Chapter 2
Food and Populations

Wildlife biologists are often responsible for monitoring populations of free-living animals within the boundaries of parks, refuges and game management units. Captive propagation programs focus on smaller confined populations but are nonetheless ultimately concerned with understanding the relationships between wild populations and their habitats.

In evaluating population numbers with repeated inventories, two questions are usually asked: ‘How many animals are in the area?’ and ‘How many animals do we want in the area?’ Conservation programs are evaluated by gains in a population of threatened or endangered species or by declines in populations of pests and invasive species. Game management programs often aim to sustain or increase the accessibility and harvest of a population with minimal adverse effects on other resources such as plant and animal communities. Wildlife monitoring typically entails the collection of data at three levels of detail with a wide variety of techniques, from aerial surveys, capture and release of individuals, to tissue sampling of harvested animals:

- numbers and locations of individuals;
- demography (e.g., proportions of age, sex and reproductive classes);
- individual condition (e.g., body mass, growth rate, health).

Wildlife nutrition links the details of demography and individual condition to the response of a population. In this chapter we discuss the response of a population to changes in food supply and environmental demands on individuals.

2.1 Population Growth and Animal Density

The number of animals in an area changes with time and can be described as a mathematical function of time (t). Time scales for populations can be measured in minutes or hours for microbes that replicate rapidly (Chapter 6), but are typically recorded in months or years for fish and wildlife species. The size of a population at the end of a year (N_{t+1}) is related to the number of animals at the start of the annual cycle (N_t) and the activities of animals over the year: production of young (P_t), deaths (D_t), immigration (I_t) into and emigration (E_t) out of the area (White 2000):

$$N_{t+1} = N_t + P_t - D_t + I_t - E_t \qquad \text{(Eq. 2.1)}$$

Changes in population size result from differences between rates of production (P_t) and death (D_t) if animal movement is accounted for by including the annual range or by excluding the possibility of movement by barriers such as oceans, mountains and deserts. Net population gain ($P_t > D_t$) is the outcome of the net supply of resources for growth and reproduction. Net loss or death ($P_t < D_t$) is a function of net demands on individuals, usually from adverse weather and disease after accounting for predation and harvest.

Incremental changes in a population may be either positive or negative and can be quantified as a proportion (R):

$$N_{t+1} = N_t \times (1+R) \qquad \text{(Eq. 2.2)}$$

The maximum value of 'R' is the intrinsic growth rate of the population (R_{max}), that is, its maximal rate of net production. Intrinsic rates of growth reflect life history traits of species, such as age at first reproduction, number of offspring each year, frequency of reproduction and age of senescence or last reproduction. The more rapidly a species can replace itself during its lifetime, the higher is $R_{max.}$ Populations of species with high reproductive rates can increase quickly when offspring survive to maturity. Captive propagation programs for fecund species such as green sea turtles can produce large numbers of offspring if causes of mortality in eggs such as predation, adverse weather (temperature, water submersion) and disease are removed or minimized (Miller 1997). Conversely, captive propagation of species such as whooping cranes and California condors are much slower because only two to three eggs are produced in each clutch (Johnsgard 1983; Snyder and Snyder 2000). Organisms achieve R_{max} when supplies for production greatly exceed any demands that result in death. Introductions or expansions of individuals into new ranges can permit an exponential increase in population size (N_{t+1}). Introductions of European rabbits into Australia, brown rats, pigs and goats into Polynesia, and common brushtail possums into New Zealand all resulted in rapid increases in population sizes as founding individuals were able to sustain high reproductive rates that greatly exceeded death rates (Thomson et al. 1987; Hoddle 2004).

Populations of introduced species cannot and do not continue to grow exponentially because food and space are finite. Exponential population growth that is independent of animal density can only be sustained for short periods of time (Fig. 2.1). Increasing animal density ($N_{t+1} \div$ area; individuals per hectare, individuals$\cdot$ha^{-1}) ultimately decreases the food supply for each individual (food $\div N_{t+1}$; kilojoules per animal, kJ$\cdot$animal^{-1}) and may also increase demands on individuals by increasing their exposure to diseases (pathogens $\div N_{t+1;}$ parasites per animal, parasites$\cdot$animal^{-1}) and adverse weather. Net production therefore diminishes as animal density approaches a resource limit or carrying capacity (K; Fig. 2.1A). Growth rate of a density-dependent population can be expressed in relation to the maximum or intrinsic rate of growth (R_{max}) by the ratio of N_t to K:

