern United States and western Canada (Baker 1984). Occurrence of this species overlaps the range of mule deer in the west, and they are usually associated with riparian habitats with abundant woody vegetation (Baker 1984). Coues white-tailed deer (*O. virginianus couesi*) occur in ponderosa pine and pinyon-juniper forests in southern Arizona and southwestern New Mexico. Small populations of Columbian white-tailed deer (*O. virginianus leucurus*) are found in western Oregon and Washington.

In addition to these ungulate species commonly found in coniferous forests, populations of two other species can occur locally in the west. Woodland caribou (*Rangifer tarandus caribou*) occur in portions of northeastern Washington, northern Idaho, northwestern Montana, eastern British Columbia, and western Alberta (Miller 1982). The wood bison (*Bison bison athabasca*) occurs in the Rocky Mountain States, Alberta, and other
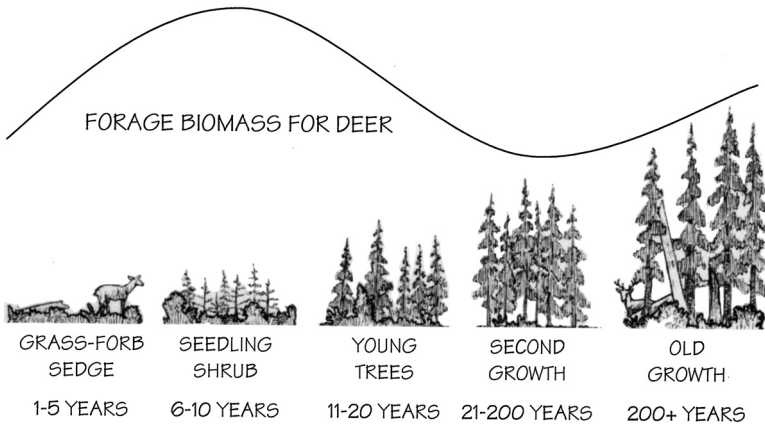
Fig. 9.1. Generalized pattern of deer forage supplies during secondary succession in coniferous forest habitat. Duration of stages represents averages for western hemlock-Sitka spruce forests of the northern Pacific coast (after Wallmo and Schoen 1981, Kie and Czech 2000).

Canadian provinces. Its status as a distinct subspecies, however, is in question (Shaw and Meagher 2000).

Habitat relationships

Ungulates and habitat seral stages

Many ungulates in western North America thrive in forests at early successional stages. For example, wildfire, prescribed burning, and clear-cut logging have resulted in increased numbers of mule and black-tailed deer in many areas (Wallmo 1978). In spruce forests of the Pacific northwest, forage for black-tailed deer is most abundant between about five and ten years following disturbance such as logging (Fig. 9.1). As forest stands start to mature and trees shade out desirable forage species, habitat value for deer declines (Wallmo and Schoen 1981, Kie and Czech 2000). In old-growth forests, openings created when large trees fall allow sunlight to reach the forest floor and forage plants for deer to become re-established (Fig. 9.1).

In coniferous forests where snow accumulation is heavy, however, such as in northern British Columbia and southeastern Alaska, new forage created by disturbance is largely unavailable to deer during winter (Wallmo and Schoen 1981). In such situations, resident deer are dependent on old-growth forests where canopy cover of trees is sufficiently dense to intercept snow and provide access to understory forage supplies, as well as a source of arboreal lichens falling from the canopy. In these areas, black-tailed

deer are climax-associated or old-forest species rather than successional species (Hanley 1984).

Moose also exhibit variable response to changes in seral stages. Large numbers of yearling moose responded to recently burned areas in Minnesota (Peek 1974), but not in interior Alaska (Gasaway et al. 1989). A lower population density of moose in Alaska prior to burning may have precluded a similar response. Areas in Alaska without a substantial understory of willow (*Salix* spp.) may not be attractive to moose following fire (Weixelman et al. 1998). Finally, woodland caribou often use climax-stage forested habitats (Apps et al. 2001). In conclusion, broad species-wide generalizations about the relationship between seral stages of habitats and ungulates are often only weakly supportable if at all.

Ungulates and food

Ruminants often are characterized by relations among body size, digestive morphology and physiology, and types of forage consumed (Fig. 9.2).
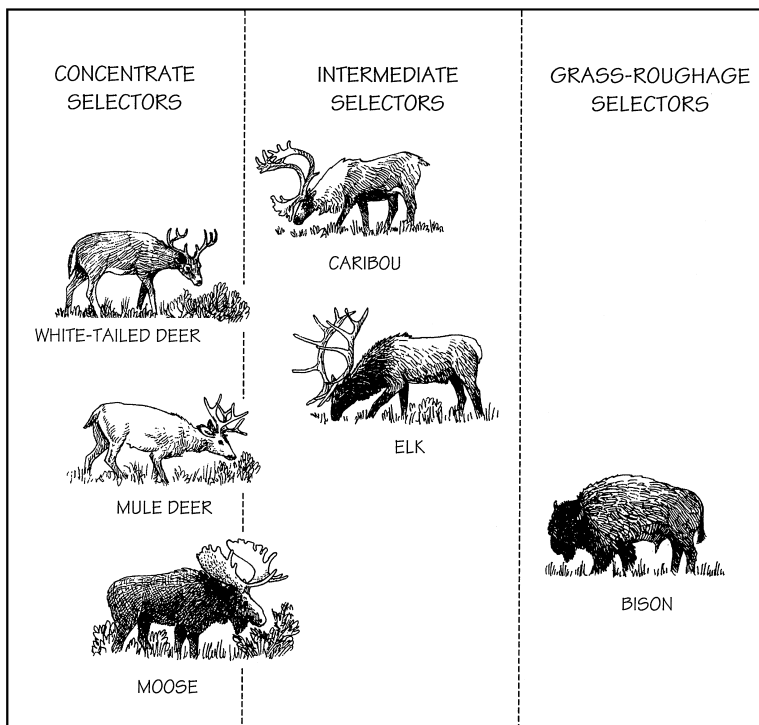

Fig. 9.2. Morphophysiological feeding types among ruminant ungulates from western coniferous forests (adapted from Hoffman 1985).

Typically, larger-bodied ruminants have proportionally larger rumens, lower feeding frequencies, longer forage retention times, and can subsist on forages of lower quality than can smaller-bodied ruminants (Hoffman 1985, Putman 1988). In addition, they have lower metabolic rates than smaller ruminants (Kleiber 1961). As such, these bulk-feeders have the luxury of ingesting fairly coarse forages of low digestibility such as dried grasses, and slowing down the rate of food passage to allow microbial digestion to break down the cell-wall constituents. Small-bodied ruminants such as mule and black-tailed deer must feed on forages in which the nutrients are more concentrated and more digestible. Even large-bodied ruminants such as moose that are adapted to feeding on highly concentrated forages exhibit digestive morphology similar to their smaller-bodied relatives (Hoffman 1985, Putman 1988). Such differences have strong allometric underpinnings (Illius and Gordon 1999).

Mule and black-tailed deer traditionally have been thought of as browsers, particularly during winter, relying primarily on twigs and other vegetative parts of woody plants. Their requirement for forages with concentrated nutrients precludes them from making heavy use of forages of low digestibility such as dried grasses, and may at times result in their preferential use of woody plant material. Nonetheless, the concept of deer as browsers by choice is perhaps one of the oldest and most persistent myths in deer ecology and management (Gill 1976). Given access to seasonally abundant, nutritious, herbaceous plants of high digestibility, deer will tend to select those species in preference to browse species of lower digestibility (Kie and Czech 2000).

Diets of Sitka black-tailed deer on Admirality Island, Alaska, ranged from 57% to 79% non-browse items such as forbs, ferns, grasses, sedges (*Carex nudata*), lichens, algae, and mosses depending on season, although during a winter with deep snow browse consumption peaked at 87% (Hanley et al. 1989). In summer, although shrubs were available to deer, concentrations of digestion-inhibiting compounds were sufficiently high to discourage consumption (Hanley et al. 1989). Diets of Columbian black-tailed deer on oak woodland-annual grass ranges in northern California included as much as 62% newly germinated annual grasses during winter when those species were green and highly digestible (Taber and Dasmann 1958). Other seasonally important forages for mule and black-tailed deer include acorns (Beale and Darby 1991), mistletoe (Urness 1969), lichens (Hanley et al. 1989), mushrooms (Beale and Darby 1991), and succulents (Krausman et al. 1997). Many of those forages are often under-represented

in diet studies because of their high digestibility or deficiencies in sampling and analytical methodology (Beale and Darby 1991).

