THE ECOLOGY OF BISON MOVEMENTS AND DISTRIBUTION IN AND BEYOND YELLOWSTONE NATIONAL PARK

A Critical Review
With Implications for Winter Use and Transboundary Population Management

C. Cormack Gates
Brad Stelfox
Tyler Muhly
Tom Chowns
Robert J. Hudson

April 2005

Faculty of Environmental Design
UNIVERSITY OF CALGARY
Calgary, Alberta

ACKNOWLEDGEMENTS

The history and enormity of issues leading to this study have touched the professional or personal lives of a broad spectrum of Americans, including federal and state civil servants and citizens who care passionately about the integrity of Yellowstone National Park, bison conservation, or protection of livestock against reinfection with a zoonotic organism nearing eradication in the industry. Given the strong polarization among interests involved in these environmental conflicts, the authors feel privileged to have been welcomed by key informants to engage in exploration of their knowledge and insights, and in many cases to have been provided with unpublished data contributing to our assessment and recommendations. Foremost among those we wish to acknowledge as contributing to the assessment is Dr. Mary Meagher, whose passionate concerns for the conservation of Yellowstone bison and the integrity of the Yellowstone Park ecosystem have been uncompromising. We encourage her to continue analyzing the as yet unrealized potential of a data set spanning more than 30 years, complimented by experience in the Yellowstone ecosystem exceeding the duration of most professional careers in wildlife management. In contrast, Rick Wallen, the current bison biologist with the National Park Service, is just beginning to develop a research and management program. We thank Rick for contributing information and his insights to the assessment and hope in return that the report contributes to the development of his program. We are grateful to both Rick Wallen and Dr. Doug Smith for the experience and insights we gained while riding the Mary Mountain Trail with them in October 2004. Finally, we wish to acknowledge the enormous contribution to the project by Traci Weller of Bozeman, Montana. Traci organized and scheduled the interviews and workshops, recorded the dialogue and prepared transcripts. Her competency and humor sustained us through the arduous interview schedule.

CONTENTS

2

REVIEW OF LITERATURE ON UNGULATE MOVEMENTS

This chapter reviews the scientific literature on temporal and spatial distribution and movements of ungulates to provide background for interpreting the movements of bison in and near Yellowstone National Park, where weather, population density, predation, hazing and winter grooming of roads influence movements. The review probes the implications of restricting movements and forced sedentarism.

Evolution of Movement Patterns

Movement patterns evolved among animal species in response to diverse ecological pressures (Dobson 1982). The fitness of an individual is dramatically influenced by its selection of a place (Alcock 1977), and particular movement patterns will be selected if they have reproductive or survival (fitness) value (MacArthur 1972). Pease and Lande (1989) stated the biogeography of a species is determined by evolution and movements of populations. They suggested the distribution of a species is often more malleable than its morphology or environmental tolerance.

Dispersal

Dispersal is an important process for improving a population's ability to respond to changing environments. Dispersal has been defined as: travel by individuals beyond their home range boundaries when they do not return (at least in the short term) as they would after brief excursions (Stenseth and Lidicker 1992); individual movements out of an area larger than a home range with no predictable return (Bunnell and Harestad 1983); and one-way movement by a population with no predictable direction (Sinclair 1992). Dispersal plays a major role in population regulation (Lidicker 1975), and spatial distribution (Taylor and Taylor 1977). Species that disperse with a low rate of return likely subsist in habitats subject to a high deterioration rate, but low movement cost, possibly due to short distances between suitable habitat patches (Baker 1978).

According to Murray's "rule of dispersal" (Murray 1967), individuals move to the first suitable uncontested site, and no further, assuming the disperser spends no longer than necessary searching for an empty location, because of the risk of travel or cost in time, or they disperse to avoid sharing home ranges. Selection favours non-dispersal in the absence of competition, but when competition exists, individuals are pressured to disperse (Waser 1985). Instead of attributing dispersal to a single cause, Dobson and Jones (1985) stated that multiple factors should be considered. Even if there is one primary cause, other factors may contribute to the magnitude of dispersal.

For dispersal to be advantageous, fitness gained from exploiting new areas must exceed the costs of moving. Dispersal may reduce disease, predation, and competition for resources (Waser 1985), but there are also potential disadvantages, including uncertainties of finding necessities (e.g. food, shelter, empty habitat, a mate, or appropriate social milieu), greater exposure to predators and competitors, loss of rare phenotypes, and less viable offspring (from breakdown of co-adapted systems, or disadvantageous genetic recombination; Stenseth and Lidicker 1992). Effective fertility may decrease if a disperser must establish a dominant position in an existing hierarchy before it can mate (Bengtsson 1978). Also, increased movement rates can be associated with greater prevalence and spread of disease (Mollison and Levin 1995).

Migration

Movement from one spatial unit to another is the least restrictive definition of migration (Baker 1978). A definition that includes a return component is used most consistently by vertebrate biologists (Stenseth and Lidicker 1992), thus distinguishing it from dispersal. To be adaptive, migratory movements must involve a change in environment, or travel over an "ecological distance" from one environment to another (LeResche 1974). Species with a high incidence of return migration should be those adapted to spatially separate habitat types that fluctuate in relative suitability (Baker 1978). Many ungulates have evolved in grassland, desert or tundra regions where food availability is highly seasonal or erratic because of drought or snow cover. Messier et al. (1988) considered the increasing energy expenditures for migration as a possible regulatory factor for the expanding George River caribou herd. In African grassland, mammal diversity is low, large concentrations of animals are typical, and long distance seasonal migrations are common (Baker 1978). In transitional zones between grassland and forest (i.e. savannah), species diversity is relatively high, animals are not highly concentrated, and migration is rare. When it does occur, migration is for relatively short distances.

Species such as wildebeest (*Connochaetes taurinus*), and caribou/reindeer (*Rangifer tarandus*), which are known for long distance mass migrations, typically also have populations that remain sedentary (McNaughton 1985, Banfield 1954). Migrants may share ranges with residents at certain times of the year. In the Ngorongoro Crater, Tanzania, there are abundant year-round food and water resources and resident wildebeest do not seem compelled to migrate (Talbot and Talbot 1963).

Opportunities to use a complementary range of habitats with limited migration distance is afforded in areas with sharp ecological gradients such as mountains. Altitudinal migration is a feature of the seasonal ecology of many ungulate species throughout western North America. Bison (*Bison bison*) use altitudinal gradients in Yellowstone and similar landscapes but used other gradients such as the prairie-parkland transition in the Northern Great Plains (Morgan 1980). The occurrence of migration in many ecosystems around the world suggests there may be common underlying causes (Fryxell et al. 1988). Large herbivores appear to migrate primarily to access high quality food and/or avoid predators, but also as an effective strategy to avoid thermal stress, insect harassment, and contact with disease and parasite vectors.

Dispersion

Dispersion is defined as the internal distribution pattern of a population (Odum 1971), or the distribution of animals in space, ignoring time, since birth (Bunnell and Harestad 1983). As the mean distance between individuals increases through dispersal, changes in dispersion may result in greater clumping, increased randomness, or more even spacing

(Stenseth and Lidicker 1992). Convergence decreases the mean distance between individuals.

Often, a population undergoes dispersion when departing on a migration, and convergence on return. If an animal migrates as a herd, then disperses into smaller social units at the destination, herding behaviour is assumed to reduce the cost of migration (Baker 1978). Natural selection appears to favour dispersion in animals when food availability is low, or convergence when food availability increases (Leuthold 1977). However, if water or other point resources are limiting, selection seems to favour convergence, whereas dispersion is favoured when water becomes less limiting.

Benefits of Dispersal

Inbreeding Avoidance

Genetic variation has been generally accepted as necessary for evolutionary adaptation of a species to a changing environment. Restriction of movement may facilitate mating of closely related individuals (Wright 1946). If a population has been outbreeding for an extended period of time, recessive deleterious mutations accumulate and deleterious effects of inbreeding become relatively high (Bengtsson 1978). Pemberton et al. (1988) reported that red deer (*Cervus elaphus*) calves homozygous for two alleles did not survive as well as calves heterozygous for both. Ralls et al. (1979) used juvenile survival of ungulates as a measure of inbreeding depression in zoos. Inbreeding avoidance is most effectively accomplished by female dispersal. Territorial behaviour of males also reduces inbreeding (Spinage 1982).

A population that has been inbreeding for a considerable time would not greatly increase fitness by changing its reproductive strategy (Bengtsson 1978). Genes required for adaptation to a particular environment may be lost or suppressed, and acquired skills appropriate in one environment may not be useful in another (Cockburn 1985). Inbreeding may be advantageous in low fecundity mammals by improving adaptation to local conditions and reducing the cost of meiosis (Shields 1983). Throughout history, bison lived in large mobile populations, which should minimize inbreeding. Inbreeding depression might be expected under the restricted management that has prevailed for the last 150 years. However, there is little evidence of problems, although the number of generations under these conditions is not great. In a recent study of bison gentics at Elk Island National Park where population structure is not manipulated, Wilson et al. (2002) found that individual males were not able to dominate breeding opportunities and successful bulls were not always the largest.

Finding Mates

Animal movements are greatly influenced by mating systems (Greenwood 1980). Ideally, dispersal should occur either at young ages before reproduction or at old ages after the reproductive contribution to the population has been completed (Morris 1982). Typically, males compete for mates and invest relatively little in rearing offspring. Conversely, females typically invest heavily in offspring and are therefore the sex limiting reproduction. In many polygynous and promiscuous mammals, young males are more likely to find mates if they adopt a disperser strategy (Dobson 1982). Males increase reproductive success through contact with many females, which can often be achieved through greater mobility. In most monogamous mammals, both males and females disperse (Dobson 1982).

In Georgia, sexual competition among male white-tailed deer (*Odocoileus virginianus*) appeared to be the primary stimulus for dispersal (Kammermeyer and Marchinton 1976). Most dispersers were young subordinate bucks of breeding age. Nelson and Mech (1999) suggested the recent range expansion and establishment of new wintering areas of white-tailed deer in North America resulted from dispersal of yearlings.

Male dispersal occurs in species that live in permanent herds, such as impala (*Aepyceros melampus*; Murray 1982), or African buffalo (Synerus caffer; Sinclair 1977). Sinclair (1977) found an increasing tendency for male buffalo to depart from mixed herds as they grew older, and those greater than ten years were permanently displaced by dominant breeding bulls. According to Prins (1989), rutting activities in mixed herds diminished a male's physical condition, while males in bachelor herds improved their condition. Distant movements of male muskoxen (*Ovibos moschatus*) on the Seward Peninsula probably improved their prospects for breeding whenever social competition was intense (Smith 1989).

In monogamous and territorial species such as dikdik (*Madoqua rhynchtragus*) and roe deer (*Capreolus capreolus*), all offspring of both sexes disperse to find mates (Hendricks 1975, Bobek 1977). Also, both sexes (although mostly males) disperse in species with loose social organization, such as southern reedbuck (*Redunca arundinum*; Howard 1986) and black-tailed deer (*Odocoileus hemionus columbianus*; Bunnell and Harestad 1983). Conversely, female Uganda waterbuck (*Kobus ellipsiprymus*) are the most active in dispersal, searching new areas for awaiting males (Spinage 1982).

During the breeding season, most mature male bison disperse to gain access to females and displace dominant bulls (e.g. Herrig and Haugen 1969, Petersburg 1973, Lott 1974, and Melton et al. 1989). Because mixed herds of wood bison (*B. b. athabascae*) are small and widely scattered, they are more likely to be encountered by nomadic males (Gates and Larter 1990). Komers et al. (1992) suggested that male wood bison accompany mixed herds for breeding, and disperse to recover from rutting activities. Once body condition is restored, the males rejoin mixed groups where there is a continuous exchange of potential female mates. Lott (1979) observed that male plains bison lose dominance if they become exhausted from rutting activities.

Access to New Resources

When resources become limited, female dispersal has been observed in red deer (Clutton-Brock and Albon 1985), southern reedbuck (Howard 1986), and roe deer (Bobek 1977). Although moose (*Alces alces*) are generally solitary, they do not exhibit female dispersal when resources become limited (Gasaway et al. 1985). Increase in population density stimulates dispersal of white-tailed deer bucks (Nelson and Mech 1984), but not females (Nixon et al. 1991, Nelson and Mech 1992). Social organization of a species influences dispersal rates (Baker 1978). In ungulates that occur in moderate sized herds, such as elk (*Cervus elaphus*) and sheep (*Ovis spp*.), females usually disperse in small groups, splitting off from the parent group and establishing an adjacent home range (McCullough 1985). Wildebeest typically occur in large herds and may disperse in large groups (Sinclair 1992). Although male African buffalo experience higher predation when they are not part of large herds, groups of three or four are able to utilize habitat patches too small for female-dominated groups that aggregate to minimise vulnerability to predation (Sinclair 1977). Gates and Larter (1990) also observed male wood bison foraging in small habitat patches not used by large mixed groups. Movement over wind-packed open habitat would have much higher energetic costs for male bison because foot loadings in snow are much higher in males than females (Telfer and Kelsall 1984). Lott and Minta (1983) suggested lack of group fidelity in bison may facilitate dispersal in a Great Plains environment with fluctuating rainfall and forage resources.