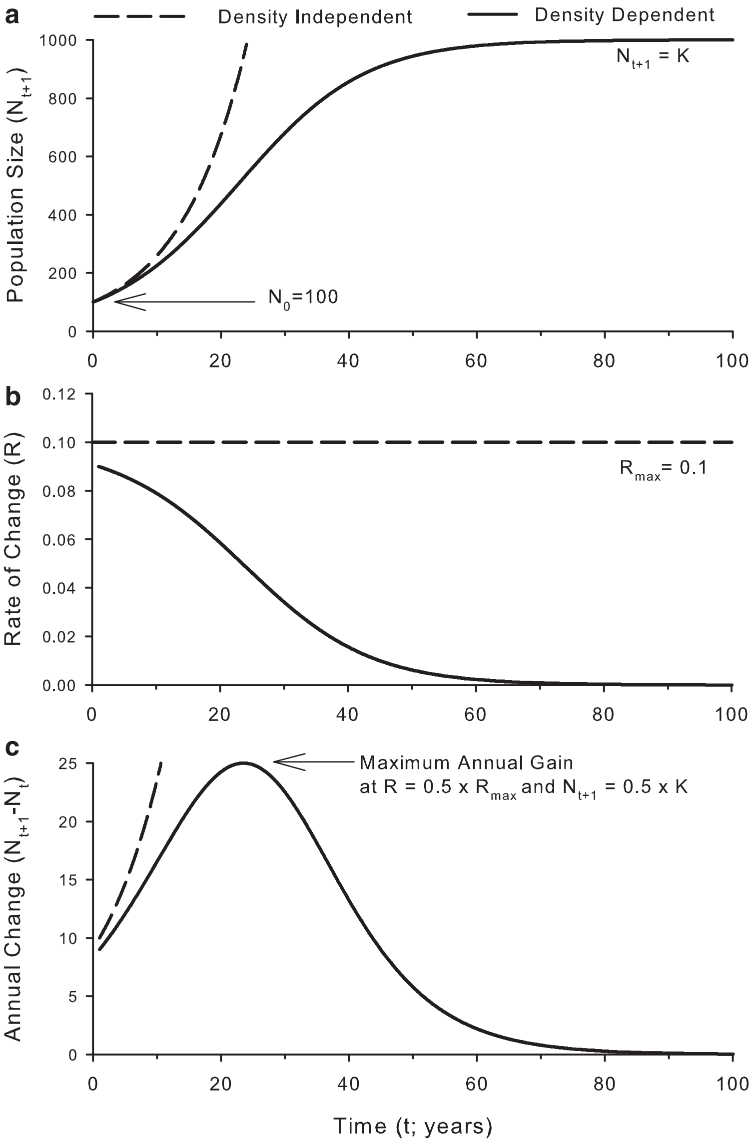

Fig. 2.1 Patterns of population growth in wildlife. **a** Changes in population number (N_{t+1}) from an initial size (N_0) of 100 individuals. Patterns are independent of animal density (*dashed line*) or dependent on a resource that limits the total number of individuals (K; *solid line*). **b** Annual rate of change in the population (R) varies for density-dependent populations. Density-independent populations grow at the maximum intrinsic rate (R_{max}). **c** Absolute annual change in population size over time. Density-independent populations increase exponentially whereas density-dependent populations reach a maximum annual gain when R is 50% of R_{max}. The maximum sustainable harvest of the population by humans (maximum sustainable yield) theoretically can be achieved at the maximum annual gain when the population is at 50% of K

$$R = R_{max} \cdot (1 - (N_t \div K)) \qquad \text{(Eq. 2.3)}$$

The size of density-dependent populations is therefore expressed as:

$$N_{t+1} = N_t \cdot (1 + R_{max} \times (1 - (N_t \div K)) \qquad \text{(Eq. 2.4)}$$

The intrinsic growth rate (R_{max}) of a population determines the time required to reach a particular number of animals and thus the rate at which the population uses food and space. Maximum annual gain in the population is achieved when R is 50% of the intrinsic growth rate ($R = 0.5 \times R_{max}$) and the population is 50% of carrying capacity ($N_{t+1} = 0.5 \times K$; Fig. 2.1B, C). The size of a sustainable harvest by humans is therefore dependent on the replacement rate of the species in relation to its consumption of food and other resources. Fast-growing species such as chinook salmon can provide large annual harvests from nutrient-rich habitats such as the Gulf of Alaska (Mundy 2005; Rodger 2006). Slower growth and lower fecundity make species such as Saiga antelope more vulnerable to overharvesting in semi-arid steppes that are not very productive habitats (Baskin and Danell 2003; Milner-Gulland et al. 2003).