Ungulates and cover

Cover is a loosely defined term, but, in its broadest sense, refers to vegetative, topographic, or other types of environmental structure that enhances reproduction or survival of animals (Bailey 1984). Functions of cover can include concealment and escape from predators, refuge from human disturbances, and shelter from thermal extremes (Patton 1992). Cover also may influence the availability of forage through subtle behavioral mechanisms associated with avoiding predators (Kie 1999, Kie and Bowyer 1999). Of particular interest in forested habitats, however, is the role overstory tree canopies play in intercepting snowfall, and ameliorating thermal extremes during winter.

Even small-bodied ungulates such as mule deer exist across a wide range of temperature gradients averaging from below −15° C during winter in the Rocky Mountains to above 30° C in the summer in the southern end of its range (Wallmo 1981). Thermoregulation is accomplished by shivering, changing posture, erecting hair, and by making use of environmental temperature variations afforded by different habitats and topographic features (Mackie et al. 1982). Moreover, cervids are adapted to cold winter temperatures because of the thickness of their winter coats.

The lower boundary of the thermal neutral zone for black-tailed deer in winter pelage was measured at −10° C (Parker 1988). Below that temperature, deer have to expend energy, for example by shivering, to maintain a constant body temperature. Larger-bodied ungulates such as elk and moose are adapted to even colder winter temperatures and more northern environments. The lower boundary of the thermal neutral zone for moose lies somewhere below −30° C (Renecker and Hudson 1986).

The management of forested habitats to provide overstory tree canopy as thermal cover is a long-established paradigm in the northwestern U.S. (Black et al. 1976). Recent research, however, reported that elk in northeastern Oregon lost less body mass during winter when tree canopies were removed (Cook et al. 1998). The ability of elk to absorb solar radiation in opened stands of trees on sunny days may have reduced the need for metabolic thermoregulation and the accompanying expenditure of energy.

Canopy cover in forested habitats does serve other important roles in some instances, however. Previously discussed is the value of old-growth

forests in intercepting snow cover and providing access to forage for black-tailed deer during winter in southeast Alaska (Hanley 1984). In addition, snow depth has a great influence on the movements of mule and black-tailed deer (Mackie et al. 1982). Snow depths of 25–30 cm may impede movements of mule deer in Colorado, and depths >50 cm may completely prevent their use of areas (Loveless 1967). During the heaviest snow accumulations in the Bridger Mountains, Montana, mule deer were restricted to only 20% to 50% of their winter range (Mackie et al. 1982). Forested habitats, therefore, may provide refugia for ungulates during periods of heavy snowfall and extremely low temperatures.

Finally, cover may be very important in forested habitats as concealment from predators and human disturbances. Elk in northeastern Oregon will concentrate in areas away from heavily traveled roads (Rowland et al. 2000); but, in contrast, mule deer in this region attempt to distance themselves from elk and move closer to roads with heavy traffic, where they use vegetative and topographic cover (Wisdom 1998). In such instances, the vertical structure of cover in forested habitats is more important than the amount of overstory canopy.

Ungulates and water

Water usually occurs in sufficient abundance in western coniferous forests to have little effect on the distribution and abundance of ungulates. Furthermore, ungulates in arid and semi-arid environments are adapted to a scarcity of free water. For example, mule deer in Arizona typically visited sources of water once a day and consumed five to six liters of water per visit during the hot summer months, while visitation rates and the amount of water consumed per visit declined during cooler seasons (Hazam and Krausman 1988). Mule deer also obtain water from succulent plant material, dew on the surface of plants, and from metabolic processes. Feeding at night in hot, arid environments not only provides relief from thermal stress but may also be timed to take advantage of diel cycles in plant water content (Taylor 1969). Whether mule deer require free surface water has been debated (Rosenstock et al. 1999, Severson and Medina 1983). Nonetheless, when access to free water is severely restricted in penned white-tailed deer, they reduce their consumption of forage (Lautier et al. 1988). Therefore, although deer in the wild may exist for some periods of time without access to standing water, this poses marginal survival conditions (Severson and Medina 1983).

The abundance and spacing of water sources influence the distribution of mule deer in arid environments. In Arizona and New Mexico, mule deer are usually found within 2.4 km of free water (Wood et al. 1970). Mule deer in northern California averaged 1.19–1.55 km away from water sources, with a mean greatest distance of 2.46 km (Boroski and Mossman 1996). Female mule deer drink more water than males during late summer (Hazam and Krausman 1988). Females are often found closer to sources of water than males, presumably because of demands of lactation (Bowyer 1984, Boroski and Mossman 1996). In many instances, however, females remain close to water sources year-round (Fox and Krausman 1994).

Ungulates and landscapes

Many ungulates are considered well-adapted to habitat edges (Leopold 1933, Clark and Gilbert 1982, Hanley 1983, Kremsater and Bunnell 1992). For example, in California where food and cover occurred in small patches, mule deer did not have to travel far to meet their daily requirements and home ranges were correspondingly small (Leopold et al. 1951). Life-history characteristics in deer, such as the size of the home range, may be related to landscape pattern in more complex ways than simply as a function of the amount of habitat edge.

Size of home ranges in mule and black-tailed deer is correlated with heterogeneity of habitats at a broad spatial scale in California (Kie et al. 2002). The amount of habitat edge measured within 2000 m of the center of the home ranges for 80 female deer (an area larger than most of those home ranges) accounted for 27% of the variability in the size of the home range. Large amounts of edge resulted in small home-range sizes (Fig. 9.3). Spatial heterogeneity, however, measured at the same spatial scale (as indicated by the abundance of different habitat types, the distance between habitat patches of similar type, the shape of the patches, and the amount of structural contrast between patches) accounted for 57% of the variation in home-range size (Kie et al. 2002).

When spatial heterogeneity was measured at smaller scales more closely corresponding to the size of the home ranges, less of the variation in home-range size could be explained (Fig. 9.3). This result has important implications in resource selection studies (Kie et al. 2002). If ungulates perceive potential habitats at scales greater than those they eventually choose as a home range, analysis of habitat selection within the home range may yield biased results. The home range already includes landscape attributes that an individual has selected, whereas other avoided
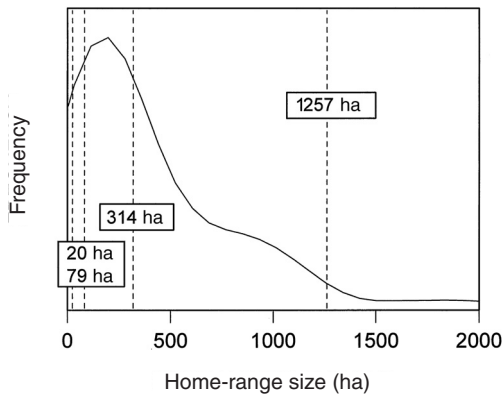
Fig. 9.3. Smoothed frequency distribution of home-range sizes for 80 female mule deer in California (after Kie et al. 2002). Landscape metrics representing spatial heterogeneity were measured at four scales: 20, 79, 314, and 1257 ha (within 250, 500, 1000, and 2000 m from the center of each home range). Home-range size was most closely correlated with landscape metrics measured at the largest spatial scale (1257 ha) even though the majority of the home ranges were smaller in size.

features lie outside the home range. Basing habitat availability on habitats contained only within the home range is circular logic because some degree of selection already has occurred.

Sexual segregation in ungulates

The concept that the sexes use space differently is not new. Charles Darwin (1871), citing previous work by C. Boner, hypothesized the following about red deer (*Cervus elaphus*): "Whilst the horns are covered in velvet, which lasts with red deer for about twelve weeks, they are extremely sensitive to a blow; so that in Germany the stags at this time somewhat change their habits, and avoiding dense forests, frequent young woods and low thickets." Main et al. (1996) summarized previous literature and classified concepts about sexual segregation into three groups: body-size, reproductive-strategy, and social-factor hypotheses.

One body-size hypothesis posits that smaller-bodied females more efficiently use habitats with closely cropped forages, thereby excluding larger males through inter-sexual competition. Sexual segregation between male and female red deer on the island of Rhum in Scotland increased when the population density of females increased, lending support to this hypothesis (Clutton-Brock et al. 1987a). Recent manipulative

experiments, however, have cast doubt on that model (Conradt et al. 1999). A newer body-size hypothesis has been proposed whereby male deer may perform better on areas with lower-quality forage than would be ideal for females because of larger rumen sizes (Barboza and Bowyer 2000, 2001). This allows males to increase their intake of less digestible forages and slow passage rates to extract more nutrients. Faced with highly digestible forages, males would actually do less well faced with the possibility of bloat. Conversely, lactating females have the ability to increase post-ruminal components of the digestive system necessary to extract the nutrients from a high-quality diet required for lactation (Fig. 9.4; Barboza and Bowyer 2000). This body-size hypothesis may explain those instances of sexual segregation where males are found in areas characterized by forage that would appear to be less than optimum for females.