Benefits of Migration

Access to Shifting Resource Availability

Many migrations occur during transitions between seasons (winter/summer at high latitudes and wet/dry seasons in the tropics) indicating this may be a response to changes in resource availability. Rapid, long distance movements are characteristic of large herbivores that evolved in grassland ecosystems. McNaughton (1985) described the Serengeti region of East Africa, comprised of 27 ungulate species and over three million individuals. The open grasslands receive low annual precipitation that support shortgrass, while wooded grasslands receive higher rainfall that support tall, highly lignified grasses. The primary grazers are wildebeest, zebra, Thomson's gazelle (*G. thomsonii*), buffalo and topi (*Damaliscus korrigum*). Annual movements occur in nomadic herds of wildebeest, plains zebra (*Equus burchelli*) and eland (*Taurotragus oryx*). Although most gazelle (*Gazella spp*.) are nomadic, they travel shorter distances. Buffalo, topi and gazelle occur as resident herds throughout the savannas. Impala, topi, hartebeest (*Alcelophus buselaphus*) and giraffe (*Giraffa camelopardalis*), which include browse in their diet, remain in wooded grasslands year-round (Baker 1978). Some eland also remain, while others migrate with zebra herds. Among seasonal migrants, there is relatively little mortality through starvation, but non-migrants such as impala, giraffe, kudu (*Tragelaphus strepsiceros*) and waterbuck all experienced considerable starvation mortality at the end of a dry season in South Africa (Hirst 1969).Wildebeest migrate to open grassland for the wet season to feed on shortgrasses, which are easily digestible and nutrient rich (Fryxell et al. 1988). When water sources evaporate during the dry season, and the food value of tropical grasses declines (Sinclair 1975), wildebeest must migrate to wooded grasslands for water and green grass.

Migration during the dry season by white-eared kob (*Kobus kob leucotus*) in Boma National Park, Sudan, allowed access to green grass and water when these resources were scarce elsewhere in ecosystem (Fryxell and Sinclair 1988*b*). Because Lechwe antelope (*Kobus spp*.) feed on floodplain grasses and herbs, movements coincided with the annual expansion and contraction of flood waters across broad river basins (Fryxell and Sinclair 1988*b*). These animals disperse during flooding, and then converge when waters subside.

On the Eurasian steppes, east of the Caspian Sea, antelopes such as dzeren (*Procapra gutterosa*) and dzheiran (*Gazella subgutterosa*), and wild asses (*Equus hemionus*) congregate in winter (Formozov 1966). Forage is locally abundant where the ground lacks snow cover. If severe winter reduces food availability, these animals undergo dispersive migration.

In southern California, migratory female mule deer (*Odocoileus hemionus*) used habitats with higher forage quality than non-migratory deer (Nicholson et al. 1997). However, migrants were exposed to increased predation during the seasonal movements and experienced higher mortality during dry years. Moose typically converge on a common range during winter and disperse into separate ranges during summer (Hundertmark 1998). In Laurentides Provincial Park, Quebec, DesMeules (1964) observed that as snow depth increased, moose became more dispersed and confined to coniferous cover. Under deep snow conditions, singles or small groups of moose could use scattered winter forage more efficiently (Houston 1968).

An eastern European tundra moose population formed in the 1950s (Pulliainen 1974) spent the summer on the arctic coast then migrated south to find adequate vegetation for sustenance during winter. In southeastern Norway, migrating moose used habitats of lower quality but higher quantity browse than resident moose (Histol and Kjeljord 1993). There was no data to indicate which strategy provided a nutritional advantage. Mutual cooperation in trail breaking and cratering in snow is an advantage of herding behaviour for caribou and bison (Helle 1984, Telfer and Kelsall 1984). Cooperative trail maintenance in snow to access resources may also be important for white-tailed deer (Telfer and Kelsall 1984, Messier and Barrette 1985).

Predator Avoidance

In many ungulate species, parturition coincides with movements away from predators (Fryxell et al. 1988). Migratory animals tend to outnumber sedentary compatriots, in some cases by an order of magnitude. One explanation for this phenomenon is that migrants are less vulnerable to predators that are unable to follow migratory herds. Also, pregnant females that disperse in a heterogeneous environment before calving force predators to search larger areas. Some ungulates that experience deep snow conditions may converge to evade predators.

Above average grass productivity in the 1970's allowed the migratory wildebeest population in the Serengeti to increase; non-migratory kongoni (*Alcelophus buselaphus cokii*), topi and impala were apparently unaffected (Sinclair 1979) suggesting that wildebeest were regulated by food, while non-migrating species were regulated by predation (Fryxell and Sinclair 1988*a*). The migratory strategy of wildebeest may decrease their vulnerability to regulation by sedentary lions (*Panthera leo*) and hyenas (*Crocuta crocuta*). During the period that their young are immobile and dependent, these predators are limited by resident prey because they are unable to follow migratory herds. Migratory species associated with open grasslands are unreliable prey; therefore predators are restricted mainly to wooded grasslands.

In the Masai Mara National Reserve, Kenya, Cooper et al. (1999) monitored spotted hyenas that fed mainly on resident topi and Thomson's gazelle during the first half of the year. Upon arrival of the migratory herds of wildebeest and zebra, hyenas switched to wildebeest, which provided them a superabundance of food for about three months. After the migratory animals departed, there was a period of reduced prey abundance due to temporary dispersion of resident ungulates. Parturition for zebra, wildebeest and gazelle is December to January. Impala, hartebeest, giraffe and other non-migratory ungulates calve in October while accompanied by seasonal migrants. This suggests an adaptation in parturition time by resident ungulates to minimise predation on offspring.

Bighorn sheep forage in large dispersed groups in open habitat adjacent to steep cliffs as a predator-evasion strategy (Risenhoover et al. 1988). Security depends on sightability of predators and availability of escape terrain. Bleich et al. (1997) studied mountain sheep (*Ovis canadensis*) in California to help determine causes of sexual segregation in ungulates. Mature rams and ewes were segregated from December to July. Mature males usually occupied sites with more abundant and higher quality forage than ewes; however, predators were substantially less abundant on ranges used by ewes with lambs than on those used by mature rams. Mixed groups occupied steeper slopes, rougher terrain and habitats that are more open when lambs were very young. Results supported the hypothesis that female ungulates, which have greater vulnerability to predation due to smaller body size, minimize their risks and risks of their offspring to predation by using habitats with greater opportunities to evade predation than mature males.

Long distance migration of the George River caribou herd of northern Quebec and Labrador reduced its accessibility to wolves (*Canis lupus*) during the four to five months when pup-rearing restricted their movements (Messier et al. 1988). As the herd expanded, sedentary populations of caribou in the region declined (Brown et al. 1986). Barren-ground caribou herds migrate from the boreal forests of Manitoba, Saskatchewan, Alberta and the Northwest Territories, to calving grounds in the tundra of Nunavut. Calving grounds were described by Kelsall (1968) as poor in vegetation and unattractive to males and non-breeders, which selected better vegetated sites at lower latittudes. Calving areas provided some refuge from tundra wolves, which preferred to den closer to the treeline (Heard and Williams 1992). Fancy and Whitten (1991) suggested that female caribou from the Porcupine herd selected calving areas north of the mountain foothills in northeastern Alaska and northern Yukon, primarily to reduce predation exposure. Highest calf mortality occurred in years when calving was closer to the foothills, where wolves and grizzly bears (*Ursus arctos*) were abundant. In Denali National Park, Alaska, offspring from caribou that migrated to calving grounds experienced only half the wolf predation that calves born in other areas (e.g. lowland spruce forests) experienced (Adams et al. 1995). In south-central Alaska, Ballard et al. (1987) determined that calving caribou were usually unavailable to wolves because wolves remained within their territories and did not follow migrating caribou into calving areas.

Maternal female woodland caribou sought high elevation slopes for calving in Spatsizi Provincial Park, northern British Columbia (Bergerud et al. 1984), west-central Alberta (Edmonds and Smith 1991), and Wrangell-St. Elias National Park and Preserve in Alaska (Barten et al. 2001). Calving grounds were partially out of the range of wolves and bears, however, food resources were more limited at those locations compared to lower elevations. These females appeared to sacrifice food abundance and/or nutrition to provide safety for their offspring.

Many caribou populations that disappeared in British Columbia since the early 1900s were non-migratory (Seip 1992). He suggested wolves might have eliminated the sedentary Quesnel Lake herd because wolf numbers were sustained at high densities by moose. In contrast, the neighbouring Wells Gray herd, which migrated to mountainous summer ranges away from moose and wolves, was increasing. Tweedsmuir-Entiako caribou that used low elevation forest had very low calf survival (Seip and Cichowski 1996). In contrast, those migrating into alpine and subalpine areas experienced higher calf survival, and calves born on islands had the lowest mortality. Migratory caribou form large aggregations to “space away” from predators at calving time, whereas less mobile woodland caribou that disperse from each other “space out” from predators (Bergerud and Page 1987). This type of behaviour has been observed in Spatsizi Provincial Park of B. C. (Bergerud et al. 1984), west-central Alberta (Edmonds 1988, Edmonds and Smith 1991), northeastern Alberta (Fuller and Keith 1981), central Saskatchewan (Rettie and Messier 1998), Manitoba (Brown et al. 2000), and Quebec and Labrador (Brown et al. 1986). In 1978, before coyotes arrived, only 15% of parturient female caribou dispersed into the Gaspe uplands. By 2002, this rose to 70% and calf survival improved (Mosnier et al. 2003).

Home range sizes of moose cow/calf pairs became significantly smaller in an experimental area of Alaska after removal of brown bears (Ballard et al. 1980), suggesting these moose used dispersion as a predator avoidance tactic.

The formation of concentrations of white-tailed deer in winter (yarding) may be due to predator avoidance rather than a food acquisition strategy (Nelson and Mech 1981). Reduced philopatry during winter may also be a mechanism for predator avoidance. Trail networks are maintained to access forage and evade predators (Telfer and Kelsall 1984, Messier and Barrette 1985). Parker et al. (1999) suggested that white-tailed deer tend to decrease home range size to a minimum, regardless of forage availability, to reduce encounters with predators. In northeastern Minnesota, deer that converged near human habitation during winter experienced less wolf predation (Hoskinson and Mech 1976). In southern Sweden, roe deer form small matriarchal groups in winter when predation risk is high (Wahlstrom and Liberg 1994). Mountain goats (Oreamnos americanus) occupy some of most rugged terrain in North America, effectively reducing predation from grizzlies, wolves and cougar (Felis concolor; Chadwick 1983). During the period after wolf eradication in the Greater Yellowstone Ecosystem, bison and elk became more sedentary (Berger 1991).

Use of Space

Familiar Area

Familiar area is the entire range an animal has prior knowledge of, either from direct perception, previously memorized sensory contact, or from social communication. Animals can therefore navigate from one point to any other point within a familiar area (Baker 1978). Once familiarity is developed, elk show high fidelity to seasonal home ranges (Knight 1970, Craighead et al. 1972). The period of delay before moose immigrate into vacated habitat is likely because familiarity needs to be developed (LeResche 1974). There are many ungulate species where few individuals leave the population, including elk (Houston 1982), red deer (Clutton-Brock et al. 1985), reindeer (Skogland 1985), and African buffalo (Sinclair 1977). Winter range of red deer in northern Scotland extended from sea level to 520 m, and summer range was >520 m (Darling 1937). The migration pattern was flexible and they migrated to low elevations in summer if weather became inclement. In spring, daily altitudinal return migrations occurred, from lower elevations at night to higher levels by day. Baker (1978) surmised that these red deer were aware that higher altitudes provided greater shelter from adverse weather, a gradual succession of new food, and protection from biting insects during spring and summer; they responded to prevailing conditions by migrating to the part of their familiar area they assessed would offer optimum conditions for that particular situation.

Male white-tailed deer left their mothers and began making exploratory movements at one year of age (Nelson and Mech 1984). This led to formation of home ranges by their first breeding season; the short dispersal distances were affected by early movement experiences. New white-tailed deer wintering areas can be established when an adult female, possibly with her daughters, abandons the traditional area and spends the winter in a new location (Lesage et al. 2000*a*). Dispersers would likely select new wintering areas near summer range or along migratory routes to former wintering areas. Migration could develop at this intermediate stage of new wintering area formation. Female offspring, and to lesser extent male offspring, establish winter home ranges peripheral of their mothers (Hoskinson and Mech 1976, Nelson and Mech 1999) causing wintering areas to expand over time. Sweeney et al. (1971) radio-collared 64 white-tailed deer and observed their behaviour when pursued by hunting dogs. These deer had relatively large familiar areas; only six travelled more than two kilometers beyond their home range, and all except one individual returned to their respective home ranges after the chase.