2.2 Individual Demands and Food Limits

The relationship between population growth and resource use can be demonstrated with a simple model of food consumption by deer (Family Cervidae) (Fig. 2.2). If the average energy consumption is $20.3\,\text{MJ} \cdot \text{d}^{-1} \cdot \text{animal}^{-1}$, the deer population will consume $4{,}058\,\text{MJ} \cdot \text{d}^{-1}$ early in the growth trajectory (200 animals) and 2.5 times more when the population is at the maximum annual gain (500 animals, 50% of K; Fig. 2.2). If food availability for the area is $19{,}000\,\text{MJ} \cdot \text{d}^{-1}$, approximately 50% of the annual food production would be used by a population maintained at 500 animals. The unused food could be returned to the environment by decomposition or consumed by other species. This unused reserve of annual food production may also serve as a safety margin against increasing demands on the deer population.

Resource limitation is one aspect of the realized nutritional niche (Chapter 1) for a population. Energy consumed by 1,000 deer at the rate of $20.3\,\text{MJ} \cdot \text{d}^{-1} \cdot \text{animal}^{-1}$ would exceed the upper limit of food availability set at $19{,}000\,\text{MJ} \cdot \text{d}^{-1}$. The herd could only attain a size of 1,000 animals if the average energy consumption decreased when the population approached this food limit. In fact, the average energy consumption is a weighted average of the rates for different classes of animals within the population. In our example, the model population of deer is comprised of males (115 kg), non-breeding females (65 kg), breeding females (80 kg) and sub-adults (35 kg) that expend $293\,\text{kJ} \cdot \text{d}^{-1} \cdot \text{kg}^{-0.75}$ body mass at maintenance (no net gain or loss of body mass). If males and non-breeding females require 2.1 × maintenance to support normal activity as well as body maintenance ($615\,\text{kJ} \cdot \text{d}^{-1} \cdot \text{kg}^{-0.75}$), growing

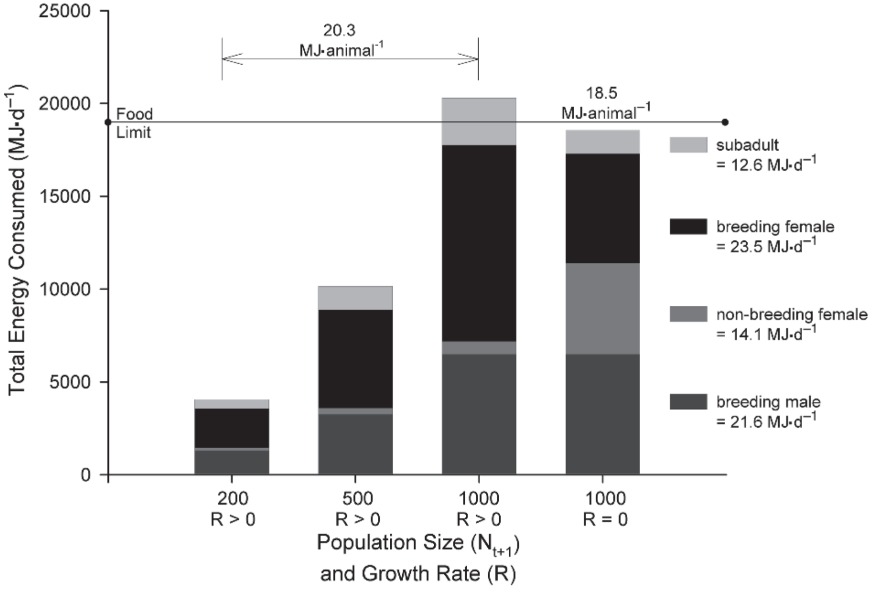

Fig. 2.2 The effect of food limitation on the demography (age class structure) of a model population of deer. The model shows total energy consumption of the population as it grows ($R > 0$) from 200 to 500 to 1,000 individuals. A population of 1,000 animals can be supported ($R = 0$) below the food limit (*solid line*) if the average consumption declines from 20.3 to 18.5 MJ • animal^{-1}. The proportion of breeding females in the population is usually reduced by food limitation because those individuals have the highest demands for energy. In this model of declining food consumption, demography changes as follows for a population of 1,000 animals: sub-adults 200 to 100; breeding females 450 to 250; non-breeding females 50 to 350; and males 300 to 300

sub-adults and breeding females would require 3 × maintenance (879 kJ • d^{-1} • kg$^{-0.75}$). In terms of daily energy requirements, growing sub-adults are projected to use almost as much as the larger non-breeding females. Breeding females use energy at the highest rates in this population even though they are smaller than males (Fig. 2.2). Such high demands for growth and reproduction are difficult to support as food becomes limited; populations near their food limits cannot support the same proportions of individuals with high productive demands. In our hypothetical population, the percentage of sub-adults declines from 20% to 10% and that of the breeding females drops from 45% to 25% as the population approaches K and population growth (R) declines to zero (Fig. 2.2).