The reproductive-strategy hypothesis suggests that the need to bear and raise young poses constraints on habitat use by adult females, thereby limiting their use of space. For example, adult female white-tailed deer in Texas occurred more often in dense chaparral habitats when they had young than did adult males. Males did not have the same anti-predator constraints and were free to use more open savannah habitats where preferred forbs were abundant (Kie and Bowyer 1999). This hypothesis has been suggested for a variety of other ungulates including moose (Miquelle et al. 1992) and bighorn sheep (*Ovis canadensis*; Bleich et al. 1997).

Social factors also have been advanced as mechanisms to explain sexual segregation, whereby behavioral differences might lead to separation of the sexes. Main et al. (1996) rejected many of these hypotheses, but recently several authors have reinvoked such hypotheses to explain sexual segregation (Conradt 1998*a*, 1998*b*, Mysterud 2000, Ruckstuhl and Neuhaus 2000). These studies posit behavioral mechanisms such as activity time-budgets that may be associated with segregation, but do not demonstrate actual spatial separation at specific spatial and temporal scales (Bowyer et al. 1996).

Managing forested habitats for ungulates
Habitat seral-stage matters
Some species of forest-dwelling ungulates such as woodland caribou require mid- to late-seral habitats. Other species, such as mule deer, can take advantage of early-seral communities as foraging habitats but black-tailed deer in southeastern Alaska may require climax forests in some instances (Hanley 1984). In addition, even though some ungulates can take
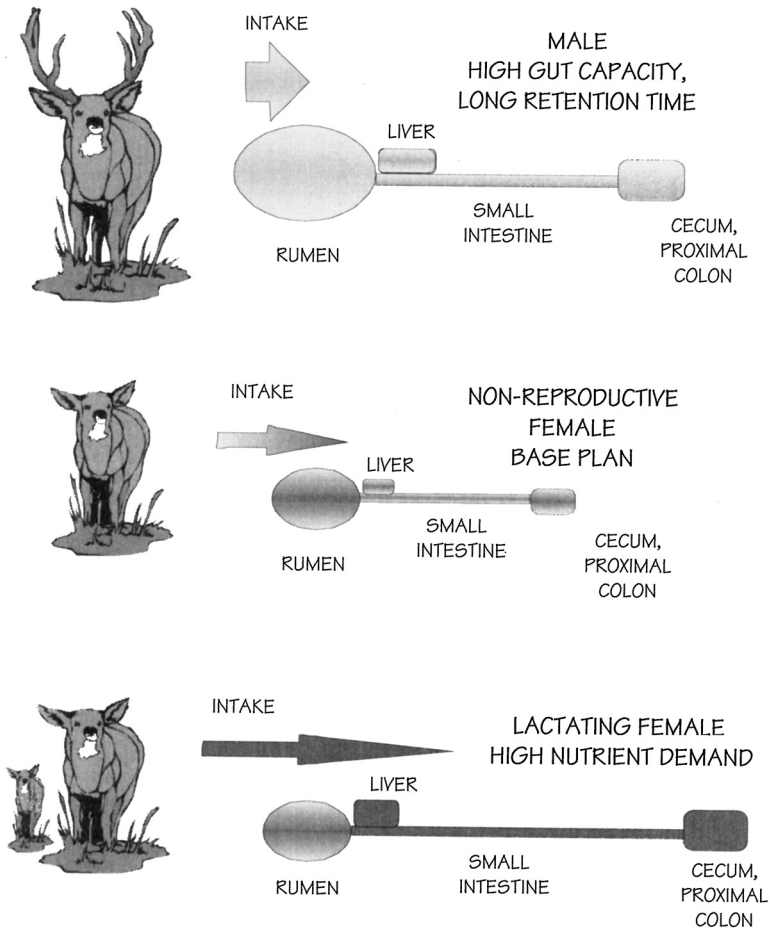
Fig. 9.4. Model of intake and digestive function in non-reproducing females compared with large males and lactating females, which provides a nutritional basis for sexual segregation in polygynous, dimorphic cervids. Width of arrows reflects amount of food intake, length of arrows indicates rate of digesta passage, and shading indicates density of nutrients in food. Diagrams of the digestive tract are shaded to reflect potential changes in fibrosity of food for males, and increases in post-ruminal size (especially the length of the small intestine) and function of lactating females (Barboza and Bowyer 2000). Barboza and Bowyer (2000) provide a complete description of the model and its components.

advantage of early-successional stage habitats following logging, forest practices that speed up and truncate succession (planting new trees, use of herbicides) may severely limit the time period during which those habitats are available (Leopold 1978). Furthermore, where forests have been

harvested heavily in the past, habitats at early-successional stages may now be maturing and losing value, with little opportunities for additional logging of harvestable age classes in the coming decades (Jenkins and Starkey 1996).

Large forest clear-cuts likely will not be a silvicultural option on public lands in the future because of adverse public opinion. In addition, prescribed fire at a large enough spatial scale to have a significant effect on deer populations is expensive and may see only limited use. Moreover, let-burn policies are hampered by social and political factors (Kie and Czech 2000). In reality, the extent of early- and mid-successional vegetation seen in the early twentieth century as a result of wildfire, logging, and livestock grazing is unlikely to re-occur in the foreseeable future (Kie and Czech 2000). Consequently, wildlife managers may need to develop new approaches for maximizing habitat benefits for forest-dwelling ungulates in mid- and late-successional habitats (Kie and Czech 2000).

The value of browse as forage may be limited

Concentrate feeders such as mule and black-tailed deer may benefit from abundant new growth on palatable woody plant species. Conversely, they often rely heavily on forbs, new growth of grasses, and a variety of other forages that have high concentrations of nutrients. These forages become even more important in mid- and late-successional stage habitats.

Cover is important but reasons underlying its need may differ

Ungulates are well adapted to winter weather in most instances. Overstory canopy cover of trees, thought to provide thermal cover for elk, is unnecessary for that purpose in many instances (Cook et al. 1998). Hiding and concealment cover may be critical, however, and vertical structure may be more important than canopy cover in this respect. Canopy cover of trees may be important in intercepting snow and providing access to forages during winter in some instances (Hanley 1984).

Water sources may affect the distribution of ungulates

Ungulates can exist in some arid and semi-arid habitats with little or no free water. The abundance and spacing of water sources, however, will influence the distribution of ungulates (Boroski and Mossman 1996).

Landscape structure matters

Diverse mixes of plant communities are best. In general, landscapes rich with different vegetation types, irregularly shaped patches, and a

minimum of structural contrast between patches are beneficial for deer (Kie et al. 2002), and maybe for other forest-dwelling ungulates as well.

    Male and female ungulates use space differently
The need to bear and raise offspring may often prevent females from making use of newly available supplies of forage (Bowyer et al. 2001). For example, the crushing of willows in interior Alaska resulted in a much greater response by adult male moose than by adult females (Bowyer et al. 2001). In some instances, it may be appropriate to treat males and females as different species for purposes of habitat management (Kie and Bowyer 1999).

    Direct manipulation of habitats is expensive and often yields limited
    benefits for short periods
Seeding, fertilization, and prescribed burning have all been used as tools to improve habitat for ungulates. Such activities are expensive, difficult to accomplish on a scale large enough to substantially increase deer numbers, and may conflict with other land-management goals (Kie and Czech 2000).

    Co-ordination of management objectives for ungulates with other
    resource uses can provide great benefits
In most instances, efforts directed at co-ordinating the management of habitats for ungulates with other land uses have far greater potential benefit than direct improvement of habitat. Other resource uses that can be modified to incorporate habitat management goals for ungulates include timber harvesting, revegetation following wildfire, livestock grazing, development of home sites, and disturbances associated with roads, off-road vehicles, and snowmobiles (Kie and Czech 2000).