Within enclosures, introduced moose and calves born to them died at a faster rate than resident moose (Bailey and Franzmann 1983). This was attributed to increased energy expenditure by the introduced moose while pacing fence lines, indicating a strong desire to return to familiar surroundings.

In South American Vicuna (*Vicuna vicuna*) the basic social units are mixed herds that occupy relatively small home ranges (Koford 1957). Sub-adult males leave mixed herds to accompany bachelor groups. Each male joins and departs these groups repeatedly and ranges widely. This enables a young male to have a large familiar area within which a small home range will be established once a harem is gathered.

Since the mid 1970s, nearly all mixed groups of bison on the northern range of Yellowstone National Park migrate to a wintering area west of the traditional core area in some years. Meagher (1989*b*) suggested acquired knowledge of new foraging areas and the gregariousness of bison, which facilitated learning, were the predominant factors influencing this movement pattern.

Home Range

Home range can be defined as the area traversed by an individual during normal foraging activities, mating and caring for young (Burt 1943) or the total fraction of the lifetime range of the familiar area physically visited by an animal in a given time interval (Baker 1978). For some species, home ranges vary between seasons and for most ungulate species home range selection differs between sexes. Bleich et al. (1997) suggested that male mountain sheep select home ranges with superior forage to enhance body condition and horn growth. Conversely, home range selection by females appeared to be influenced by predation risk. They concluded that sexual segregation likely results from differing reproductive strategies of males and females among sexually dimorphic ungulates. The ultimate factor determining home range size is energetic requirements (McNab 1963). According to Cederlund and Sand (1994), male moose have larger home ranges than females because of higher metabolic requirements related to sexual dimorphism, and a mating system that depends on access to dispersed females. They also stated that with large mammals such as moose, habitat patches are relatively small compared to the home range. During severe winters, the optimum strategy for large bull moose in Denali National Park, Alaska, was to remain solitary, reduce activity levels, decrease travel distances, increase bite size and inhabit a site with high forage biomass (Miquelle et al. 1992). During summer, bull moose tended to aggregate in open areas where higher forage biomass was available, while cow moose with calves dispersed in forested areas to reduce predation risk.

In African buffalo, home range size was related to quality of habitat (Sinclair 1977). Small home ranges occurred in forested or high rainfall habitat, whereas larger home ranges were likely to be in drier open areas. Buffalo density was correlated with the amount of food in patches along riverbanks, in swamps and in forest glades. To learn the locations of these habitat patches, young animals must follow adults for an extended period of time. Mackenzie wood bison used smaller home ranges where populations were expanding their range, probably due to greater access to unexploited forage resources (Larter and Gates 1990). Females had the largest home ranges. Because they aggregated in larger herds than males, females probably required more extensive grazing areas and these were distributed in widely separated patches. In autumn, bison used a greater variety of habitats when forage quality and quantity became more homogeneous on the landscape (Larter and Gates 1991*a*).

Territory

The simplest cited definition of a territory is “any defended area” (Noble 1939). Leuthold (1977) expanded the definition to include “that part of an animal’s home range from which it excludes individuals of comparable social status through active repulsion”, or “a spatially fixed area within which a given animal consistently prevents certain other individuals from engaging in certain activities”. Territorial behaviour appears to be most apparent in tropical ungulates (Spinage 1982). Leuthold (1977) described territorial behaviour of five classes of African ungulates. Small, exclusive browsers with small home ranges occupied year-round, such as dikdik (*Madoqua kirkii*), duikers (*Cephalophus spp*.) and klipspringers (*Oreotragus Oreotragus*), generally have individual or pair territories. Larger browsers or grazers, such as reedbucks (*Redunca spp*.), oribi (*Ourebia ourebia*), sitatunga (*Tragelaphus spekei*), bushbuck (*T. scriptus*) and gerenuk (*Litocranius walleri*), have larger home ranges, and typically only males are territorial. Moderate sized browsers, grazers and mixed feeders such as impala, waterbuck, and several species of gazelle and kob have fairly large home ranges and are typically sedentary but may move seasonally. Diets may change seasonally, for example, reduced foraging on grass as the dry season progresses. Male territories are a small part of the home range, and a large proportion of males occur in bachelor herds. Exclusive grazers, such as wildebeest, are highly mobile and have attenuated territories that continually reform as the herd moves. Sedentary populations of wildebeest exhibit more pronounced territorial behaviour. Buffalo and eland, which consume a wide variety of grasses and/or browse, move across extensive areas and are not territorial.

Dispersal and Density

Saturation Dispersal

Saturation or enforced dispersal is density dependent and occurs when an animal population fills its habitat to capacity (Lidicker 1975). The dynamic state of the population is stationary and most dispersal in large mammals fits this category (Sinclair 1992). Non-adaptive dispersal occurs when animals are forced from natal or established home ranges by social factors inherent in high density populations (Stenseth 1983). Movements caused by pressure dispersal usually do not extend beyond the first area of favourable conditions encountered (Caughley 1977). In some species, dispersal distance changes with density, not frequency (Cockburn 1985). Food availability is often driven by weather (White 2004) and animals confronted with a sudden drop in carrying capacity because of unfavourable weather may be forced to search for better foraging opportunities.

In Georgia, Kammermeyer and Marchinton (1976) observed that all dispersal of white-tailed deer originated from heavy concentrations around agricultural areas protected from hunting. Dispersal terminated in less densely populated wooded areas often subject to intense hunting pressure. Neither lack of food nor deteriorating habitat were mitigating factors, and dispersers were generally subordinate males. In southeastern Quebec, high-density populations were the most philopatric in winter, and were the source of most dispersers (Lesage et al. 2000*a*). Nicholson et al. (1997) found dispersal to new areas occurred more often from a high density mule deer population than a low density population.

Barren-ground caribou may exhibit a density-dependent response to forage depletion, which could potentially be delayed by a shift in winter range (Ferguson and Messier 2000). On Baffin Island, a mass emigration of caribou from the Foxe Peninsula traditional winter range to Meta Incognita Peninsula occurred. Caribou that remained on Foxe Peninsula's overgrazed range were in poorer physical condition than those migrating to relatively unexploited range on Meta Incognita Peninsula. Periodic recurrence of freezing temperatures during the early stages of spring thaw results in ice formation within snow cover rendering low-growing forage unavailable to Peary caribou (R. t. pearyi; Miller and Gunn 1978). This precursor to starvation may trigger long distance movements across sea ice on the Arctic Archipelago that are important for the survival of these caribou, and recolonization of islands where there have been severe declines. Similarly, mass movements of typically sedentary urials (*Ovis orientalis*) have been reported during times of severe drought (Geist 1971).

After about 75 years of occupying a traditional winter range in northern Yellowstone Park, bison underwent a westward "stress dispersal" during a particularly severe winter of 1975-76 (Meagher 1989*b*). Mackenzie wood bison experienced range expansions when population densities were high, suggesting the animals were responding to environmental stress (Gates and Larter 1990).

Pre-saturation Dispersal

Pre-saturation dispersal is density independent, meaning it occurs before carrying capacity is reached (Lidicker 1975). Movements occur when the population is either increasing toward saturation or decreasing from saturation levels (Sinclair 1992). Ambient dispersal is low level dispersal by young healthy animals and reproductively active adults, independent of population density. Stenseth (1983) included both pre-saturation dispersal and ambient dispersal in adaptive dispersal. Howard (1960) described innate dispersal as emigration of individuals by random diffusion that is predetermined genetically and is not in response to environmental conditions. As opposed to pressure dispersal, distances travelled during innate dispersal may be many times farther than the average home range radius (Caughley 1977).

Dispersal in some expanding populations is not necessarily pre-saturation (Sinclair 1992). Thar (*Hemitragus jemlahicus*) introduced to New Zealand dispersed from a core population that was at or above carry capacity (Caughley 1970*a*). Singer et al. (2000*b*) reported higher rates of dispersal of mountain sheep from rapidly expanding populations not at saturation levels. In contrast to white-tailed and mule deer, roe deer dispersal was inversely related to density (Linnell et al. 1998). Males maintain territories, while females live in what may be more appropriately described as home ranges (Bobek 1977). Both sexes force subordinate animals to leave when social carrying capacity is reached. In Poland, high summer forage availability resulted in smaller territories and home ranges, not density of animals (Bobek 1977). Summer carrying capacity was the determining factor of territory and home range size if winter snow depths were less than 15 cm.

Muskoxen were reintroduced to the Seward Peninsula in 1970. Bulls that wandered from areas of high muskox density served as the vanguard for expansion of traditional habitat (Smith 1989).

Innate dispersal may be operative in wood bison as pioneering mature males encounter unoccupied habitat. Mature bulls were the only segment of the Mackenzie wood bison population found in peripheral habitat patches, and competition for food was an unlikely explanation (Gates and Larter 1990).

Awareness of Destination

Exploratory Migration

Exploratory migration was defined by Baker (1978) as migration beyond the limits of the familiar area, but the animal retains the ability to return. According to Johnson (1989), exploratory migration may be a precursor to dispersal and permanent change in an individual’s home range. Exploration allows an animal to compare its potential success in an alternative setting to its present location. If exploratory movements fail to result in a new residence, the cost may be the loss of the original home range to an intruder. Red deer released in New Zealand in 1861 dispersed more rapidly along valleys than between valleys, suggesting the ability to return to vacated areas was retained (Baker 1978). Climatic changes that varied locally on the Great Plains, and rapidly changed the distribution of resources, favoured a propensity for exploratory behaviour in bison (Lott and Minta 1983).

Calculated Migration

Calculated migration is movement to a specific destination known to the animal at the time of migration, either through direct perception, previous acquaintance, or social communication (Baker 1978). They are usually regular and occur at a fixed periodicity over the course of a year. Ungulates seem to exhibit various behavioural patterns such as contact between adjacent social units and exploratory migration that increase the ratio of calculated to non-calculated migrations. Baker (1978) stated that when ungulates are introduced into unoccupied areas, the rate of movement from the release point is seldom so great that it cannot be attributed to calculated migration. The most common migrational pathway for ungulates is along the slopes of hills and mountains, following an elevation gradient, regardless of latitude (Baker 1978). In temperate regions, animals usually select higher elevations in summer and lowlands where there is less snow in winter. The reverse is true for moose in some areas where snow seldom exceeds critical depths, and calving habitat may be better in lowlands (Gasaway et al. 1983). The north-south migration of barren-ground caribou is more accurately described as perpendicular to the treeline (Banfield 1954). Elevational and latitudinal migrations involve movements along a climatic gradient; however, there are other seasonal and rectilinear migrations not necessarily related to climate.

It is quite probable that several years are required to change traditional movement patterns of moose (LaResche 1974). Calves seem to learn traditional travel routes from their mothers, which is further enhanced by the long lifespan of moose (Pulliainen 1974). Migratory systems should be maintained as long as offspring of moose that established the system persist. In many areas of Europe, summer and winter habitats are adjacent to each other and movements are not extensive. Where seasonal habitats are up to 300 km apart, traditional migration routes may be essential for survival. In Sweden, migration distances of adult moose are directly related to that of their mothers (Sweanor and Sandegren 1988). A traditional migration route in Norway has been used for at least 5,000 years even though habitat has deteriorated on the winter range (Andersen 1991). Pulliainen (1974) found that moose in various parts of Europe migrate in different directions. Moose of western Lapland migrate to the east and northeast. Moose that summer in northern Karelia, Russia migrate east for winter, whereas moose in other parts of Karelia migrate west for winter. In the Pechora River region of Russia, autumn migration occurs in two directions – north to south and east to west; these moose are noted for their uniformity of travel paths. Seasonal migrations in other parts of Russia vary in direction, apparently due to winter food availability.

Wintering female Sika deer (*Cervus nippon*) in eastern Hokkaido, Japan have mixed migration patterns (Mayumi et al. 2003). There are residents, north migrants that occupy summer range at high elevation, and east migrants that summer at lower elevation. White-tailed deer complete calculated migrations between winter and summer range (Aycrigg and Porter 1997, Van Deelen et al. 1998, Nelson and Mech 1999). Some individuals abandon traditional routes to disperse or remain in the same range year round (Nelson and Mech 1984, 1999, Aycrigg and Porter 1997, Nelson 1998). Female white-tail deer appear to transfer knowledge of migratory routes to their offspring (Tierson et al. 1985, Nelson and Mech 1999, Lesage 2000*a*). Female offspring remain closer to mothers into adulthood than males (Nelson and Mech 1984, 1999).