Individual responses to resource availability can be used to predict responses at the population level (Chapter 10). Population declines ($R < 0$) resulting from food limitation are associated with declines in body condition of individuals and reduced deposition of energy and nutrients in fat and lean mass. Poor body condition can reduce reproductive rates if body stores of fat or protein fall below the level required for breeding (Fig. 2.3). In caribou, for example, a threshold of 6–8 % body fat in mid-winter may separate reproductive from non-reproductive females

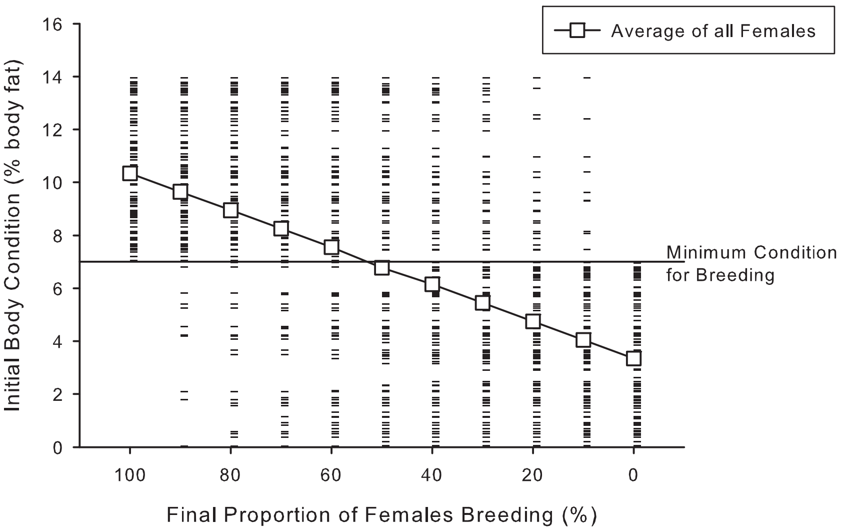

Fig. 2.3 Body condition of individual breeding animals can indicate the potential production of a population during the year. The model shows initial body fat content of 100 female deer in relation to the proportion of females breeding in the population. The simulation uses a threshold of 7% body fat for successful reproduction. Average body fat content (*open squares*) of all females declines linearly as breeding numbers and potential production decline

(Crête et al. 1993; Ouellet et al. 1997). Caribou also rely on stored body protein for fetal development (Allaye-Chan 1991; Parker et al. 2005). Similarly, snow geese rely on both body fat and protein for egg laying and incubation (Ankney and MacInnes 1978). Declines in body condition of reproductive females may therefore precede declines in population size, especially in species that use seasonal body stores to meet the high demands of pregnancy or egg production, lactation or incubation (Chapter 10). Food limitation also reduces juvenile survival, increases the age of first reproduction by constraining growth and development of young individuals and therefore decreases recruitment into the breeding cohort of the population (Eberhardt 2002). Poor body condition may increase the risk of mortality in all age classes but especially in the young and the old by increasing their susceptibility to inclement weather and disease. These differences in mortality risks among age classes may then alter the demography and the food required for the entire population.

2.3 Trophic Relationships

The flow of energy and nutrients occurs in a trophic hierarchy from primary producers such as plants to herbivores and carnivores. This transfer of energy between trophic levels depends on the efficiency of production, which is determined by the deposition of energy or nutrients in producers, and the subsequent assimilation of those products by consumers at the next trophic level. Energy that is expended by individuals for daily maintenance reduces the proportion of energy invested in replacing the population with new individuals. Consequently, ectotherms such as fish with low maintenance requirements for energy have higher production efficiencies than endotherms such as mammals and birds (Humphreys 1979). The capture of energy by consumers depends on their ability to extract energy and nutrients from food. Primary production in terrestrial plants includes energy deposited in structural carbohydrates, which are more difficult to digest by consumers than the simple structures of aquatic algae (Chapter 6). In terrestrial systems, the large investment in plant structures that have less available energy, such as wood, results in most biomass being distributed at the base of the food web. Conversely, in aquatic food webs, there is high flux of energy through the base, resulting in relatively little biomass of primary producers and therefore an inverted pyramid of biomass (Chapin et al. 2002).