Population dynamics

Factors underpinning population dynamics of ungulates have been a topic of considerable debate (Fowler 1981, McCullough 1990, Mackie et al. 1990). Nonetheless, few life-history characteristics of ungulates are free from density-dependent effects (McCullough 1999), and managing either the harvest of, or habitat for, ungulates requires an understanding of density-dependent mechanisms. Ungulates have small litter sizes but long life spans in comparison with small-bodied mammals. Substantial maternal investment in young (especially during the neonate's first year of life) is ubiquitous among ungulates (Clutton-Brock 1991, Rachlow and

Bowyer 1994). Consequently, density dependence is an expected outcome from these and other life-history characteristics of ungulates (Stearns 1977, Stubbs 1977, Fowler 1981, Goodman 1981). Density dependence plays a crucial role in understanding the dynamics of animal populations and is embodied in most models of population growth among ungulates, yet controversy still surrounds this topic.

Detecting and interpreting density dependence

Detecting density dependence is neither simple nor straightforward (Slade 1977, Gaston and Lawton 1987, Pollard et al. 1987). Nevertheless, numerous studies of ungulates have demonstrated the fundamental role that process plays in the dynamics and regulation of populations (Klein 1968, Kie and White, 1985, Skogland 1985, Clutton-Brock et al. 1987b, Boyce 1989, Bartmann et al. 1992, Sand 1996, Singer et al. 1997). Notably, those studies supporting density-dependent mechanisms typically were conducted under circumstances where confounding variables such as predation and severe weather were unimportant or controlled (McCullough 1979, Bowyer et al. 1999). Likewise, research substantiating the importance of density-dependent mechanisms in ungulate populations typically has come from long-term studies in which populations varied markedly in size with respect to carrying capacity (K) of the environment, and appropriate vital rates for populations were collected (McCullough 1979, 1990). Herein we define K to mean the number of animals at or near equilibrium with their food supply. Although many definitions of K exist (McCullough 1979), we constrain our use to the traditional meaning of this term.

What factors might lead to confusion over whether density dependence was affecting the dynamics of an ungulate population? Some obvious problems include examining a population over too small a range of densities (often over too short a time span) to bring about changes in fecundity, recruitment, or survivorship. Also, attempting to compare population density among years when the ability of the environment to support those animals (K) was fluctuating substantially will lead to uncertainty about whether density dependence was operating. We will return to the difficulty of assessing K later. We do not believe that all criticisms of density dependence can be countered by those two potentialities. We note, however, that empirical approaches have some limitations. Careful examination and interpretation of data presented to refute a well-established ecological principle, such as density dependence, are required.

Table 9.1. *Population size, carrying capacity (K), and overwinter mortality in five hypothetical populations of deer inhabiting ranges of varying quality*

Population	K (number of deer)	Population size	Number dying	Overwinter mortality (%)
A	307	321	30	9.4
B	512	507	50	10.0
C	114	124	12	9.7
D	357	362	36	10.0
E	200	214	22	10.3

Note that all populations are at or near K.

We argue that some approaches for assessing density dependence are flawed. Comparing densities among populations to evaluate parameters such as recruitment or mortality is of questionable value (Weixelman et al. 1998, Bowyer et al. 1999). For example, if five populations of deer occurred in habitats that exhibited substantially different carrying capacities (K), and all five populations were at or near K, similar population characteristics such as recruitment or survival would be expected for those populations (Table 9.1). A graph of recruitment rate against population density, however, would lead to the conclusion that density dependence was not operating (a random pattern or a linear fit with a slope near zero), when that mechanism was regulating all five populations (Fig. 9.5). Clearly, habitat quality can confound comparisons of density dependence among populations of ungulates.

Similarly, evaluating density dependence from historical changes in population size can be misleading. Environments and subsequent responses of animals can be quite variable over many years. Assuming that current populations can achieve levels attained long ago involves assuming a similar ability of the habitat to support ungulates (and that the initial population estimates were reliable), which may be incorrect. Moreover, population density can be a misleading indicator of habitat quality (Van Horne 1983). The foregoing examples simply illustrated how data related to density dependence might be viewed improperly and misinterpreted. We suggest that the problem is far more pernicious, and stems from how the basic biology of ungulates and their interactions with their environment are perceived.

We caution that the inverse relation between recruitment rate (young/adult female) and population size need not be linear to infer
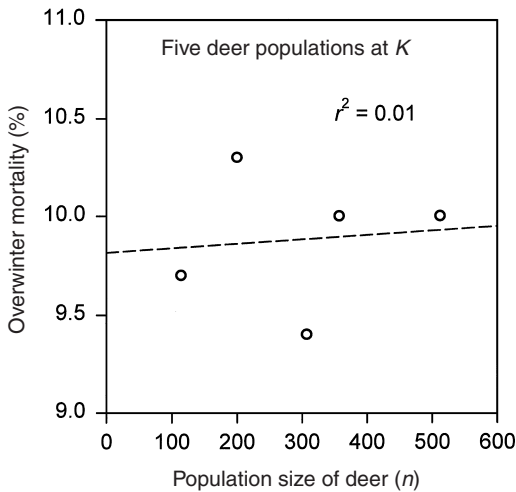
Fig. 9.5. Relationship between overwinter mortality and population size for five hypothetical populations of deer inhabiting ranges of varying quality; all populations were at or near carrying capacity (K). Population size or density should not be used to infer density dependence or independence among different populations. The standard interpretation of this relationship is that the populations are exhibiting density independence (no correlation between population size and overwinter mortality), when all are being regulated by habitat quality (e.g., density dependence) – data from Table 9.1.

density dependence; a non-linear pattern for ungulates may be common, particularly at population densities between maximum sustained yield (MSY) and K (Fowler 1981, Kie and White 1985, McCullough 1999, Person et al. 2001). Moreover, where the difference between MSY and K is small relative to the total size of the population, density dependence may be especially difficult to detect because the onset of obvious density-dependent changes is rapid, and restricted to a narrow range of densities near K.

Another potentially confusing outcome from density dependence relates to the rate of recruitment of young into the population, and the effect of that process on the age structure of the population. A high rate of recruitment (young/adult female) is not necessarily indicative of a productive, increasing population, and a low recruitment rate may not be reflective of a declining population (McCullough 1979). The interaction between population size and recruitment rate (young/adult female × number of adult females) determines the number of young successfully added to the population and, consequently, the allowable harvest (Fig. 9.6). Thus, a high recruitment rate but low population size, and a low
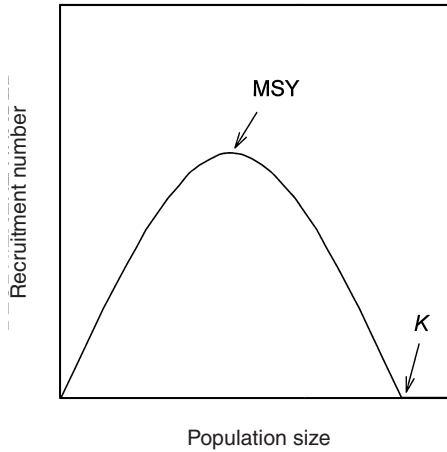
Fig. 9.6. Parabolic relationship between recruitment number (i.e., number of young successfully added to the population) and population size of adult or other reproductive females, showing populations sizes that yield maximum sustained yield (MSY) and carrying capacity (*K*; adapted from McCullough 1979). The parabola need not be symmetrical to infer density dependence.

recruitment rate but a high population size both yield a low number of recruits and, concomitantly, little population change. A population at moderate size and with a modest recruitment rate, however, would produce the greatest number of recruits and maximal amount of population increase (the relation between recruitment number and population size is parabolic, Fig. 9.6).

Further, a population exhibiting a high rate of recruitment might be overharvested and declining, whereas one with a low recruitment rate might be relatively stable near *K*. Likewise, a population with a wide base to an age-class pyramid (numerous recruits and fewer adults, thought to indicate a stationary population) might be either overharvested and declining markedly or increasing rapidly. A population with a small base to a similar age pyramid (few recruits and more adults, thought to identify a declining population) may represent a relatively stationary population at or near *K* (McCullough 1979). Caughley (1974) warned long ago that the age structure of a population should not be used to infer changes in population size without an independent estimate of size for that population. He also wondered why age structure would be useful if an independent assessment of population size was available. We note that the failure to comprehend these inherent relationships among population parameters

can lead to misinterpretations as to whether density dependence is operating.