Nomadism

Nomadism refers to movements where no fixed directional pattern or destination is apparent. In the Serengeti, rapid desiccation and senescence of vegetation at the beginning of the dry season results in a sharp decline of food quality (Sinclair 1974).

Movements are directed to any area where rain can be seen or heard by the animals, but only those storms producing rain within the familiar area of a wildebeest herd seemed to initiate movement (Talbot and Talbot 1963). Late in the dry season, nomadic ungulates are usually concentrated in high rainfall locations where green forage persists (McNaughton 1985). In the savannah-grassland environment, there are continuous fluctuations in rainfall, grazing, nutrient availability and fire. These generate pulses in primary production that result in a potentially rich, but temporally and spatially unpredictable food sources for grazing ungulates. The evolution of highly mobile nomadic lifestyles contributes to dominance of grazing ungulates in this ecosystem because this behaviour is essential for effective exploitation of a constantly shifting resource base. In heterogeneous landscapes where high rainfall areas or lakeshores provide dry season refuges, resident herds may duplicate many features of the migrations of the major grazers, but on a smaller scale.

Movements of some ungulate species occur at irregular intervals. In sub-arid or arid regions of Africa, there may be large-scale unpredictable movements of ungulates (Leuthold 1977) such as springbok (*Antidorcus marsupialis*) (Bigalke 1966), addax (*Addax nasomaculatus*), oryx (*Oryx gazella*), and several species of gazelle (Dorst and Dandelot 1970). After evaluating historical accounts from early observers, Roe (1970) was unable to confirm any consistent directional migrations among the large North American bison herds. He defined irregular migration as either movements that were possibly quite regular, but not necessarily associated with any direction or season, or erratic movements that occurred in any direction or season. McCullough (1985) described bison as nomadic with migration apparent in some populations. These patterns have been reconstructed for herds in western Canada (Morgan 1980). Northern Yellowstone bison that move between summer and winter ranges may be at an intermediate stage of migration development (Meagher 1989*b*).

Range Expansion

Range expansion is the outward dispersal of individuals beyond the limits of the traditional area of distribution for a population. Increases in low density populations may be confused with supposed range extensions (LeResche 1974). Often, range retraction of one ungulate coincides with range expansion of another. When large mammalian herbivore species experienced dramatic population declines in Lake Manyara National Park, Tanzania, compensatory responses of other species resulted in overall constancy of herbivore biomass (Prins and Douglas-Hamilton 1990). As moose extended across most of Labrador during the latter half of the 20th century (Chubbs and Schaefer 1997), the Red Wine Mountains caribou herd coincidentally declined (Schaefer et al. 1999). Caribou formerly existed on Isle Royale. They were replaced by moose that invaded the island in the early 1900s (Allen 1979).

Post-Glacial Colonization

There have been five global cooling periods since the last ice age (John 1977). The most recent, often referred to as the “Little Ice Age”, lasted from approximately 1300 to the mid 1800s. It was followed by a warming period, with a cool interruption from 1900 to 1920. Indirect effects of recent climate change on vegetation through fire may be more important than direct effects on species distribution, migration, substitution and extinction (Weber and Flannigan 1997). As the favourable climatic region for many species shifts northward, large climatic disturbances will disrupt life cycles of the original inhabitants, facilitating entry of new competitors. According to Peterson (1955), Asia was the original centre of moose dispersal and the widely distributed subspecies *Alces alces pfizenmayeri* approaches the ancestral type. Since the last glaciation, moose at their widest distribution covered almost all of Europe excluding the Mediterranean (Kurten 1968). In northeastern Siberia and Alaska, moose of the subspecies *A. a. gigas* remained in Beringia during glaciation (Kistchinski 1974, Peterson 1955). Other moose in North America found refuge in west central U.S.A. (*A. a. shirasi*), south of the present day Great Lakes (A. a. andersoni), and the Atlantic seaboard (*A. a. americana*; Peterson 1955). After glacial retreat, *A. a. gigas* moved into the Yukon, *A. a. shirasi* extended its range northward, *A. a. andersoni* moved north and west from Ontario to the edge of treeline and the Yukon, and *A. a. americana* expanded north on the eastern side of the continent. Before 1875, these subspecies were still geographically separated. Since then, all have colonized huge tracts of land to the point where they now overlap, suggesting that post-glacial dispersal has continued until recent times, or is still progressing.

Kelsall and Telfer (1974) cautioned against assuming moose were completely absent from many regions where low populations may have existed in widely scattered locations. It is possible that moose have always inhabited the same regions in Quebec, or extended their range northward within the last century because of habitat changes (Brassard et al. 1974). Moose may have been sparsely distributed in central British Columbia before undergoing a rapid population increase in the early 1900s (Spalding 1990). LeResche et al. (1974) described moose distribution in Alaska. In the Brooks Range on the Arctic Slope, and on the tundra of northern and western Alaska, moose were apparently very scarce at the turn of 20th century. They did not inhabit Colville River delta on the northern coast until about 1890 to 1910, and then became common by the 1950s. Along the northwestern and western coast of Alaska beyond treeline, where moose were essentially absent at the turn of century, there was a gradual population increase, similar to the central Brooks Range. Much of the Seward Peninsula was devoid of moose until the 1940s. Apparently, moose invaded the coastal rain forest of southeastern Alaska and British Columbia by moving down river valleys before 1900 (Klein 1965).

Since the Second World War, moose have expanded their range in all directions in Europe (Pulliainen 1974). In northwestern Russia, dispersal to the north led to formation of a “tundra population” of moose. In southern Russia, moose extended their range into steppe habitat, of which only a small percentage is forested. Some individuals have wandered to the Caspian Sea, Sea of Azov and the northern Caucasus.

The maximum southerly extension of woodland caribou range coincided with the end of the “Little Ice Age” (Bergerud and Mercer 1989). A moose/white-tailed deer community in Nova Scotia switched to a moose/woodland caribou community during this period of global cooling. After warming recommenced, deer recolonized Nova Scotia and expanded northward and westward in Canada (Telfer 1967). The last lichen-rich habitats caribou occupied in eastern North America were generally the most recent to be invaded by white-tailed deer (Bergerud and Mercer 1989).

Northward range extension of mountain goats (*Oreamnos americanus*) in southeastern Alaska was possibly due to mild winter conditions and cessation of hunting in 1977 (Aumiller and Ballard 1986). There was also a similar black-tailed deer northward range expansion in Alaska (Roberson 1986).

Multivariate morphometric analyses of cranial and post-cranial skeletal data from late Pleistocene, Holocene, and living populations of European and North American bison were used by Van Zyll de Jong (1986) to study bison systematics. Results supported the premise that all forms could be considered as one variable chronospecies, *Bison bison*. A large diverse bison population occupied the Beringia refugium before the onset of the last glacial cycle (Shapiro et al 2004). After the Bering Strait re-established at the beginning of the Holocene, the Siberian bison population became extinct. When the ice-free corridor reopened between Alaska and the North American interior, Van Zyll de Jong (1986) suggested that *B. b. occidentalis* from Beringia probably met and hybridized with the more southerly *B. b. antiquus*. The modern prairie bison, *B. b. bison* evolved from this intergrade, probably during the Hypsithermal (5000-7000 b.p.) when extensive grasslands developed. *B. b. athabascae* displays greater morphometric resemblance to *B. b. occidentalis* and has affinities with woodland habitats more associated with ancestral forms. Shapiro et al. (2004) used ancient DNA and Bayesian techniques to reconstruct the genetic history of bison throughout the late Pleistocene and Holocene. During deglaciation, the first bison into the ice-free corridor were evidently of southern origin, and the authors concluded that modern bison are mainly derived from a clade originating south of the ice sheet, distinct from Beringian bison.

Human Disturbance of Habitat

Human activities on the landscape often modify habitats in ways that result in profound changes in ungulate distribution, often leading to species substitution. Habitat alteration has been an important factor in the widespread distribution of white-tailed deer across North America (Waller and Alverson 1997, Hosley 1956, Kramer 1972). Northward expansion of deer in Ontario coincided with logging and settlement (Dawson 1963). Deer rapidly expanded northward between Lake Superior and the Quebec border after 1900, reaching maximum limits of expansion about 1940. Following fire control and regrowth of forest habitat, deer populations declined and range contracted. Deer expanded their range at the turn of last century from southern Quebec across the Gaspe Peninsula, following human disturbances such as logging, agriculture and wolf control (Lesage et al. 2000*a*). In northern Alberta, white-tailed deer are closely associated with nutritious agricultural crops (Prescott 1974). Similar trends have been reported in Eurasian species of deer. In Yakutia, Russia, agricultural activities have facilitated northerly and westerly expansion of roe deer (Egorov 1965).

Extensive prairie lands of northwestern Minnesota were cleared and drained for agriculture in the early 1900s (Phillips et al. 1973). By the mid-1930s much of the farmland was abandoned and subsequently developed into large expanses of willow, aspen and marsh. Since then, moose have invaded these new habitats and expanded westward.

Kochy and Wilson (2001) detected a strong correlation between anthropogenic nitrogen deposition and forest expansion in several northern Great Plains parks. Where the limiting resource for plants is nitrogen, tall woody species with large receptor surfaces are better able to intercept airborne particulate nitrogen than grasses. Trees, shrubs and browsing ungulates should benefit most, while grazers such as bison would be at a disadvantage. Over the last six decades, forests near large metropolitan centres in high deposition areas, such as Elk Island and Prince Albert National Parks in Canada, expanded ten times faster than forests in low deposition areas such as Wood Buffalo or Jasper National Parks.

Archaeological evidence indicates that bison did not invade the region east of the Mississippi River until some time after the year 1000 (Roe 1970). Bison habitat was enhanced by aboriginal use of fire, which may have contributed to significant range expansion.

Translocation

Wildlife management agencies often remove individuals of a species from one location and place them in another to repatriate a species into former range, augment existing populations with additional animals, or introduce exotic species into new range. Immigrants to islands are usually strong competitors (Ricklefs 1979). Most invaders exhibit ecological release as populations grow rapidly and occupy a variety of habitats, many of which are not inhabited on the mainland. For six species of deer introduced into Victoria, Australia, the number of individuals introduced (propagule size) was a significant predictor of success (Forsyth et al. 2004). Nine introductions of four or fewer individuals failed, whereas six of seven introductions with seven or more individuals succeeded. Migratory species were less likely to become established than non-migratory species, species with wider climatic tolerances were more likely to have wider spatial ranges, species with larger spatial ranges had higher population growth rates, and species with larger original range sizes had larger total range sizes. A similar propagule size threshold (six individuals) was apparent for ungulate introductions to New Zealand (Forsyth and Duncan 2001).

Eruptive oscillation in ungulates occurs when a large discrepancy exists between the number of animals the environment can support and the number of animals actually present (Riney 1964). Most basic interactions between an animal and its environment exist, regardless of whether the species is newly introduced or re-introduced, native or exotic, wild, domestic or feral. In an established population, eruptive oscillation can occur when the environment suddenly becomes more favourable, such as following a disturbance (e.g. logging, overgrazing, fire), or when the number of animals in a population is significantly reduced. Riney (1964) described four stages of a typical ungulate introduction. Initially, mortality is low, the population increases rapidly, and vegetation quality in critical parts of the habitat begins to decline. In the second stage, vegetation quality continues to decline and the population exceeds its carrying capacity. Reproduction remains high because the large proportion of younger age groups in the population creates a reproductive time lag of several years. Even if mortality of young starts to increase, the total population continues to rise. The physical condition of individual’s declines, especially in critical periods of the year, and in the latter part of this phase animals can be in poor condition even at the most favourable times of the year. Large-scale mortality is apparent by the third stage, especially when a critical resource becomes limited, such as water in drought years. Overpopulation continues in the early part of this stage, and later food resources in the most heavily utilized parts of the range begin to recover. In the final stage, the population adjusts to the carrying capacity of the habitat. In the early part of stage 4, a population can be slightly below carrying capacity, but not so low as to initiate an eruptive cycle. The time between the start of stage one and the peak of stage two will be longer if the nucleus population is able to disperse into areas progressively more remote from the release site. In general, the minimum time between initiation of the oscillation and an eruptive peak is 15-20 years for medium sized ungulates (reedbuck, impala). For red deer in New Zealand it is approximately 20 years. The rate of dispersal is an important factor affecting the oscillation period. Caughley (1970*a*) listed several examples of probable irruptive fluctuations of ungulates. When he tested Riney's model on Himalayan Thar, introduced to New Zealand in 1904, results supported the model.

Caribou were repatriated to Southampton Island in northern Canada in 1967. The population increased almost 100 fold by 1983 (Heard and Ouellet 1994). Instead of extending their range radially from a zone of high density, as in Riney's model, caribou spread over the entire island; density increased only after all apparent habitat was occupied.