The relationship between the numbers of prey and predators depends on the amount of energy in the prey and the efficiency of transfer between trophic levels. A predator such as a coyote (Family Canidae) would be able to satisfy its energy demand for 2.23 MJ•d^{-1} with fewer grouse (Family Phasianidae) at 10.8 MJ•prey item^{-1} (0.2 kills•d^{-1}) than voles (Subfamily Microtinae) at 0.13 MJ•prey item^{-1} (16.6 kills•d^{-1}). The size of the prey population required by a population of predators is further increased by the low efficiency of production between trophic levels. If the coyote captures only 1% of the energy in the available prey, the coyote would need to hunt from a prey base of 223 MJ•d^{-1}, which is equivalent to 21 grouse or 1663 voles each day.

Figure 2.4 models the energetic equivalents of a predator–prey relationship between a group of 50 coyotes and 1,000 grouse. Prey populations vary with annual changes in weather and food abundance that alter their rates of production (P_t) and

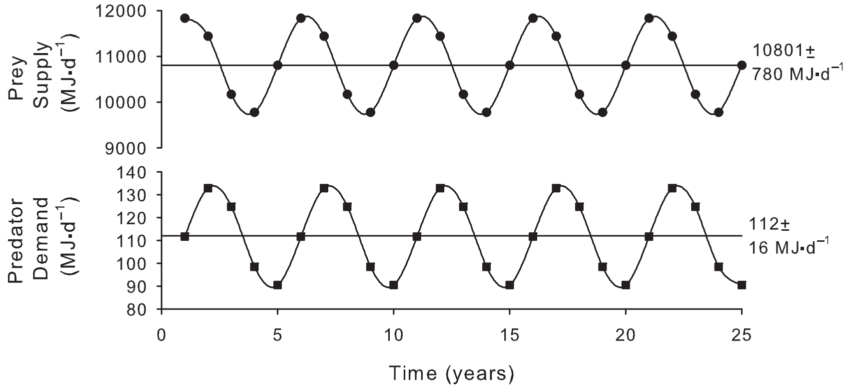

Fig. 2.4 Model of fluctuating prey supply and predator demand for energy. Average energy supply is based on 1,000 grouse predated by 50 coyotes. Predator demands are modeled with a lag of 1 year from the prey supply. Lag times vary with life history parameters such as fecundity, age of maturation and survival of the predator

death (D_t) (Bayliss and Choquenot 2003; Hudson et al. 2003). In our model the grouse population oscillates by 10% every 5 years (Fig. 2.4). Predator populations are obliged to follow the fluctuations in the supply of their food, as observed in the predator–prey cycles for lynx and snowshoe hares (Sinclair and Krebs 2003) and for barn owls and field voles (Taylor 1994). Recruitment of young into a population of lynx declines dramatically 1 year after the peak in snowshoe hare abundance (Mowatt et al. 1996). Our model of energy demands for coyotes and their population size lags behind the changes in prey supply by 1 year (Fig. 2.4).

The relationship between the numbers of predators and prey also depends on the life history parameters of each species (R_{max}), and the size and age class structure of each population. Fecund consumers that mature quickly, such as rodents and some songbirds, may respond more rapidly than ungulates and large carnivores to fluctuations in the environment and the food base (Fryxell and Sinclair 2000). The persistence of a population of prey is also dependent on its food supply and its rates of birth and death. If the food supply can support birth rates, then deaths from predation may maintain the population of prey at a level well below the food limit, as in management strategies for sustainable harvest by humans (Fig. 2.1) (Sinclair and Krebs 2003). High predation rates in small areas constrain populations of forest-dwelling caribou well below their food limits (Jenkins and Barten 2005; Wittmer et al. 2005). However, the relationship between a predator and one species of prey tends to disappear as alternative food sources become available. Figure 2.5 extends our model of 50 coyotes to include 20,000 voles as a secondary prey when the availability of the primary prey is reduced from 1,000 to 700 grouse. Multiple prey items with different patterns of abundance allow generalist predators such as coyotes to substitute one food for another as each choice declines or to meet the increasing costs of reproduction from a broader food base (Bothma and Coertze 2004).