The foregoing descriptions of relations among population size, recruitment rate and number, age structure, and population change may seem simplistic and unnecessary given that those theoretical predictions have been understood for nearly a century, and substantial empirical support exists for them. Unaccountably, this approach for evaluating the population ecology of ungulates is not as widely accepted or practised by managers as might be expected. For instance, some authors have suggested that northern populations of ungulates may not exhibit density dependence (Bergerud et al. 1983, Gasaway et al. 1983, Bergerud 1992, Boertje et al. 1996). Population models that do not include density dependence, however, have ignored much of the biology of ungulates. This approach may risk either a theoretical error or a management catastrophe. Why should this be the case, and what has underpinned this controversy?

Population density, severe weather, management options, and controversies

One problem in understanding population dynamics of ungulates is the potential for an interaction between animal density and severe weather (Bowyer et al. 1986, Sæther 1997, Bowyer et al. 2000). We argue that even where populations of ungulates are reduced to low numbers because of severe weather, there will be effects from density-dependent mechanisms. Individuals in populations near K tend to be in poor physical condition because of intense intra-specific competition (McCullough 1979). Such individuals typically are on a low nutritional plane and often exhibit low rates of reproduction and survivorship, and exacerbated wear on teeth (Skogland 1984, Bowyer et al. 1999). Populations at high densities with individuals in poor physical condition also may be more susceptible to diseases and parasites than those at lower densities and on higher nutritional planes (Eve and Kellogg 1977, Sams et al. 1996). Conversely, animals in populations that are at or below MSY characteristically are in good physical condition resulting from limited intra-specific competition and display high rates of productivity and survival (Fig. 9.7).

Animals in poor physical condition are more likely to be helped or hindered by a variable climate than are animals on a high nutritional plane, which are better buffered against climatic extremes (Fig. 9.8, Bowyer et al. 2000). Consequently, correlations between climatic variables and measures of physical condition, fecundity, or survivorship of animals are
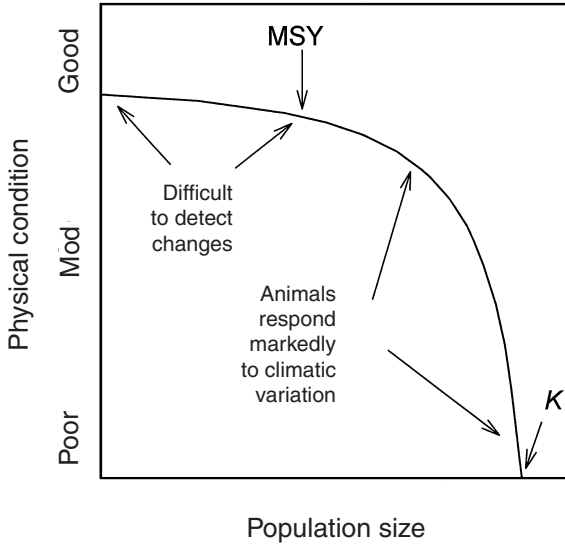
Fig. 9.7. Relationship between physical condition of individuals and population size. Note that changes in physical condition and subsequent effects on reproduction and survivorship may be difficult to detect below maximum sustained yield (MSY), whereas changes in population size between MSY and carrying capacity (K) can be marked.
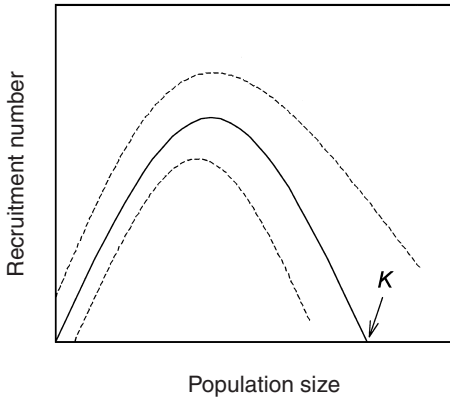

Fig. 9.8. Relationship between increasing variation in recruitment of young and population size of adult females (adapted from McCullough 1979, Bowyer et al. 2000). Variation in recruitment increases from maximum sustained yield (peak of parabola) and carrying capacity (K) because a variable environment has a disproportional ability to help or hinder ungulates in poor physical condition (Fig. 9.7).

expected to be stronger for populations at or near K compared with animals in better physical condition from populations well below K (Figs. 9.7 and 9.8). Hence, a population at K could exhibit high correlations between population parameters and climatic variables. Such an outcome might be interpreted as density-independent limitation when density-related effects are regulating that population. Cause and effect cannot be inferred from correlation (Bowyer et al. 1988). Likewise, teasing apart effects of density from climate in evaluating population parameters may be problematic. Partial correlations for weather-related variables often are robust because they possess a greater range of values than does population density, which often fluctuates about some long-term K.

How then can density-dependent and density-independent effects be discriminated? Assuming a variable climate, a reduction in variance of climate-related effects on population parameters with a substantial lowering of population density with respect to K would be evidence of density dependence (Fig. 9.9); a high and equal variance across a wide range of population densities would be support for density independence. This latter outcome means that climatic effects are so severe they have overwhelmed the ability even of animals in good physical condition to
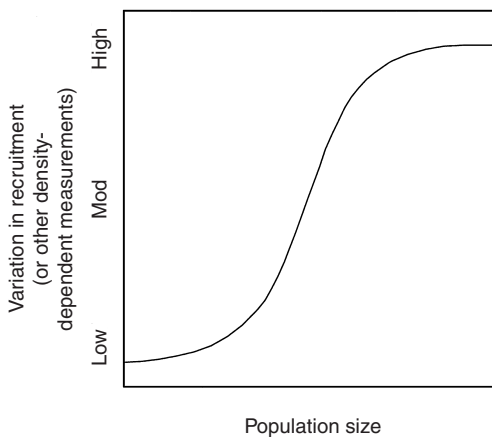

Fig. 9.9. Predicted variation in recruitment or other density-dependent (DD) measurements with increasing population size under conditions of density dependence. The increased variability is caused by interactions between changing physical condition of individuals with increasing population size (Figs. 9.8 and 9.9) and variable environmental conditions. A population limited by density-independent factors such as severe weather should exhibit uniformly high variability across a wide range of population sizes.

compensate by using body reserves. We caution, however, that animals on a sufficiently high nutritional plane may not respond as expected to severe winter conditions with reduced reproduction (Bowyer et al. 1998), or may rebound quickly from overwinter mortality. Ungulates possess an impressive array of adaptation for coping with winter (Telfer and Kelsall 1984).

Long-term data sets necessary to examine factors underpinning population regulation are seldom available (McCullough 1990). Yet, understanding causes of mortality and recruitment are essential for managing populations of ungulates. For instance, low productivity could be dealt with effectively by increasing harvest if a population were experiencing strong density dependence (assuming that was a primary management objective), but such a solution could send populations limited by severe weather or predation spiraling toward a low-density equilibrium or even extirpation. We further caution that too heavy a harvest, even where strong density dependence occurred, could lower recruitment number and population size, driving the population below MSY. This outcome could potentially cause managers to conclude that there was not a density-dependent response; for example, that population size and number of recruits declined rather than increased with increasing harvest (Bowyer et al. 1999). Likewise, too light a harvest relative to K, or harvesting a population that had overshot K, would lead to a similar conclusion – no density-dependent response when that phenomenon was regulating the population. Too often management agencies reduce harvest to compensate for low recruitment without knowing where the population is with respect to K. Where such a population is approaching K, that management results in a further depression in recruitment in the following year as the population nears K (Fig. 9.6). Clearly, change in population size is a necessary metric for assessing density dependence, but should not be used as the sole criterion.

Other pitfalls exist in managing populations of ungulates. If a population exhibits density independence and is reduced by climatic extremes to some low number from which it typically recovers under more hospitable conditions, then that surplus constitutes the allowable harvest (assuming compensatory mortality) – the surplus often determines the harvest under conditions of density independence (Leopold 1933). Conversely, under density dependence, the harvest determines the surplus. For example, recruitment number would increase as the population was harvested back from K toward MSY (Fig. 9.6). Moreover, the sex ratio of the harvest

would be relatively unimportant in the dynamics of a population experiencing strong density independence. This occurs because severe density-independent events are thought to kill without regard to sex, age, or physical condition (animals that constituted the surplus would die from causes other than hunting anyway). Under density-dependent circumstances, a far different situation occurs.