A bull and cow moose released in 1878 and two bulls and two cows released in 1904 founded the entire moose population of Newfoundland, covering the whole island by 1945 (Pimlott 1953). The spread of moose was characterised by a 25 year period of rapid dispersal and low density, followed by a period of build up to high densities.

Growth of a reintroduced muskoxen herd in the Arctic National Wildlife Refuge of northeastern Alaska occurred in three stages (Reynolds 1998). Slow growth in 1969-70, immediately after release, was followed by a decade of irruptive rapid growth. In the final stage, the population declined and stabilized in the regions of initial occupation, concurrent with emigration of mixed-sex groups into additional regions.

Wood bison repatriated west of Great Slave Lake (Mackenzie Bison Sanctuary) closely followed Riney's model (Larter et al. 2000). Increases in density and intraspecific competition were followed by expansion into new range. The expansion population benefited from better quality forage and lower calf mortality.

Biophysical Constraints

The range inhabited by a species is generally surrounded by ecological and/or physical barriers (Allee and Schmidt 1966). Dispersal is significantly influenced by the inherent power of movement by individuals (vagility; Odum 1971). Corridors offer relatively little resistance to dispersal, whereas filter routes allow passage of only some species (Vaughn 1972). Beringia filtered ungulates maladapted to temperate conditions, while the Panama isthmus filtered ungulates poorly adapted to tropical conditions.

Terrain and Landscape

High elevation may restrict dispersal because of slope, low temperature, or low atmospheric pressure. Wild sheep, ibex (*Capra sp.*) and yak (*Bos grunniens*) are unable to range much higher than 5800 m because of lack of oxygen, not because of low temperature or food availability (Allee and Schmidt 1966). The direction that mountain ranges extend also has an important effect on dispersal. East-west ranges in Eurasia such as the Pyrenees, Alps, Carpathians, Caucasus, Hindu Kush, Himalaya, Tien Shan and

Altai intensify climatic barriers. During periods of global cooling, higher rates of extinction occurred in Eurasia because these mountain ranges became more of a barrier to animals seeking warmer climates than the north-south New World mountain ranges (John 1977). South of the Sahara in Africa, there are no extensive mountain ranges and species distribution is widespread (Allee and Schmidt 1966). In southeastern Alaska several small moose populations are restricted to river valleys (LeResche et al 1974). Moose invaded the Yakutat area by the Alsek River in the 1920s or 1930s following the retreat of glaciers that previously blocked the valley (Klein 1965). In southcentral Alaska, moose were isolated from Prince William Sound by both glaciers and Miles canyon on the Copper River. A population was established on the Copper River delta through a series of transplants (LeResche et al. 1974).

Waterbodies pose a significant barrier to island colonization unless they freeze, or the distance is short enough for animals to swim. Moose were able to cross to Isle Royale and woodland caribou to the Slate Islands when Lake Superior froze between these islands and the mainland (Allen 1979). Moose were unable to cross to good quality habitat in Newfoundland without human intervention.

Habitat Type

Geist (1971) described the effect of habitat stability on ungulate movements. *Caprinae* habitat in mountains is typically comprised of stable climax grass communities. Some grassland created by fire is slow to revert to forest. Habitat is discontinuous and patches are linked together by migration routes. During warmer drier periods, montane grassland habitats expanded, then as forest cover spread in cooler, wetter periods, probably allowing mountain ruminants to continue normal movements between shrinking patches. Under natural conditions, virtually all range is occupied. Because dispersal does not usually lead to discovery of new habitat, it is more advantageous for home range knowledge to be transmitted from one generation to the next, and for yearlings to follow other adults after weaning.

Presently, bighorn sheep populations occur in small isolated groups because of catastrophic declines in the late 1800s and early 1900s (Singer et al. 2000*a*). They probably occurred in a naturally fragmented distribution with population centres located on rugged mountainous terrain. When dispersal did occur, it was typically into contiguous habitat already occupied by other bighorns, and rarely into unoccupied habitat. Although they occasionally engage in exploratory behaviour, successful colonization is unusual. Efforts to increase bighorn sheep populations have included extensive translocations, but many have resulted in small, sedentary and stagnant or declining populations that avoid travelling through timber. Despite the low success rate, over half of extant populations are the result of translocations (Gross et al. 2000). Sedentariness is considered one of the largest problems challenging long-term persistence of bighorn sheep populations (Risenhoover et al 1988).

In contrast to bighorn sheep and other mountain caprinids, several species of cervids, such as moose, select fluctuating, early successional habitat, and are more capable of expanding their distribution (Geist 1971). Movements of yearling moose driven off by cows after weaning often appear erratic (Houston 1968). New home ranges are established through individual exploration of transient habitat that is linked to permanent habitat.

According to the Bell-Jarman Principle, body size determines forage selection of ruminant species (Renecker and Schwartz 1998). Forest vegetation tends to concentrate nutrients in leaves, buds and twigs, and provides cover from predators. Ruminants that select dense forested habitats are generally small, solitary and laterally compressed. Small ruminants select for high quality browse that passes rapidly through the digestive system because of relatively high metabolic requirements (Renecker and Schwartz 1998), and they tend to evade predators by hiding (Estes 1974). Open habitats lack high quality food that small ruminants require, and make them conspicuous to predators. An exception to this rule is the moose, the world's largest cervid, that must select food patches that permit high rates of intake, especially in winter, when food quality deteriorates and movement through snow is energetically costly. Another exception to the Bell-Jarman Principle is the giraffe, the world's largest ruminant. Here, dense food patches are individual acacia or other trees.

Open plains may provide extensive food patches, and vigilance behaviour allows escape from predators. Ruminants adapted to open plains are generally large and gregarious. Bison are bulk feeders able to digest large amounts of low quality fibrous forage in voluminous rumens (Houston 1982, Hudson and Frank 1987, Hanley 1982). Plains species often depend on open environments such as grasslands where bulk food is abundant, but low in nutritional quality, and avoid predators by running (Estes 1974). To consume enough forage, minimal time must be spent searching. When nutritional quality of grass reaches intolerably low levels because of desiccation, the mobility required to take advantage of irregularly distributed rainfall that produces fresh grass is facilitated by large body size. In forested habitat, rapid locomotion is hampered, especially for larger mammals. Of the large African ruminants, only the buffalo and okapi occur in the African rain forest (Allee and Schmidt 1966). Dispersal in forest may be limited because of sparsely distributed food and obstructed escape from predators.

Human Predation

Unparalled in the fossil record or on other continents at the same time, the extinction of more than half of the large mammals in the Americas was attributed to direct effects of human predation (Alroy 2001), or a combination of human predation and climate change (Ward 1997). Archaeological evidence indicates large human populations has been present in the Americas since 13,400 years BP, coinciding with the beginning of the mass extinction period. Alroy's simulation of human population growth, hunting patterns, and population dynamics of 41 large herbivores (30 now extinct) indicated that human density had to be less than 0.13/km^2 for all species to survive. However, this was an order of magnitude lower than the observed range of hunter-gatherer densities.

The keystone herbivore hypothesis suggests that large grazing mammals maintain open grasslands, and if these herbivores are removed by human predation, grasslands may succeed to other vegetation types such as shrubland or forest (Owen-Smith 1987). Zimov et al. (1995) applied this concept to Siberia, western Alaska and Beringia using a simulation model that suggested human predation could also have indirect constraints on ungulate dispersal. In Beringia, semi-arid grass-steppe largely converted into wet moss tundra after much of the grazing megafauna consisting of bison, muskoxen, horses (*Equus spp*.) and mammoths (*Mammuthus primigenius*) disappeared. This coincided with improved human hunting weaponry at the end of the Pleistocene. Grasslands have high rates of evapo-transpiration that reduce soil moisture and are adapted to grazing. Mosses are lower in productivity, increase soil moisture and are vulnerable to damage by trampling. Human predation may have caused a biome shift from steppe to tundra hindering the re-establishment of grazing ungulates.

Kay (1998) proposed that before their populations were devastated by introduced diseases, aboriginal people of North America were the ultimate keystone predator. Native Americans were highly efficient predators who could rely on a variety of alternate food when meat was unavailable. There is evidence that humans suppressed moose, bison, elk, deer and muskox populations to very low levels in historical times (Fritz et al. 1993, Krech 1999, Isenberg 2000). The shrub-steppe region of western Montana, central Idaho and southeastern Washington was considered a game sink mainly because of human predation (Martin and Szuter 1999). Aboriginal harvest may have limited growth of moose numbers on the Colville River, Alaska, until the 1920s when humans moved to the coast, and hunting pressure on the river was relaxed (LeResche et al. 1974). However, there remains debate and uncertainty about the extent to which human predation altered wildlife populations and distributions (Yochim 2001).

In Norway and Sweden, moose hunting was formerly restricted to nobility, and poachers were severely punished (Markgren 1974). After hunting rights were granted to commoners in Sweden in 1789, the moose population was almost exterminated; this trend was similar in Norway and Finland. Since 1830, hunting restrictions and predator reductions in Scandinavia resulted in moose dispersing to most of the present range limits by the end of the 19th century. During human famines, many moose populations in Europe were severely depleted, and in southern, western and central parts of Europe, they were exterminated by the13th century (Pulliainen 1974). After 1850, when moose distribution was at a minimum, numbers increased when protective measures and wolf control were implemented. Moose reintroduced near Warsaw, Poland have expanded their numbers and wandering individuals have been seen in neighbouring countries.

Moose distribution contracted during the 19th century in Siberia. Subsequent range expansion after the beginning of 20th century may be due to decreased hunting pressure and conservation measures (Kistchinski 1974). Murie (1934) reported that moose from the mainland were prevented several times from becoming established on Isle Royale because of hunting. It was not until the winter of 1912-13 that they successfully colonised the island.

Mountain goats that occupy the most rugged and remote terrain are less vulnerable to hunters (Rideout 1978). The mountain goat population in Glacier National Park is characterised by high density and large group sizes (Singer and Doherty 1985). After reaching peak numbers, introduced herds stabilized with little or no compensatory reproduction for hunter harvests.

Muskoxen populations have increased dramatically since the early 1900s, reoccupying much of their former circumpolar range (Reynolds 1998). Overexploitation by humans and severe weather likely caused earlier declines.

Around the time of human colonization of North America, the *B. antiquus* variety of bison dominated the Great Plains ungulate community (Guthrie 1970). It was possibly extirpated along with other large-sized bison such as *B. latifrons*, by advancing hunting societies. Modern plains bison usurped the vacated niche on the Great Plains as the dominant grazer. This new smaller form was reproductively mature at a younger age, possibly making them better adapted to human predation (Guthrie 1970, Wilson 1992). Limited range extension of plains bison into eastern and western mountain ranges suggested it was a relatively late arrival, and *antiquus* populations on the west coast disappeared without being replaced (Guthrie 1970). Van Vuren (1987) considered human hunters, particularly after obtaining the horse, quite capable of exterminating small bison populations, preventing them from establishing west of the Rocky Mountains. Hornaday (1889) documented that technological improvements in firearms and ammunition accelerated the extermination of plains bison throughout most of its range. Wood bison disappeared from the Yukon and Alaska by the early 20th century, probably because of hunting (Guthrie 1968, Stephenson et al. 2001).

Land Use Conflict

Human activities on the landscape are often incompatible with wild ungulates. Their presence may not be tolerated, or habitats may be altered in such ways that they can no longer be occupied or traversed by native species. If migrants are culled when they leave protected areas, migratory habits may be eliminated, favouring survival of non-migratory individuals (Leopold et al. 1963).

Since the 1980s most of the deciduous forest and natural open fields in eastern Hokkaido, Japan have been converted to agriculture (Mayumi et al. 2003). Increased forage resources and protection of females from hunting resulted in a Sika deer population irruption. Migrants used agricultural lands less than predicted because of aggressive deterrence by humans. In central Asia, the wild yak has lost most of its preferred alpine meadow and steppe habitat to pastoral activities (Schaller 1998).

The greatest diversity and abundance of African ungulates now occur mainly in undisturbed habitats in eastern and southern parts of the continent. Most game preserves have been established without ample consideration of the spatial movements of wildlife (McNaughton 1985). In a portion of the Kalahari within Botswana, wildebeest previously had access to three main river systems. Fences now restrict them to Lake Xau, where access has diminished because of expanding livestock production and human settlement (Williamson et al. 1988).

In the 19th and early 20th century, large numbers of sheep, goats and cattle pastured in Scandinavian forests competed with wild ungulates for forage (Markgren 1974). Agro-sylviculture, urbanization and infrastructure development, among other human activities, were considered by Perez et al. (2002) as the primary threats to Spanish ibex (*Capra pyrenaica*) conservation. Reservoirs, canals and aqueducts usually impede movements of mountain sheep (Singer et al. 2000*a*). Fences, roads, and towns have severely disrupted movements of desert bighorns (Bleich et al. 1996). Advanced fire suppression has enabled encroachment of tall shrubs and trees into early seral habitats required by sheep.