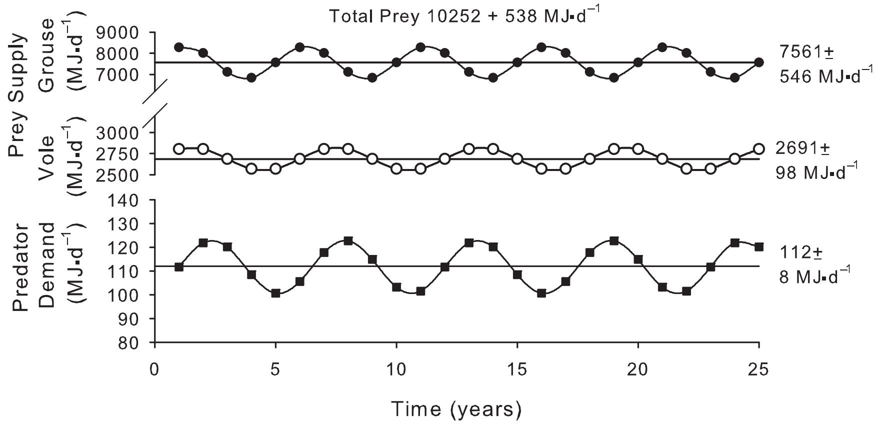

Fig. 2.5 Multiple prey items can be used to meet predator demands. The model populations for coyotes and grouse (Fig. 2.4) are extended to include 20,000 voles when grouse numbers are reduced from 1,000 to 700. The amplitude of the oscillation in predator demand is smaller than in Fig. 2.4, but the total energy demand is similar to a single prey system

An increase in the number of species of consumers and foods in a trophic system rapidly increases the complexity of trophic relationships. Trophic complexity may reinforce the structure of animal and plant communities by providing multiple feedbacks and tolerances. The number of links in a food web is not always indicative of the ability of the system to resist or recover from perturbations. Some keystone organisms exert much more influence on the organization of an ecosystem than would be predicted by their proportion of the biomass (Primack 2004). Removal of keystone predators can allow their prey to consume more plants and thus alter the plant community. Extinctions of gray wolves and grizzly bears have been associated with declines in habitat for migrant songbirds because larger moose populations have changed the structure of shrubs and trees (Berger et al. 2001a). Similarly, the reintroduction of wolves into areas from which they had previously been removed results in antipredator behavior by elk and changes in habitat selection that affect species at progressively lower trophic levels (Creel et al. 2005; Mao et al. 2005).

The absence of predators emphasizes the importance of feedbacks between the herbivore population and the plant community. Overexploitation of a food base occurs when the production of the consumer is not tightly linked to food production. The herbivore population may increase and crash repeatedly because food abundance and consumer demands are often out of phase (Fryxell and Sinclair 2000). High fecundity and rapid maturation predispose species to overutilizing habitats with low or erratic food production. Island populations of domestic sheep that produce twins tend to overconsume pastures, whereas numbers of native red deer with single births are more closely related to the cycles of plant abundance (Clutton-Brock and Coulson 2003). Slow-growing forages such as lichens may be particularly vulnerable to overconsumption. Populations of reindeer and caribou introduced to predator-free islands can increase rapidly, but eventually fall to extinction when the food base of lichens is exhausted (Klein 1987).

Large-scale movements of animals help to disconnect animal production from plant production in areas within an annual range. The food requirements of migratory birds such as Canada geese and snow geese can exceed forage production on the spring breeding grounds if more birds survive winter by feeding on agricultural fields in the south (Ankney 1996) (Fig. 2.6). Seasonal or regional depletion of the food base may be sustainable if the plants have high leaf replacement potential and if the animals show a wide range in spatial and temporal use of the area. Large grazing herds of wildebeest and zebra can exploit highly productive grasslands of the Serengeti because the consumers move to other sites as plant availability declines (Bell 1971; McNaughton 1985). Brant and barnacle geese select the growing tips of plants which delays the maturation of the plant and results in a higher-quality diet for both the migratory geese and resident European hares during summer (Van Der Wal et al. 2000; Stahl et al. 2006). Herbivores such as hippos and hairy-nosed wombats also may enhance production of some plants such as grasses, resulting in a ‘grazing lawn’ (Jeffries 1999), by removing competing plant species and by recycling nutrients from excreta (Van Der Wal and Brooker 2004). The optimum density of herbivores for plant production varies with the composition of the plant community

Fig. 2.6 Populations of migratory herbivores such as Canada geese are affected by food availability over very large geographic areas. Abundant food in wintering areas may reduce mortality and increase the number of birds that return to consume plants along the migration route and at spring breeding grounds. High densities of herbivores can damage plant communities by removing leaves and seeds, trampling stems and damaging roots at rates that exceed the rate of replacement by the plants. Low to moderate densities of herbivores may facilitate plant production by increasing the availability of nutrients such as N for plants

(proportion of forbs, grasses, shrubs) and the availability of nutrients and water to plants (Person et al. 2003; Stewart et al. 2006) (Fig. 2.6).