Recruitment rate of young for populations of ungulates exhibiting strong density dependence is related primarily to the density of adult females rather than adult males (McCullough 1979, 1984, Bowyer et al. 1999). That outcome occurs because the genders of polygynous ungulates sexually segregate for much of the year (Bowyer 1984, Bleich et al. 1997, Kie and Bowyer 1999, Barboza and Bowyer 2000, Bowyer et al. 2001). Hence, females compete more intensely with other females and young for resources than do adult males because of the spatial separation of the sexes outside rut. That difference in life-history characteristics between the sexes has profound consequences for management of ungulates, especially the sex ratio of the harvest. Populations at or near K will not respond in a density-dependent fashion from a harvest of only males (McCullough 1979, 1984). The population cannot be reduced from K toward MSY with a male-only harvest, and males become a progressively smaller portion of the total population from such a harvest regime (McCullough 1984). Consequently, obtaining the expected increase in recruitment number as a population is reduced from K toward MSY requires a harvest of adult females (McCullough 2001). At MSY, a wider variety of sex ratios can be harvested than at very low or high population densities (McCullough 1979). Harvesting females at densities below a population size that will yield MSY results in a lower recruitment number. Males should dominate in such harvests until the population exceeds the size that will produce the maximal number of recruits (MSY, Fig. 9.6). Thus, the sex ratio of the harvest for populations exhibiting density dependence should vary depending upon where the population is with respect to MSY – a daunting concept to explain to some hunters. As a further confounding factor, management agencies often judge the success of a hunting season by the total harvest (where harvest is the primary management objective). In contrast, hunters may rely more on the number of animals seen in the field or the effort necessary to kill an animal as a measure of satisfaction (Gross 1972, Lautenschlager and Bowyer 1985). For density-dependent populations, those outcomes are inversely related from K to MSY – another potential source of contention in managing ungulates.

Table 9.2. *Life-history characteristics of ungulates that reflect the relative differences in a population at maximum sustained yield* (MSY) *and at carrying capacity* (K)

Life-history characteristic	Population size at or below MSY	Population size at or near *K*
Physical condition of adult females	better	poorer
Pregnancy rate of adult females	higher	lower
Pause in annual production by adult females	less likely	more likely
Yearlings pregnant[a]	usually	seldom
Corpora lutea counts of adult females[a]	higher	lower
Litter size[a]	higher	lower
Age at first reproduction for females	younger	older
Weight of neonates	heavier	lighter
Survivorship of young[b]	higher	lower
Age at extensive tooth wear	older	younger

[a] Some species of ungulates may show limited variability in particular characteristics.
[b] In the absence of efficient predators.

Judging the relation of population size to *K*

One method to help calibrate where a population is in relation to *K* is to evaluate measures of animal condition and reproduction with respect to population size (Table 9.2). We admonish that such an approach has limitations, but may offer the only data readily available to help determine harvest or to decide whether to manipulate habitat. Measures of animal condition tend to lag behind the ability of the habitat to support them. Thus, a population irruption that resulted in an overshoot of *K* (Leopold 1943, Klein 1968, Caughley 1970) might be detected far too late to implement meaningful management. Such an overshoot holds the potential to reduce *K*, further confounding interpretation of animal condition. We discuss the potential for low to moderate densities of herbivores to have a positive effect on their forage later in this chapter. Moreover, an overharvested population may exhibit limited variability in some parameters (for example, litter size may become fixed at some maximum) as the population is driven from MSY toward low density or extirpation. This outcome also makes estimating where the population is with respect to *K* difficult. Forage-based measures of *K* exist (Hobbs et al. 1982, Stewart et al. 2000) as do indices of habitat quality based on foraging intensity (Riney 1982). Nonetheless, some metrics require a substantial knowledge of the habitat and nutritional requirements of animals to be of value. Others, such as

indices of overgrazing and hedging of trees and shrubs, often lag behind population density of ungulates (Caughley 1977).

K should not be considered a seasonal phenomenon. Most northern ungulates cannot obtain a maintenance diet during winter because of the low quality of forage during that season (Mautz 1978). Body reserves accumulated during spring and summer are essential for reproduction and may help buffer the animal against extreme conditions in winter (Schwartz and Hundertmark 1993, Bowyer et al. 2000). Variation in corpora lutea counts with population density (Teer et al. 1965) would not occur if forage in spring and summer were not in short supply. The world is not completely green (Slobodkin et al. 1967); not all plants are suitable forage for herbivores (Bryant and Chapin 1986). Similarly, inadequate winter forage may exhaust body reserves too rapidly to allow even animals in good condition to survive severe winter weather (Mautz 1978). Thus, animals may balance the need for resources acquired during the growing season with the availability of winter forage. Consequently, K might be set by a variety of conditions related to the quality of summer and winter ranges (Bowyer et al. 1986, Schwartz and Hundertmark 1993). K cannot be determined from either summer or winter alone in a seasonal environment.

Habitat manipulation and population density

Effective manipulation of habitat requires knowledge about the size of the ungulate population with respect to K. For instance, a population held well below K by predation is not limited by available forage, and manipulation of habitat to enhance animal numbers will not likely be successful (Fig. 9.10). A time lag may exist from when the manipulation occurs and the maximal production of forage (Weixelman et al. 1998). But, unless further management is implemented to eliminate other limiting or regulating factors (such as predation or harvest), manipulations of habitat likely will fail to produce the expected results (Fig. 9.10). Conversely, appropriate manipulation of habitat to enhance animal numbers for populations near K holds great promise for increasing population size and allowable harvest (Fig. 9.10). Clearly, the lack of consideration of density-dependent processes can lead to management failures and undermine public confidence in future manipulations of habitat.

Predation and population density

Determining where an ungulate population is in relation to K (Table 9.2) is also key to understanding when management of predators (Gasaway
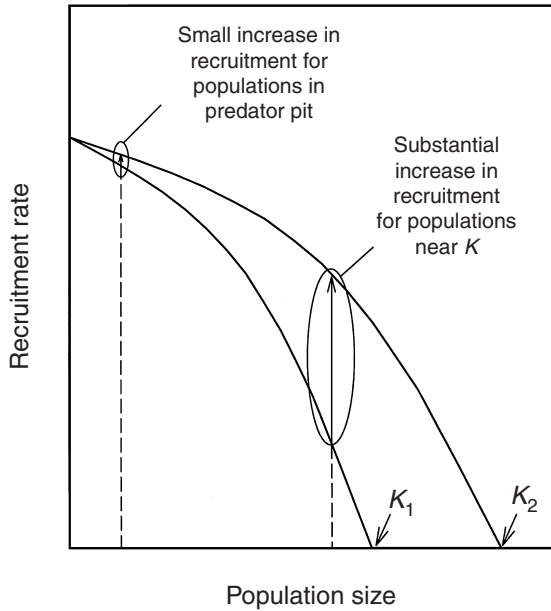
Fig. 9.10. Variation in recruitment rate (young/adult female) with increasing population size relative to changes in carrying capacity (K) caused by habitat manipulation. Note that a substantial improvement in recruitment rate occurs as habitat manipulation such as fire or logging increases carrying capacity from K_1 to K_2. A much smaller change in recruitment would result for populations held at low densities by predation (in a predator pit) because those individuals are not limited nutritionally.

et al. 1983, 1992, Hatter and Jans 1994, Van Ballenberghe and Ballard 1994, Boertje et al. 1996) is likely to affect population dynamics of their primary prey. This perspective is necessary because whether mortality of prey is compensatory or additive changes with population density (Fig. 9.11). Females attempt to produce more young than the environment can support at densities between MSY and K, an antithetical result for those who believe in behavioral regulation of ungulate populations or in group selection (McCullough 1979). Many young produced at high population densities with respect to K are born to mothers with few body reserves and, consequently, neonates exhibit low body mass and survivorship (Schwartz and Hundertmark 1993, Keech et al. 2000). In theory, the loss of another young or adult from the population allows survival of an individual that would not otherwise have been recruited into the population. Nonetheless, many of those young born at high population density are predisposed
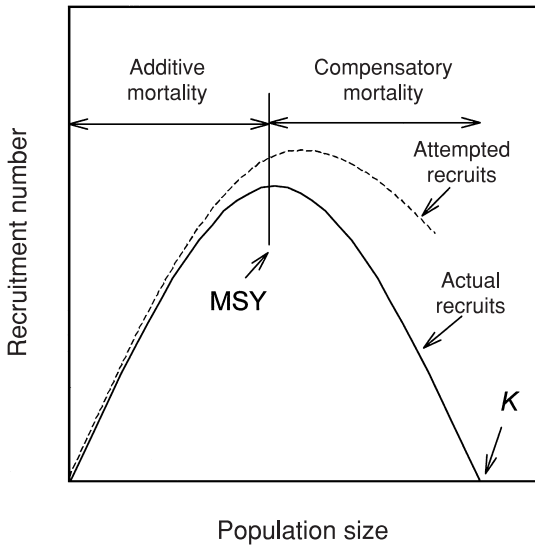
Fig. 9.11. Changes in recruitment number and attempts to recruit young with increasing population size of adult females. Note that individual females attempted to reproduce at a higher level than can be supported by the environment from densities ranging from maximum sustained yield (MSY) to carrying capacity (*K*), but that attempts to recruit young parallel the recruitment number below MSY because females are in good physical condition (adapted from McCullough 1979). Consequently, mortality tends to become increasingly compensatory from MSY to *K* (open area) but is largely additive (horizontal lines) below MSY.

to mortality from a variety of sources including predation, and would have perished anyway had they not been killed by a predator – mortality was compensatory.