The dispersal capacity and reproductive ability of tule elk (*Cervus elaphus nannodes*) have made them effective colonizers, but their range includes some of the richest agricultural land in California (McCullough et al. 1996). Conservation measures have rescued them from extremely low numbers and tule elk now survive in scattered populations. In the Greater Yellowstone Ecosystem, about three-quarters of bison, elk and pronghorn migration routes have been lost (Berger 2004), primarily due to lack of tolerance for bison outside of protected areas, winter feeding of elk, an increase in the local human population, and loss of habitat.

Competition

Elton and Miller (1954) identified two principal components of competitive interactions. Exploitation occurs when organisms utilize common resources that are in short supply, and interference occurs when organisms seeking those resources have their access limited by others. Krebs (1972) suggested that the first indication of competition between two closely related species is that their spatial distributions do not overlap. The second indication is when one species is absent and the other occupies a wider range of habitats.

The "Competitive Exclusion Principle" states that complete competitors cannot coexist (Hardin 1960). Competitive exclusion is a transient phenomenon because the poorer competitor is always eliminated (Ricklefs 1979). When it occurs it is likely intermittent and not always evident (Weins 1977). Outcomes of competitive interactions are not always predictable because conditions influencing form and intensity of competition vary locally (Boer 1998). Organisms are able to increase competitive ability if they evolve interference mechanisms or become more efficient exploiters of a common resource. Ungulates of North and South America evolved independently for millions of years until the land bridge emerged five million years ago, allowing faunal exchange. Because northern immigrants to the southern continent were superior competitors they caused the disappearance of many South American ungulates (Simpson 1950).

Within goat (*Capra spp*.) and sheep genera, species often divide mountain ranges in half and restrict overlap to a narrow zone (Schaller 1977). The Kuban ibex and Dadestan tur (*C. cylindricornis*) have partitioned the Caucasus into eastern and western halves. On the Gadabar Ghar massif in Pakistan, the markhor (*C. falconeri*) occupy the western half while wild goat (*C. aegagrus*) occupy the eastern half.

Although elk are primarily grazers, they may also include browse depending on food availability (Houston 1982). Moose introduced to Colorado from 1978 to 1993 compete with native elk herds for willow (Boer 1998). Houston (1968) suggested that moose dispersed at low densities may have a competitive edge over herd species such as elk in winter because moose are able to use scattered forage more efficiently than large concentrations of elk. According to Cowan (1950), when elk were introduced into Banff and Jasper National Parks in 1917 and 1920, moose, mule deer and mountain sheep were the ancestral ungulate community. Elk food preferences overlapped with the original ungulates and competition increased as elk numbers grew. Elk dominated moose and mule deer in competitive interactions probably because of their diversity of diet. Mountain sheep populations remained stable probably because of spatial separation and minimal competition between elk and mountain sheep. Elk apparently out-compete moose in some conditions (Cowan 1950, McMillan 1953, Flook 1964). High elk numbers using riparian habitat in summer may reduce the amount of willow browse available to moose in winter when elk have migrated elsewhere (Martinka 1969, Telfer and Cairns 1986). In the Yakutia region of Russia, well defined competition between elk and moose for willow in streambeds only becomes important at high densities (Egorov 1965).

In Wind Cave National Park, South Dakota, the greatest spatial overlap between mule deer and elk was during summer (Wydeven and Dahlgren 1985). Competition was expected to be low because mule deer selected forbs and browse, while elk consumed graminoids. However, elk may have displaced mule deer from portions of the park through agonistic behaviour and competition for browse during periods of high elk density. During winter there was lower potential for competition because of different spatial distribution and food habits, but competition could be possible if severe winters cause elk to browse more extensively. In central Montana, competition between mule deer and elk appeared to be most intense during spring and summer (Mackie 1970). Direct competition between elk and pronghorn (*Antilocapra americana*) could increase in autumn and winter if increasing numbers of elk fed more extensively on forbs.

In northern Montana, white-tailed deer range expansion into mule deer habitat coincided with decreased mule deer populations (Martinka 1968). Higher deer densities may increase competition between the two deer species during severe winters. In Alberta, much of the southern mule deer range has been invaded by white-tails (Soper 1964). The reverse is evident in the Dos Cabezas Mountains of southeastern Arizona where mule deer appeared to be the superior competitor (Anthony and Smith 1977).

Although Fisher and Gates (in press) found no evidence of wood bison and woodland caribou competition in the Yukon during winter, there is potential for exploitative competition during autumn when significant use of lichens by bison was observed in the Mackenzie Bison Sanctuary (Larter and Gates 1991*a*).

Guthrie (1970) theorized on bison evolution and competition. Bison occupied the large bovid grazing niche in northern Eurasia. In the warmer south (including tropical regions) it was occupied by wild cattle species such as auroch (*Bos primigenius*), zebu (*B. indicus*), banteng (*B. banteng*), kouprey (*B. sauveli*) and gaur (*B. gaurus*), and buffalo genera, consisting of *Syncerus* and *Bubalus*. An exception was the yak, a species of wild cattle that was able to invade the cooler Himalayas. Because of diet similarity between *Bison* and *Bos* they become biotic barriers to each other. Although bison did not penetrate southern Eurasia because of competitive exclusion, there was no such limitation in North America. Bison underwent considerable range expansion and phylogenetic change in the New World that was unparalleled in the Old World. In the northern environment of Eurasia and Alaska, *B. priscus* existed almost unchanged throughout the latter half of the Pleistocene until its extinction by either rapid evolution or elimination (Guthrie 1970). This form of bison appears to have flourished as the dominant ungulate in northern regions (Guthrie 1968). When bison dispersed into the North American interior, the complex ungulate community it encountered (dominated by horses) was not competitive enough to prevent colonization, possibly resulting in the decline of horses during the late Pleistocene (Guthrie 1970). The fossil record suggests that there is insufficient specialization of Bison to allow stable sympatric distribution of more than one form for any extended periods of time. The modern plains bison and European counterparts (*B. b. bonasus* and *B. b. caucasus*) replaced the earlier forms either through direct competition, or passive replacement whereby the indigenous form became extinct and the niche was immediately occupied by a new variety.

Alternate Prey

Two species may be in "direct competition" for resources or exhibit "apparent competition" if they share a common predator (Holt 1977). In a single prey scenario, a predator's numbers are limited by one feedback pathway. The addition of an alternate prey species may increase the density of the predator by expanding its resource base, leading to heavier predation on the original prey species. Thus survival of the most vulnerable prey can become independent of its own carrying capacity, yet indirectly and critically dependent upon the carrying capacity of the less vulnerable prey. In South Africa's Kruger National Park, Harrington et al. (1999) implicated lion predation as the cause of a roan antelope population crash. Influx of zebra into antelope range during drought conditions may have led to an increase in lions.

Simkin (1965) hypothesized that caribou could decline from apparent competition with moose if wolves are the shared predator. In British Columbia where moose expanded after 1900, providing a greater prey biomass for wolves, subsequent higher predation on caribou may have resulted in local extinctions (Bergerud and Elliot 1986). Seip (1992) suggested that increasing wolf predation was the major cause of the declining caribou populations in the Quesnel Lake and Wells Gray Provincial Park area of southeastern British Columbia.

Alternate prey may include other ecotypes of the same species, such as migratory and resident caribou (Schaefer et al. 1999). The Red Wine Mountains caribou population of central Labrador declined drastically from the 1980s to the 1990s, while the adjacent migratory George River herd grew and expanded its range. Subpopulations of the Red Wine Mountains herd with the greatest range overlap with the George River herd experienced the highest mortality. Schaefer et al. (1999) concluded that refuge from other ungulates, including other caribou, were important for persistence of some caribou populations.

Augmentation of existing endangered woodland caribou populations along the southern parts of its former range in Idaho has been implemented as a conservation measure. In addition to loss of habitat, failure to reverse the caribou decline may be attributed to an increased cougar population resulting from an expanded white-tailed deer prey base (Zager et al. 1996).

While many mule deer populations throughout western North America seem to be declining, white-tailed deer populations are increasing (Robinson et al. 2002). In south central British Columbia, the main cause of mortality in both species was cougar predation. The lower survival rate of mule deer was directly linked to a higher predation rate compared to white-tailed deer. The disparate survival and predation rates were consistent with the apparent-competition hypothesis. Moose appeared to be declining in the Mackenzie Bison Sanctuary while the reintroduced wood bison population was erupting, and wolves were probably increasing (Larter et al. 1994). The proportion of moose in the wolves' diet was significantly higher than its availability. In an adjacent area with less wolf activity, moose densities were twice as high.

Food Availability

Ungulate distribution and home range size are strongly influenced by habitat productivity and forage resources that are often distributed in a patchy environment (Ford 1983). The botanical environment of Beringia during the late Pleistocene appeared to have inadequate forage productivity to sustain the abundance of large ungulates (Hopkins et al. 1982). According to Laxton et al. (1996), this paradox is reconciled by localized "hotspots" of loess-fed soils conducive to extremely productive grasslands capable of sustaining large ungulate populations in an otherwise impoverished ecosystem.

Winter food profoundly influences moose distribution (Kelsall and Telfer 1974). Even where a variety is available, only a few selected plant species are consumed in large quantities. Some genera such as willow are important at both the southern extremities of moose range, which are characterized by greater food diversity, and the northern periphery where choices are much more reduced. Moose have been observed wintering above the treeline in river valleys where willows are present (Kelsall 1972).

Lyman and Wolverton (2002) reviewed archaeological evidence and concluded that bison were never abundant west of the North American continental divide. Van Vuren (1987) suggested a contributing factor might have been low carrying capacity. Physical barriers are an unlikely constraint as Haines (1967) described potential avenues for bison immigration westward through the Rockies.

Mack and Thompson (1982) discussed the phenology of dominant plant species in intermountain grasslands as an explanation for lack of bison. Grasses and large herbivorous mammals with hypsodont dentition first appeared in the Eocene and evolved together (Stebbins 1981). Basal meristems, small stature, high shoot density, rapid turnover of deciduous shoots, below ground nutrient reserves and rapid growth are characteristics of grasses adapted to convergent pressures of both aridity and grazing (Coughenour 1985). Grasslands east of the Rocky Mountains are dominated by rhizomatous/stoloniferous species (Daubenmire 1978). Tall, tussock-forming caespitose grasses from boreal regions are adapted to conserve energy and immigrated from the north into the intermountain trough (Daubenmire 1975). Much of the ice-free mid-continent east of the mountains was occupied by bison; after the last deglaciation, they proliferated. The chronology of calving and maximum milk production in bison is well suited to staggered phenology of grasses in this part of the continent, where different grasses become available to bison throughout the year (Peden 1976). In contrast, it is unlikely that large herds occurred in open steppe west of the Rockies where dominant grasses aestivate during much of the summer and are intolerant of grazing and trampling. Caespitose grasses may have persisted through the Quaternary because large-hooved congregating mammals did not override macroclimatic selection for this grass form. Although small herds of elk occurred west of the Rocky Mountains (Rickard et al. 1977), their distribution was probably also restricted in similar ways, and only became common in areas after wolves were eradicated (Lyman and Wolverton 2002).

Following livestock and exotic introductions, tussock grasslands of New Zealand have experienced massive replacement by alien rhizomatous grasses since mid-nineteenth century (Godley 1975). No indigenous rhizomatous grasslands in temperate regions display human-induced change to such degree. This suggests that the extent of co-evolution of large mammalian herbivores and plants in these grasslands may be predicted to some extent from characteristics of the dominant grasses. Steppe from Ukraine to Kazakstan is an apparent exception where most dominant grasses are caespitose, despite a long association with saiga (*Saiga tartarica*), camel (*Camelus dromedarius*), gazelle (*Gazella sp*.), wild ass and auroch. Eurasian caespitose grasses have adaptations to mammalian grazers, but little is known about how their selection forces compare with bison.

Climate

Snow Accumulation: Snow restricts forage availability, increases energy costs of foraging, alters habitat selection and movement patterns, and increases energy costs of locomotion (Fancy and White 1987). Snowfall effects can be offset by an abundance of food and cover (Edwards 1956), and topography where snow can be blown away or melted (Stelfox and Taber 1968). When Telfer and Kelsall (1984) used chest height, foot loading and behaviour to calculate indices of snow coping ability for several North American ungulates, those with higher indices occurred in snowier regions. Of the species studied, pronghorn, short-grass plains specialists, had the lowest indices. Elk, white-tailed deer and bison tolerate the shallow soft snow of the southern boreal forest. Caribou had the highest indices of snow coping ability and, as expected, subsist further north, where snow cover is deeper and persists longer. On mule deer winter range in Middle Park, Colorado, snow that was over 46 cm deep essentially excluded them from large areas (Gilbert et al. 1970). The capacity of white-tailed deer fawns to survive their first winter could influence species distribution in north eastern North America (Lesage et al. 2000*b*). The quality of winter range would likely be important for maintenance and expansion of northern populations. They did not penetrate the boreal forest biome in Quebec apparently because of excessive snow depths (Prescott 1974).