2.4 Environmental Variation

Variation in the environment changes populations of species throughout the trophic chain, from primary producers to apex predators, over different scales of time. The environmental conditions of temperature, light, water and nutrients in both soil and water drive the primary production of microbes, algae and plants in both aquatic and terrestrial habitats (Chapin et al. 2002; Diana 2004). Changes in environmental drivers within a year produce weather patterns and seasons, whereas changes in annual cycles produce climatic patterns. Climatic patterns include interactions between atmospheric pressure and ocean temperature that affect both summer and winter weather in the northern (North Atlantic Oscillation) and southern (El Nino Southern Oscillation) hemispheres.

Weather patterns have two basic effects on animal populations. They change:

1. supplies for primary plant production and the trophic chain; and
2. demands on individuals and the risk of death.

These effects are modified by the timing, duration and intensity of environmental changes in relation to the life history demands of each species in the animal community.

The duration and timing of weather conditions favorable for primary plant production vary with geographical region. Consequently the opportunity for animal production also varies with geography and thus climate. Short seasons are tightly linked to photoperiod at high latitudes whereas seasons are less distinct or differentiated towards the equator. At high latitudes, seasonal breeding is often synchronized or cued by the light cycle. Changes in day length accompany primary plant production, which coincides with lactation or incubation, and maximizing growth rates of young in a short but regular season in the Arctic. In arid environments, the window for plant growth may be limited by less regular events such as rainfall. Timing of reproduction and the ensuing production of plants and prey in deserts are therefore cued by rainfall rather than light (Wingfield et al. 1992). Further details on the adaptations of animals to the timing of food supplies and the implications of climate change are presented in Chapter 11. Mule deer that extend across a large North American geographical gradient reproduce approximately 1 month earlier in northern populations than in southern desert populations (Bowyer 1991). In temperate zones, changes in the timing of seasonal rainfall and plant growth can result in shifts in the timing of breeding by birds (Nussey et al. 2005). Increases in the length of the European summer provide longer periods for growth by red deer that enhance body size of males and the maturation of females (Post et al. 1999). Therefore, weather effects on primary production interact with both demography and population size, and are thus components of density-dependent growth.

Severe weather events such as storms and ice expose animals to greater demands for thermoregulation and body maintenance. Animals living at high density close to the food limit of their population are likely to be more vulnerable to the unpredictable risks of adverse weather than well-fed animals. Individuals that are stressed by exposure and low food availability also may be the most vulnerable to disease. Diseases that rapidly debilitate individuals are more likely to affect populations at high than low density and produce sudden declines in the population. Conversely, chronic conditions (e.g., intestinal parasites) or non-lethal infections that reduce fecundity or lifespan may only reduce annual production (Albon et al. 2002; Joly and Messier 2004b). Disease may render some animals more vulnerable to predation. The loss of these potentially infective individuals to predation rather than disease may reduce the overall death rate (D_t) by reducing the rate of transmission of the disease (Hudson et al. 2003). The combined effects of adverse weather, disease and predation can be additive, resulting in large mortality events. Winter die-offs of caribou are reported for herds confined to small foraging areas by heavy snows and extreme cold (Tyler 1986).

Direct and indirect effects of environmental variation change population patterns from the smooth curves in Fig. 2.1 to the more erratic patterns in the model in Fig. 2.7. This model demonstrates that population size is the result of a dynamic balance between multiple factors that produce a net supply or net demand that respectively decreases or increases the population (Bayliss and Choquenot 2003).