As populations are reduced from *K* toward MSY, the proportion of mortality that is compensatory declines with the decrease in "excess" young that females attempt to foster. Females are in sufficiently good physical condition at low densities that many reproductive attempts are successful (Fig. 9.11). Indeed, for populations below MSY, most females conceive and have the necessary body reserves to successfully provision young. Thus, any decimating factor (Leopold 1933), including predation, becomes additive because those neonates would have been recruited had they not been killed. Whether one species of predator or another kills those young is inconsequential – mortality is additive. Hence, a suite of mortality factors near *K*, where mortality is mostly compensatory, might have a limited effect on the dynamics of an ungulate population. That same combination

of mortality sources at or below MSY, where mortality is primarily additive, may have a profound effect on the dynamics of the population and unexpectedly send it declining rapidly toward low density.

Interpreting effects of predation and whether predator control is warranted to meet particular management objectives also requires information about the relationship of the population to K (Table 9.2). For example, a heavy loss of young to predation in an ungulate population near K is not a cause for concern. Those neonates would not likely have been recruited in the absence of predation. Conversely, that same outcome for a population at or below MSY would indicate that predators might be regulating the population, and predator control may be needed to increase the population (assuming that was the management objective). Additive and compensatory effects of predation and harvest on dynamics of ungulate populations are complex, and cannot be understood without considering density-dependent mechanisms (Fig. 9.11).

Ecosystem processes

Ungulates are more than merely products of ecosystems. These large herbivores may serve as regulators of ecosystem processes at several scales of time and space (McNaughton 1985, McNaughton et al. 1988, Hobbs 1996, Kie and Lehmkuhl 2001, Singer et al. 2003). For example, research conducted in coniferous forests in Olympic National Park in western Washington indicated that herbivory, primarily by elk, reduced plant standing crop, increased species richness of forbs, and helped determine the distribution of several shrub species (Woodward et al. 1994, Schreiner et al. 1996). Although the presence of a large number of ungulates in a single herd at a specific location may have profound effects on vegetation, herbivory by large herbivores more strongly affects ecosystems through modification of basic processes, including rates of nutrient turnover, competitive interactions among plant species, and rates and trajectories of successional pathways (Hobbs 1996, Pastor et al. 1997, Augustine and McNaughton 1998). Thus, grazing and browsing by ungulates act primarily as chronic rather than as episodic disturbances, although irruptions and crashes of some populations have occurred episodically (Klein 1968). Population densities of ungulates are also important to consider when examining effects of herbivory (Bowyer et al. 1997). Densities of herbivores and intensity of their foraging may determine whether herbivory increases nutrient cycling and plant productivity (Molvar et al. 1993,

Kielland et al. 1997) or negatively affects plant communities by driving changes in successional pathways (Pastor et al. 1997).

Effects of ungulates on nutrient cycling

Ungulates can increase rates of nitrogen mineralization through consumption of palatable plant species and subsequent fertilization via urine and feces (McNaughton 1992, Seagle et al. 1992, Molvar et al. 1993, Pastor and Cohen 1997). Ungulates increase nitrogen (N) cycling by adding readily available N for microbes, positively affecting conditions for N mineralization, and by changing litter quality (Hobbs 1996, Kielland et al. 1997). Deposition of urine and feces by ungulates affects nitrogen cycling by offering an accelerated alternative to decomposition as a pathway for nitrogen turnover, because nutrients from urine and feces are in forms that are readily accessible by plants (Ruess and McNaughton 1987, 1988, Ruess et al. 1989, Pastor et al. 1993, Frank et al. 1994, Hobbs 1996). Indeed, plants with an evolutionary history of grazing show elevated responses in growth to urea and ammonia, relative to other forms of inorganic N (Ruess 1984, Ruess and McNaughton 1987). Moose browsing on diamondleaf willow (*S. pulchra*) in Alaska increased the rate of nitrogen turnover (Molvar et al. 1993) and litter decomposition (Kielland et al. 1997). Moreover, moose browsing on paper birch (*Betula resinifera*) resulted in more rapid processing of litter by stream insects (Irons et al. 1991).

Nitrogen in feces is positively correlated with forage quality, and fecal nitrogen for cervids is known to increase with increasing forage quality (Leslie and Starkey 1985, Hodgman and Bowyer 1986, Bowyer et al. 1997). High-quality forage promotes fecal decomposition and nitrogen mineralization by microbes, which reduces ammonia losses via volatilization (Ruess et al. 1989). Thus, selection for high-quality forage also has effects beyond the level of herbivore nutrition (Ruess and McNaughton 1987, Ruess et al. 1989, Turner 1989, Frank and McNaughton 1993, Hobbs 1996, Frank and Evans 1997). Grazing by large herds of migratory ungulates such as elk and bison increased the rates of N mineralization in soils in Yellowstone National Park (Frank et al. 1994, Frank and Evans 1997). Moreover, Day and Detling (1990) reported that bison fed selectively on plants that had previously been fertilized by urine.

Ungulate movements within home ranges and following migration tend to concentrate nutrient deposition, because ungulates do not use their environment uniformly (Hilder and Mottershead 1963, McNaughton 1983, 1985, Senft et al. 1987, Coughenour 1991, Ward and

Saltz 1994, Hobbs 1996) and feces tend to be deposited in areas of greater use (Etchberger et al. 1988). Consequently, N consumed over large areas often becomes concentrated spatially and amplifies nutrient returns in areas selected by ungulates (Ruess and McNaughton 1987, Ruess et al. 1989, Turner 1989, Frank and McNaughton 1993, Hobbs 1996, Frank and Evans 1997). For instance, migrations of elk during winter resulted in net movement of N from summer to winter ranges (Frank and McNaughton 1993, Frank et al. 1994, Hobbs 1996).

In forested systems, where foraging is concentrated on woody plants, selective browsing may reduce nutrient cycling (Bryant et al. 1991), particularly when ungulates are at high population densities (Bowyer et al. 1997). Forage selection and litter decomposition are determined by nutrients, structural carbohydrates, lignin, and secondary metabolites (Meetemeyer 1978, Swift et al. 1979, Melillo et al. 1982, Flanagan and Van Cleve 1983, Pastor et al. 1984, Bryant and Chapin 1986, Pastor et al. 1988, Bryant et al. 1991, Pastor et al. 1993). Plant species with high levels of secondary metabolites are not only poor-quality food for herbivores, but also produce low-quality litter. This is because the same chemical properties, such as secondary metabolites, lignin, waxes and cutins, and low nitrogen concentrations, that reduce their quality as food also reduce their value for soil microbes (Flanagan and Van Cleve 1983, Moore 1984, Pastor et al. 1984, 1988, Bryant et al. 1991, Pastor et al. 1993). Soil fertility also declines as the biomass of unpalatable species sequesters increasing amounts of nutrients and as decomposition rates decline because of low litter quality (Bryant et al. 1991). Moreover, chemical defenses of many woody species are correlated directly with their ability to tolerate nutrient stress, and slow-growing species such as white spruce (*Picea glauca*) can persist in nutrient-deficient soils (Bryant et al. 1983, Coley et al. 1985). Those shifts in the dominance of woody species from those that are palatable to herbivores to species that are more chemically defended and less palatable have resulted from high population densities of moose (Pastor et al. 1988).

Important components of determining effects of herbivory on ecosystems are nutrient supplies within the system (Bryant et al. 1991) and population densities of herbivores that feed upon them (Bowyer et al. 1997). Moose populations in interior Alaska are often held at low population densities by predation (Gasaway et al. 1983, 1992), which may prevent heavy browsing and weaken selection toward the dominance of unpalatable species (Molvar et al. 1993). Molvar et al. (1993) suggested that moose act as keystone herbivores that mediate rates of nutrient

cycling in northern ecosystems. This observation is consistent with studies of moose herbivory in northern ecosystems, where browsing by moose at low population density increases rates of N turnover (Molvar et al. 1993, Kielland et al. 1997), plant productivity (Molvar et al. 1993), and litter decomposition (Kielland et al. 1997). Conversely, moose at high population densities influenced successional processes, shifting communities from palatable hardwoods to unpalatable conifers with high levels of secondary defense compounds. This ultimately led to slower cycling of nutrients in the systems (Bryant et al. 1991, McInnes et al. 1992, Pastor et al. 1997).