Moose are uncommon or absent in eastern Quebec where snow depth regularly exceeds 500 cm (Brassard et al. 1974). In nearby Labrador, slow dispersal of moose may be due to deep snow (Mercer and Kitchen 1968). Studies in Canada and Russia suggest that moose travel easily in snow up to 60 cm in depth, but are impeded by soft snow up to 100 cm, which is the approximate chest height of an adult (Kelsall and Telfer 1974). Nasimovich (1955) described areas in Russia where 70 cm of soft snow is prevalent and there are no moose. They may occupy regions of deep snow if there is adequate food or tree canopy, but not at high altitudes and latitudes where trees are open-growing and branched to the ground. Moose are sparsely distributed or absent in high snow fall areas adjacent to the Sea of Okhotsk and Kamchatka (Kistchinski 1974). Singer and Doherty (1985) found a significant negative correlation between mean monthly snow depths and mean monthly elevation of collared mountain goats.

Aridity: Extinction of desert bighorn sheep populations in California is more likely in low elevation mountain ranges (less than 1500m), where precipitation is below 200 mm, there are few natural springs, and where there is range overlap with domestic sheep (Epps et al. 2004). These findings suggest desert bighorns are vulnerable to climate warming and it has already affected their distribution. Lower temperatures associated with high elevation mountain ranges alleviate water requirements for sheep and provide a longer growing season. The distribution of desert bighorns has probably fluctuated for centuries, expanding in cool wet periods and contracting to higher elevations as climate became warmer and drier.

In Kruger National Park, severe population declines of roan antelope (*Hippotragus equinus*), sable antelope (*H. niger*), tsessebe (*Damaliscus lunatus*), kudu (*Tragelaphus strepsiceros*), waterbuck, warthog (*Phacochoerus africanus*) and eland occurred during a period of extreme reduction in dry season rainfall from 1977-1996. This coincided with a rise in regional temperature (Ogutu and Owen-Smith 2003). Zebra, giraffe, wildebeest and impala populations remained stable. Species that remained abundant possessed diverse feeding habits. Forage production during the dry season had a greater influence on ungulate population dynamics than forage production during growing season. Grazers were more affected by rainfall variability than browsers because the herbaceous layer is more sensitive to moisture than woody vegetation. The southern limits of Roan antelope, sable antelope, and tsessebe reach Kruger National Park and may have been undergoing range contraction in response to increasing aridity and habitat change. Protected areas are increasingly becoming surrounded by fences and other barriers to movements that otherwise might be made by large mammal populations in response to habitat changes. Habitat use by white-eared kob was constrained by the availability of water as herds were rarely observed farther than 10 km from water sources (Fryxell and Sinclair 1988*b*). The aridity of the hypsithermal period is a possible explanation why moose did not disperse through mountains to occupy the interior plateau of British Columbia at that time (Kelsall and Telfer 1974).

Temperature: Many mammals are more sensitive to heat in summer than cold in winter (Allee and Schmidt 1966). The Shirasi moose has not dispersed westward along the corridor of the Okanagan highlands in southern British Columbia and northern Washington to potentially suitable habitat in the Cascade Mountains or the central coastal rain forest (Kelsall and Telfer 1974). The presence of moose in similar habitat in British Columbia and Alaska suggests hot summer temperatures may be preventing them from occupying these areas by high summer temperatures.

Disease

According to Hess (1996), highly contagious diseases of intermediate severity present the greatest conservation risk to wildlife populations. Severe diseases tend to disappear rapidly because either the local population dies out or dispersal is too low to spread the disease across the metapopulation. When a shared parasite effects species differently and influences the outcome of interactions, parasite-mediated competition may be the result. A lack of evidence of elk, moose, or caribou in North America from before the Pleistocene indicates that they were very late immigrants from Asia (Scott 1937). Certain parasites that have evolved a stable relationship with North American deer of the genus *Odocoileus* cause mortality in cervids that invaded the continent during the Pleistocene (Kelsall and Telfer 1974). Examples include *Elaeophora schneideri*, which is benign in mule deer, but causes mortality in elk (Hibler and Adcock 1971), and the meningeal nematode (*Parelaphostrongylus tenuis*), which does not harm white-tailed deer, but is lethal to moose and caribou (Anderson 1972). *P. tenuis* is potentially a limiting factor for woodland caribou in eastern and central Canada (Anderson 1972, Pitt and Jordan 1994). Some translocations of woodland caribou such as at Michipicoten Island in Lake Superior have been considered successful, but no reintroductions have persisted where high white-tailed deer populations exist with meningeal worm (Bergerud and Mercer 1989).

Kelsall and Telfer (1974) noted that moose are conspicuously absent in the deciduous biome and southward extension of the deciduous-coniferous transition of the Appalachian Mountains. South of deep snow regions, white-tailed deer diets consist of a high proportion of mast and herbage (Murphy 1970). There appears to be an empty niche for a browser, however *P. tenuis* may be limiting moose dispersal (Kelsall and Telfer 1974). Whitlaw and Lankester (1994) questioned whether this parasite actually restricted the distribution of moose in Ontario. Although populations consistently declined when deer densities exceeded 5/km^2, the effect of *P. tenuis* could not be separated from other factors known to influence cervid numbers. In areas where moose and deer coexisted, and *P. tenuis* was endemic, moose still persisted (often at low densities) and no catastrophic declines or extinctions had been observed.

Bighorn sheep are highly susceptible to pneumonic pasteurellosis from contact with domestic sheep and catastrophic mortalities have resulted (Foreyt and Jessup 1982). Bighorns now occupy about one third of their historic range (Gross et al. 2000). Epizootics are able to kill up to three-quarters of a population in a single year and reduce recruitment for an additional three to seven years. Disease has a more profound influence on sheep survival than habitat loss or fragmentation. Simulated population dynamics in the South Dakota Badlands ecosystem that were subjected to a range of conditions showed that in the absence of disease, extinction rates were low and insensitive to rate of colonization or area of suitable habitat.

Migration Initiation Thresholds

Factors that stimulate migration are quite dependent upon the animal's expectation of improved environment at a particular time of year, and this would change with the time of year (Baker 1978). Leuthold (1977) stated that migratory populations (or portions of them) may become sedentary as environmental conditions ameliorate.

Snow

The presence of snow has a significant effect on an individual's mobility and food availability. Heavy snowstorms cause mule deer to migrate to winter range (Russell 1932). For most Kaibab mule deer, seasonal migration from high plateau summer range to lowland winter range is triggered by the first persistent snow cover, usually in November (Barlow and McCulloch 1984). Where persistent snow cover occurs, white-tailed deer migrate between summer and winter ranges (Messier and Barrette 1985, Nelson 1995, Van Deelen et al. 1998). Hoskinson and Mech (1976) suspected that in northern Minnesota, fall migration was triggered by a combination of snow accumulation and low temperature. In the Adirondack Mountains of New York, Tierson et al. (1985) observed deer began movements to winter range when snow depths approached 38 cm. In New Brunswick, this occurred when snow depths exceeded 30 cm in hardwood stands (Drolet 1976). Although white-tailed deer typically yard together in winter, concentrations may not develop if snow conditions do not inhibit travel (Moen 1973). In prairie and agricultural habitats of South Dakota, where temperatures are cold and there is little snow, Sparrowe and Springer (1970) reported that up to 30% of white-tailed deer remained dispersed during winter. Where persistent snow cover is absent, white-tailed deer are quite sedentary (Larson et al. 1978, Lincoln 1992, Loudon and Brinklow 1992).

In Wells Gray Park, British Columbia, Edwards and Ritcey (1956) observed that moose spent the summer at high elevations up to the timberline. Autumn migration was triggered by snowfall, and depths increasing faster at higher altitudes caused moose to gradually descend. The critical snow depth appeared to be 75cm. Knowlton (1960) also suggested that winter snow depths in Montana initiated movements of moose downward from upland summer range. Scandinavian moose carry out regular winter migrations from mountains to valleys but if there is little or no snow they may remain at high altitudes (Pulliainen 1974). In the Kisloretsk area of the Russian Lapland Game Preserve, the majority of moose migrate to the southwestern part of the preserve and deep snow is regarded as the primary cause. In the central and southern Ural Mountains, moose that summer on western slopes migrate along valleys to eastern slopes where snow is shallower. Although this movement usually occurs during November and December, migration is as late as February in winters with little snow, and ceases when snow reaches 20-30 cm. Autumn moose migration in Sweden seemed to be triggered by 40 cm of snow (Sandegren et al. 1985).

The first heavy snowfall of the season possibly caused the fall migration of barren-ground caribou to begin (Kelsall 1968). A composite threshold of snow depth, hardness and density for movement within winter range was determined by Pruitt (1959) for barren-ground caribou. They prefer snow that is soft, light and thin and the migration threshold seems to increase as winter progresses.

Plant Phenology

In temperate ecosystems, protein content and digestibility of plant material is positively correlated with latitude and elevation (Van Soest 1983). Although temperate ungulates may not encounter more abundant vegetation by migrating to higher elevations or latitudes, they may obtain higher quality forage (Skogland 1984, Langvatn and Albon 1986). Migrating cervids gain fitness from prolonged access to newly emerging forage along an ascending altitudinal gradient during early summer (Mysterud et al. 2001). Russell (1932) suggested that migration of mule deer from winter to summer range was related to plant growth. Moose increased their use of open lowlands in spring where earlier snowmelt promoted green-up (Hauge and Keith 1981). High quality forage is required soon after winter due to increased demands of cows and the negative energy balance of both sexes. In tropical India, the home range of gaur may be large enough to encompass a valley and surrounding hillsides (Schaller 1967). Migration to higher elevations before the hot season allows the gaur to access green grass. After calving, the timing of migration of female saiga to spring feeding grounds coincides with green-up (Bannikov et al. 1967).

Serengeti ungulates experience a shifting mosaic of available forage that can be exceptionally rich due to localized rain showers, but it is not sustained (McNaughton 1985). These animals concentrate on actively growing grasslands, and then abandon them as grasses desiccate. Lack of correlation among productivity patterns of three stands on the Serengeti plains separated by only 4-10 km demonstrated the low predictability of productivity pulses. Productivity ranging up to $40 g/m^2/day$ in such pulses may provide a substantial food potential to grazers, but its occurrence in space and time is highly variable. The ability of gazelles to track a pulse of productivity was demonstrated by a close relationship between their density and primary production over the duration of such a pulse.

Spring movements of Montana moose from winter ranges to higher elevations may be stimulated by disappearance of snow or by green-up of growing plants (Peek 1962, Knowlton 1960). Migration of Kenai Peninsula moose from winter to spring range, followed by slow dispersal to upland summer-fall ranges is likely related to plant phenology (LeResche 1974).

Blood (1963) and Murie (1944) observed that mountain sheep followed the ascending snowline in spring feeding on fresh sprouting vegetation.

Thirst

Prolonged dry weather may compel ungulate populations to search for water and lush forage. In Montana, Peek (1962) observed greater use of upland habitat by moose during dry summers. Except during brief periods of parturition and breeding herds of saiga are usually migrating (Bannikov et al. 1967). In mid summer there may be continuous movement in search of food and water on the Eurasian steppes. During exceptionally dry summers, migrations extend further westward. Some species are able to direct their movements according to rain events. Wildebeest are adapted to feed on grass less than 10 cm in height, particularly freshly sprouting (Talbot and Talbot 1963). They drink every day if water is readily available, but cannot exceed five days without it. During the dry season, wildebeest may travel more than 80 km/day if food and water are widely separated. Wildebeest react to the sound of thunder 25 km away by moving toward it. Migration may also be initiated toward dark cloud-capped storm columns up to 80 km away. Antelopes and wild asses leave the Gobi desert at the onset of winter because of thirst when open water freezes (Allee and Schmidt 1966).

Reproduction

Movements of some species are influenced by their reproductive condition. Barten et al. (2001) observed that parturient cows of the Mentasta caribou herd in Alaska migrated to elevations higher than the usual range of bears and wolves, whereas non-maternal females remained at lower elevations. Also if females lost their offspring, they rejoined non-maternal females and predators at the lower elevations. Parker (1972) reported that non-pregnant barren-ground caribou were less likely to migrate to calving grounds. Similarly, non-pregnant saiga females often accompany males instead of migrating with females to calving grounds (Bannikov et al. 1967).