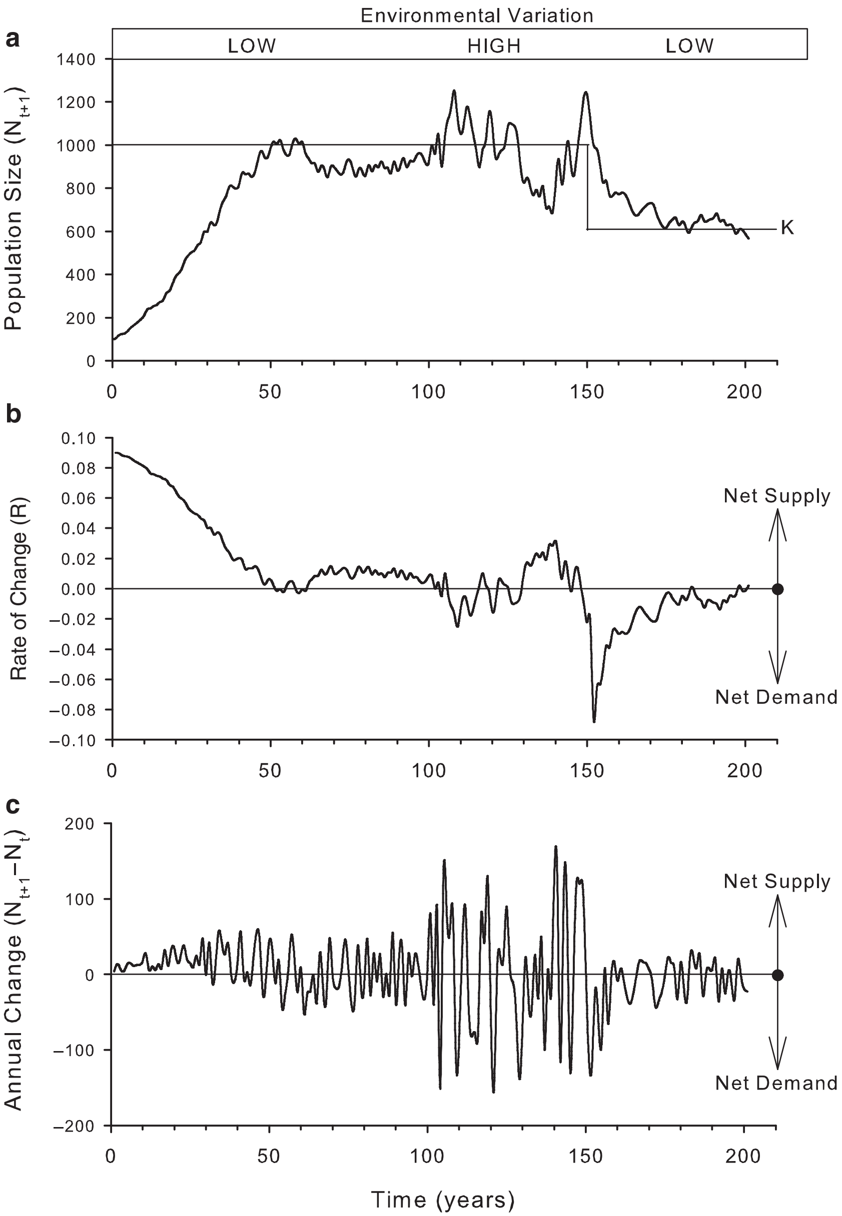

Fig. 2.7 Environmental variation affects population trends and resource limits. The density-dependent model of population growth in deer (Fig. 2.1) is extended to include periods of random variation in growth rate (*R*). Population size (**a**) is stable after 50 years during periods of low environmental variability (5% variation in *R*) similar to a benign climate. Increased variability in growth rate (15% of *R*; **b**) of a large population results in dramatic changes in the annual growth of the population (**c**). The limit for the population (*K*) is shifted from 1,000 to 600 animals at 150 years to simulate a sudden change in the habitat such as fire (**a**). Growth rate (*R*) is negative (**b**) as the population declines to the new resource limit within 50 years (**a**)

Although populations can grow in conditions of both low and high environmental variability, greatest annual changes in numbers occur when populations are large and near their food limit. Large herds are susceptible to small changes in net supply. Conversely, small populations are vulnerable to the net demands of mortality events such as adverse weather or acute diseases that reduce the number of breeding individuals. The long-term effects of a population on its plant and animal communities interact with environmental drivers to alter the food available to the population (Fig. 2.7). The nutritional niche realized by individuals is therefore an outcome of the characteristics of both the population and the environment.

2.5 Summary: Populations

Animal populations increase to limits of food and space availability in a density-dependent pattern. Animal populations are groups of individuals with different body sizes and food requirements. The adequacy of food supplies for any group of animals in the wild or in captivity depends on the number of animals and their demands for energy and nutrients in the prevailing environmental conditions. A small fraction of the energy available in a population of plants or prey is consumed by the next trophic level because energy is expended for non-productive processes at each level and because the consumer may only capture a portion of the production. Weather drives changes in primary plant production and secondarily affects risks of debility and death for animals. Environmental extremes can increase the vulnerability of small populations to greater demands (e.g., predation) and the risk of large populations to starvation.