Effects of ungulates on plant productivity

The herbivore-optimization model (Fig. 9.12) predicts that one effect of moderate levels of herbivory on plant production is the enhancement of net primary production of forage plants over ungrazed plants (McNaughton 1979, 1983, 1985, 1986, McNaughton et al. 1988, Georgiadis et al. 1989, Hik and Jefferies 1990, Frank and McNaughton 1992, 1993). Where grazing and browsing by ungulates act to increase the cycling of a nutrient in limited supply, the result may be an overall increase in
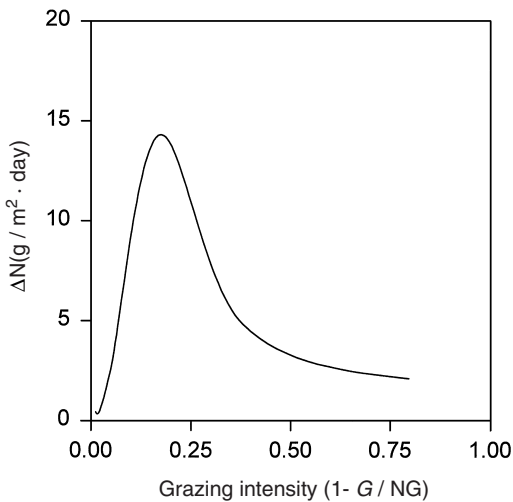

Fig. 9.12. Example of a herbivore optimization curve, illustrating the relationship between increase in grazing intensity and change in above-ground productivity in grasslands, where G = biomass in grazed areas, NG = biomass in ungrazed areas, and ΔN = increase in productivity measured in grams per square meter per day (after McNaughton 1979).

annual net primary productivity (ANPP; McNaughton 1976, 1979, 1983, 1992, Seagle et al. 1992, Frank and Evans 1997, de Mazancourt et al. 1998). Milchunas and Lauenroth (1993) reported that 17% of studies they reviewed showed elevated ANPP in areas grazed compared to areas where grazing was excluded. Williams and Haynes (1995) also noted increased rates of herbage production and increased soil nitrate, phosphate, and organic carbon with inputs of feces compared to control plots.

Adaptation of plants resulting from an evolutionary history of herbivory that provides capacity for re-growth following defoliation involves many factors. These include low stature, deciduous leaves, rhizomatous growth, linear leaf elongation from intercalary meristems, high shoot density, below-ground nutrient reserves, and rapid rates of transpiration and photosynthesis (Coughenour 1985, Hobbs 1996). Moreover, browsing in autumn and winter released stems from apical dominance, resulting in re-growth of larger stems with larger leaves during the following spring and summer (Bergstrom and Danell 1987, Molvar et al. 1993, Bowyer and Bowyer 1997). Likewise, vegetative reproduction by adventitious growth appeared to be enhanced by browsing (Grime 1977). Moose browsing on diamondleaf willow in interior Alaska caused significant increases in the growth of willow stems and leaves (Molvar et al. 1993). Moreover, moose exhibited preference for re-growth of willow stems that had been browsed the previous winter (Bowyer and Bowyer 1997). Compensatory growth in plants is also dependent upon favorable environmental conditions, such as moisture and nutrient availability. Thus, soil characteristics are also important in allowing for compensatory growth following defoliation (Mack and Thompson 1982).

Effects of ungulates on succession and plant species diversity

Browsing by high densities of ungulates can result in decreases in the diversity of plant species (Olff and Ritchie 1998, Riggs et al. 2000). Conversely, low to moderate levels of herbivory by ungulates can enhance species diversity in plant communities by directly reducing the abundance of preferred forages and indirectly influencing competitive interactions among plants (Hobbs 1996, Augustine and McNaughton 1998). Selective browsing can reduce plant species diversity by changing the composition of communities dominated by woody plant species, often increasing the abundance of unpalatable species (Bryant et al. 1991).

In general, plant species richness decreases with even moderate levels of herbivory in nutrient-poor systems and increases in nutrient-rich

systems (Proulx and Mazumder 1998). High population densities of large herbivores can contribute to the dominance of conifers and grazing-resistant or unpalatable species (Bryant et al. 1991, Bowyer et al. 1997, Kielland et al. 1997). For example, high population densities of moose on Isle Royale have existed for long periods of time. Selective feeding on deciduous species of willow, aspen (*Populus* sp.), birch (*Betula* sp.) and other palatable hardwoods has resulted in forest composition that has become dominated by white spruce (Pastor et al. 1997, Jordan et al. 2000). Similarly, intense browsing by white-tailed deer in deciduous forests of the eastern U.S. shifted the herbaceous layer toward grasses, unpalatable herbaceous plants, and browse-tolerant woody plants (Tilghman 1989, McShea and Rappole 2000). Browsing by elk and mule deer in the Blue Mountains of Eastern Oregon and Washington resulted in the suppression of palatable understory shrubs when compared with exclosures (Riggs et al. 2000).

Effects of ungulates on other wildlife

Successional changes across landscapes and changes in plant species composition resulting from ungulate herbivory modify habitat for other species of wildlife. Dense populations of white-tailed deer in the northeastern U.S. altered forest stand development by reducing or eliminating young tree seedlings, shrubs, and herbaceous plants (Tilghman 1989, deCalesta 1994, McShea and Rappole 2000). Reduction in the height of woody vegetation with increased density of white-tailed deer reduced the abundance and species richness of birds that traditionally nest at intermediate levels of the canopy (deCalesta 1994). Moreover, deer densities >7.9 deer/km² had a significant negative effect on bird populations (de Calesta 1994, McShea and Rappole 2000).

How successional changes in the northwestern U.S. affect songbirds or small mammals has yet to be determined. Effects from loss of habitat with reduction in deciduous species of woody vegetation, however, likely reduce or remove habitat components necessary to other species of wildlife. Many neotropical migrants are relatively well represented in grand fir (*Abies grandis*) communities in the Blue Mountains of the Pacific Northwest. Although some species nest in forest canopies, many use shrubs and saplings either in burns, clear-cuts or under mid- to late-successional canopy in coniferous forest (Riggs et al. 2000). Some shrub-nesting species are relatively sparse or scarce in the Blue Mountains, and are likely linked to herbivory by ungulates as has been reported for

deciduous forests in the eastern U.S. (deCalesta 1994, McShea and Rappole 2000, Riggs et al. 2000).

Research needs

Use of forested habitats by ungulates has been studied extensively in the past. Additional research is needed, however, to understand how landscape patterns and characteristics affect behavior, life-history strategies, and other physiological and ecological traits of ungulates. Also, research on the influences of large-scale fires on habitat quality and long-term trends in ungulate populations is needed. Studies also will be needed to determine how post-fire management and rehabilitation practices affect ungulates (Mackie et al. in press).

Determining where a population of ungulates is with respect to K still remains a major challenge. That knowledge is essential for the wise management of populations and in determining when predator control may be effective. Interactions with harvest and severe weather may further complicate matters. Sorting among those factors and how they relate to the size of ungulate populations in relation to K is a fundamental management need. Moreover, there is a need to develop spatially explicit models for ungulate populations (Bowyer et al. in press).

Understanding how ungulates interact with their environment and their role in trophic cascades is an important research need. Evidence exists that ungulate foraging and their deposition of urine and feces may have either positive or negative effects on nutrient cycling and other ecosystem processes. Knowledge of how the population density of ungulates influences those processes is essential. We cannot manage all components of diverse ecosystems, and defining the role of keystone species, such as ungulates, is critical to the future management of coniferous forests (Bower et al. in press).

Summary

Wild ungulates play important roles in coniferous forests throughout western North America. Not only do they respond to habitat changes at the landscape scale, but they also have important effects on basic ecosystem processes, thereby acting as keystone species. Furthermore, the dynamics of ungulate populations are complex. A complete understanding of how ungulate numbers are regulated over time requires

consideration of interactions among climate, predation, and density dependence. The failure to integrate all of these concepts into a cohesive management framework is likely to lead to an incomplete understanding of their role in forested ecosystems.

Acknowledgments

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