In southeastern Oregon, sexual segregation of mule deer supports the hypothesis of sexual segregation (especially around parturition) to enhance reproductive fitness (Main and Coblentz 1996). Maternal females selected areas with adequate food, permanent water nearby to satisfy lactation demands and steep slopes as escape terrain from coyotes. Males travelled more widely to exploit superior foraging opportunities.

Group Size

There may be minimum group sizes that cause animals to undertake movements. In the Pechora River area of Russia, seasonal migrations discontinued when moose reached low densities in the 1920s and 1930s, then migrations resumed after the end of the Second World War when the population rebounded (Pulliainen 1974). Indian elephants (*Elephas maximus*) in Malaya live in discreet home ranges that overlap with other herds (Mohamed Khan bin Momin 1969). If a group was reduced to three individuals or less, they travelled away from the home range to join another herd.

Multi-Species Resource Use

Resource Partitioning

When two closely related species of similar size meet in the same region they tend to compete for resources and only persist together if they are ecologically separated by habitat and/or food preference (Schaller 1977). The differential use of resources by species is termed resource partitioning (Schoener 1974), and it may ultimately be caused by competitive interactions (Connell 1980). Often, species of prey differ in their vulnerability to predation in a particular habitat. Predator-mediated resource partitioning results when one of the prey species responds by moving to a different habitat (Lingle 2002). Wet season food selection by nomadic grazing ungulates in the Serengeti suggests resource partitioning (McNaughton 1985). Wildebeest concentrated on vegetation forage with a green standing crop of between 40-80g/m2, and gazelles on 20-40g/m^2. Buffalo were bimodal in their eating habits using swards of low standing crop and 80-100g/m^2. They tend to occupy fairly restricted home ranges and do not undergo extensive movements. Bimodality occurs because some herds experience the onset of the wet season at different times than others. Generally, buffalo resided on the most productive sites, followed by wildebeest, then gazelle on the poorest ranges. During the peak of the rainy season, the three major nomadic grazers (wildebeest, zebra and gazelle) were spatially segregated. Wildebeest and zebra occurred in the wettest areas, while gazelles occupied the driest areas.

Dry season food selection of the four major grazers was separated by species, composition, standing crop and structural properties of the vegetation. Buffalo and zebra fed in tall vegetation where green forage was diffusely distributed, gazelles grazed short vegetation with a low standing crop, and wildebeest used grazing lawns of high biomass concentration. Sinclair (1977) noted that wildebeest were potential competitors with buffalo in the dry season, when both used riverine grasslands. Buffalo were able to use forest glades as an ecological refuge if competition became excessive which wildebeest, topi, kongoni and hippopotamus (*Hippopotamus amphibious*) avoided.

Species also followed one another in grazing succession as new arrivals consumed forage avoided by previous grazers (Vesey-Fitzgerald 1960). For example, dry season feeding patterns of gazelle were closely associated with sites previously utilized by wildebeest (McNaughton 1976). Schaller (1977) summarised ecological separation of Caprinae species in mountainous regions of Eurasia. Although some species generally preferred certain types of forage (e.g. goats selected browse more than sheep) most specialization appeared to be in habitat selection. Where sheep and goat species co-occurred, sheep were found mainly on undulating terrain, while goats were on precipices. In the Himalayas, thar are cliff dwellers that may travel above the timberline, while serow (*Capricornis sumatraensis*) are more associated with dense cover. Where ibex or bharal (*Pseudois nayaur*) occur above the timberline, thar are found mainly in wooded gorges that ibex and bharal avoid. In the Altai, where thar are absent, ibex occupy cliffs in the wooded zone. In the Alps, Ibex live at higher elevations than chamois (*Rupricapra rupricapra*), and where mouflon/urial (*Ovis orientalis*) have been introduced, they occupy the lowest slopes. In the eastern Caucasus, chamois may range higher than the tur, but when they share the same elevation, tur are more often found in shady valleys that chamois avoid. In Baluchistan, markhor (*Capra falconeri*) are on cliffs whereas urial occur on talus slopes, and ibex are on cliffs above argalis (*O. ammon*).

Northern portions of white-tailed and mule deer range overlaps with southern portion of moose range. In parts of western North America, all three share sympatric zones. Because moose are generally associated with boreal coniferous forest, white-tailed deer with deciduous brush forest, and mule deer with more open grassland-parkland, the sympatric ranges may be comprised of marginal habitat for all three species (Prescott 1974). As browsers that consume a number of similar food items, there is potential for competition where they coexist. Differences in food preferences, seasonal spatial segregation and different abilities to cope with snow and cold provide evidence of resource partitioning (Boer 1998). Snow depths of about 30 per cent less than chest heights seriously impeded both white-tailed deer and moose in Nova Scotia and New Brunswick, but moose, being taller, had an advantage in deep snow. Northern and elevational limits for white-tailed and mule deer are influenced primarily by winter conditions, and mule deer can apparently tolerate winters of greater severity (Kramer 1972). The main determinant of moose distribution appears to be browse availability (Prescott 1974). In New Brunswick and Nova Scotia high moose densities tend to be limited to elevations above 150m (Dodds 1974). An altitudinal separation over part of the year may allow moose to survive in areas of deer abundance. Because moose are adapted to cope with deeper snow, they seasonally occupy areas uninhabited by *P. tenuis* infected deer.

In mountainous areas of northwestern North America, moose and deer are more segregated than in other parts of sympatric range probably because of elevational effects on vegetation communities and snow accumulation (Telfer 1978). Moose and deer differ in wintering area selection by choice of overstorey cover and understorey browse. Where moose and mule deer share the landscape, they seldom compete in same area during winter. Mule deer converge in valley bottoms, while moose are more dispersed. In the Maritimes-Maine region, moose and white-tailed deer reduce spatial overlap, as moose winter on upper slopes greater than 180 m in elevation, while deer are more often on lower slopes under 180m in elevation (Prescott 1974).

Elk have less tolerance for snow depth than moose and this may be a determining factor for the proximal distribution of these two species in winter (Stevens 1974). Both have been able to maintain high populations in Elk Island National Park where they reside together in close proximity (Holsworth 1960). In Wind Cave National Park, South Dakota, habitat selection, spatial distribution and food habits of mule deer differed extensively from both bison and pronghorn (Wydeven and Dahlgren 1985). Elk and bison had low distributional overlap and food habits differed. Similar resource partitioning between these two species has been observed in Elk Island National Park, Alberta (Telfer and Cairns 1979).

On Yellowstone National Park's northern range, Singer and Norland (1994) compared niche relationships and diet among elk, bison, bighorn sheep, mule deer, and pronghorn antelope during the periods of 1967-1970 and 1986-1988. By the latter period, total ungulate numbers nearly tripled. Although bison used a wider variety of habitats as their population increased and diet and habitat overlap increased with other species, Singer and Norland (1994) found little evidence of change in competitive interactions between species. Although food habits and habitat use patterns of pronghorn and mule deer overlap where they are sympatric, there was nearly complete spatial segregation and limited opportunities for competition (Wood 1989). Where overlap occurred, it usually resulted from movement of pronghorn into mule deer habitat.

Lingle (2002) studied predation and habitat separation of white-tailed and mule deer in southern Alberta. Although they are closely related species that tolerate a wide variety of habitats and frequently coexist, in this study area mule deer used more rugged and open terrain, while white-tails occupied gentler terrain. In response to coyote predation, mule deer moved to and up slopes, and white-tailed deer moved down and away from slopes, which led to habitat segregation of the two species. Similar mechanisms have been proposed for segregation of African ungulates (Jarman 1974, Sinclair 1975). Risk of predation may also lead to convergence of ungulate species such as Thomson's and Grant's gazelles (*Gazella granti*) (Fitzgibbon 1990).

Although woodland caribou often share the landscape with other ungulates such as moose, deer, elk and bison, they occupy a much different ecological niche. Certain adaptations permit caribou to exploit a nutrient-poor niche on the landscape where other ungulates are unable (Thomas and Gray 2002). According to Kelsall (1968), caribou are physiologically adapted to cope with low protein forage. Lichens, which form the bulk of the winter diet, are high in digestible carbohydrates for energy value, but low in protein and minerals.

The musk deer (*Moschus moschiferus*) of Eurasia shares the landscape with reindeer and also depends on lichen for sustenance. The musk deer is a small cervid that requires shelter during winter and there appeared to be little overlap in distribution with reindeer outside of mountain taiga (Egorov 1965). Cumming et al. (1994) described habitat partitioning by moose and woodland caribou in north western Ontario. Autocorrelation of winter track locations demonstrated that wolf tracks were most often associated with moose tracks, and the two ungulates appeared to disassociate from each other. Cumming (1975) found that predation rates on caribou varied according to distance from wolves.

Results from a study in north eastern Alberta by James (1999) supported the following three predictions of a spatial separation hypothesis: (1) caribou and moose selected different habitat types, while moose and wolves selected the same upland habitat type; (2) wolf predation on caribou was higher near habitats selected by moose (3) scat analysis showed that relative predation on caribou was less than their relative frequency in the environment. In west-central Alberta, wolves selected habitats with young vegetation and waterways with abundant moose (Kuzyk 2002). In contrast, caribou preferred forest 120-160 years of age (Szkorupa 2002), and avoided cutblocks (Smith et al. 2000) and perennial streams (Oberg 2001).

In a study of range relationships of muskoxen and Peary caribou on Banks Island, Northwest Territories when both species were increasing, Wilkinson and Shank (1974) detected little overlap in distribution and most of the feeding time was spent in different plant communities. Similar results were observed in later studies of caribou/reindeer – muskox interactions (e. g. Smits 1989, Biddlecomb 1992, Schaefer et al. 1996, Ihl and Klein 2001).

In the Aishihik Lake area of the Yukon, Fischer and Gates (submitted) observed strong patterns of niche partitioning during winter between woodland caribou and wood bison. Although both species are grazing ruminants, specific morphological, physiological and behavioural adaptations determine foraging niche at the landscape, range overlap, feeding site, and diet composition levels.

Commensalism

Commensalism occurs when populations of two species may interact in such a way that one population benefits but the other is unaffected (Odum 1971). In the Serengeti, long distance migrants follow each other in a sequence led by zebra, then wildebeest which are followed by Thomson's gazelle (Gwynne and Bell 1968). The rapid passage, hindgut digestive system of zebra is relatively efficient for extraction of nutrients from low quality forage. High grass stem consumption and trampling by zebra reduce plant competition for light and stimulate greater production of grass leaf. Because wildebeest feed mainly on grass leaf, they experience improved habitat suitability when following zebra. The combined action of zebra and wildebeest enhances availability of dicotyledonous plant material that gazelles prefer. Although large grazers may facilitate access to forage for smaller grazers, smaller grazers may drive the succession from behind by high-grading pastures (Farnough et al. 2002). Predation also may partially explain the grazing succession (Sinclair and Norton-Griffiths 1982).

Although waterbuck consume the same types of grass in forest habitat as African buffalo, the smaller waterbuck is able to forage where the grasses are widely scattered (Sinclair 1977). As the buffalo requires large food patches that allow high rates of intake, Sinclair (1977) suggested that its feeding activities in the forest could be both competitive and facilitative for waterbuck. During earlier times, pronghorn may have been at least as numerous as bison in western North America (England and DeVos 1969). Pronghorn underwent dramatic decreases, but there is little reference to excessive slaughter similar to bison. The diet of pronghorn consists mainly of browse and forbs, which may increase under heavy grazing. It is possible that moderate overgrazing by bison improved habitat for antelope.

Chapter Summary

Animal species move in response to diverse ecological pressures (Dobson 1982). The primary benefit to adopting a movement strategy appears to be the ability to respond to a changing environment. Environments can change through variation in resource availability, which is often weather related, predation pressure, interspecific or intraspecific competition, or disease. These changes ma be atributed to a range of natural variability in the environment and can be modified by human activity. Movement strategies allow species to find new resources, escape predation pressure, find new mates and improve reproductive potential. Movement can be costly, however, because of uncertainties of finding necessities, greater exposure to predators and competitors, loss of rare phenotypes, and less viable offspring (Stenseth and Lidicker 1992).

Success of a movement strategy depends on the environment in which the population persists. Many species of ungulates have populations within the same environment that adopt either a movement strategy, such as migratory movement tracking seasonal changes in resource availability, or are sedentary, adapting to a particular niche in the environment. Both strategies have costs and benefits, yet both can be successful. Changes in the environment can make either of these strategies more successful than the other; however, movement strategies may be best for highly variable environments. Ungulate species will adapt movement strategies, whether long distance migratory movements or sedentary, in response to their environment. Although one particular pressure may be the primary cause of movements, movement strategies are typically an adaptation to multiple pressures.