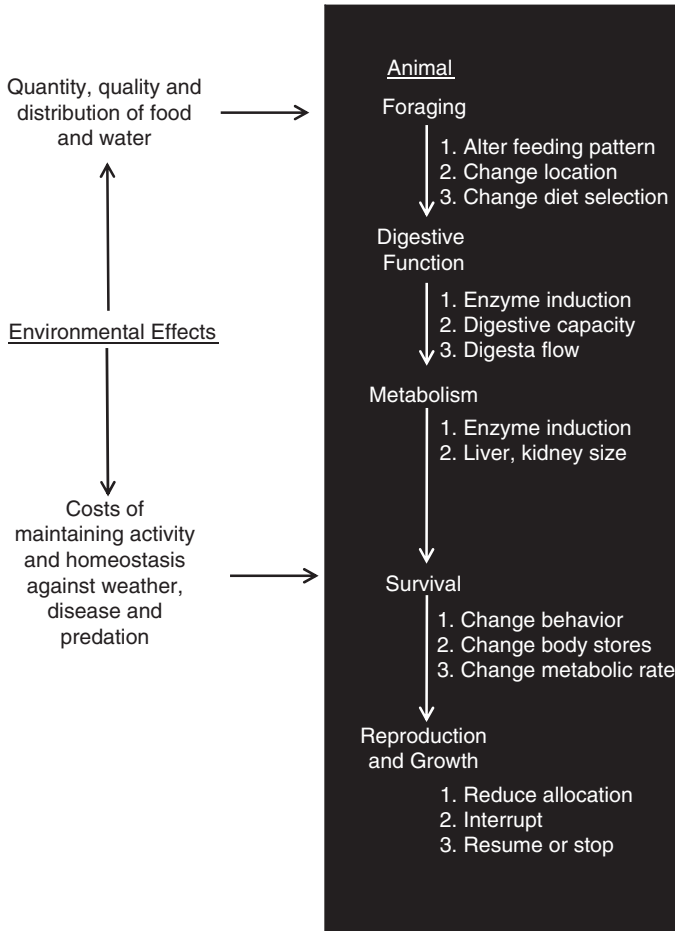


## Chapter 11

# Integrating Nutrient Supply and Demand in Variable Environments

Environmental variation alters the supply of food and water as well as the requirements of animals for these resources (Fig. 11.1). Changes in food intake can affect all components of energy and nutrient balance, which ultimately affects growth and reproduction. The ability to tolerate and resist adverse environmental changes depends on the plasticity of the animal, from its foraging activities (behavioral plasticity) to its production (physiological plasticity). For example, brown bears have some behavioral plasticity to tolerate disturbances from wildlife watchers by altering the times and locations at which they feed on salmon (Rode et al. 2007). Polar bears also can change their foraging behavior by moving onshore when there is insufficient sea-ice cover to allow foraging on seals. The ability to accommodate a change in foraging conditions depends on the duration of the change, the breadth of the animal's dietary niche, the availability of alternative foods and the energy demands of the animal. Decreases in sea-ice cover are associated with poor survival of young polar bears and with increasing conflicts between bears and humans as the bears begin to seek terrestrial foods often near settlements in order to meet their demands for maintenance and growth (Regehr et al. 2007).

Physiological plasticity allows animals to respond to changes in the supply of nutrients. Increased food intakes may require concomitant increases in the capacity of the digestive tract in order to hold more food and absorb more nutrients, and increases in the abilities of the liver and kidney to clear more absorbed metabolites. Seasonal reductions in food abundance may force animals to reduce their food intake and rely instead on their stores of energy and nutrients. Animals can minimize the increased costs of survival under adverse conditions by reducing the energy expended on core functions such as movement and thermoregulation. Bears reduce activity and body temperature when they enter winter dormancy. The ability to respond to changes in food supply or survival costs is determined by the time required to respond and the physiological range over which the response can be sustained. Animals are stressed with potentially negative consequences when they cannot meet the demands of their environment and their life history. Growth and reproduction may be slowed, interrupted or abandoned when stressors cannot be avoided or accommodated by changes in location or food intake (Fig. 11.1). Storms, for example, increase the concentration of stress hormones in breeding



**Fig. 11.1** Effects of environmental variation on energy and nutrient flow in animals

songbirds, which alters their allocation of energy from reproduction to survival as they temporarily abandon nesting (Wingfield and Ramenofsky 1999). Similarly, stressful winters with heavy snowfalls are associated with pauses in reproduction of female caribou and their annual production of calves (Adams and Dale 1998).

Behavioral and physiological responses are integrated to maximize the likelihood of survival and reproduction. This integration involves multiple levels of response from genes and metabolic pathways at the cellular level to growth and reproduction of the whole animal. Therefore, responses are integrated over time scales that range from seconds to years as each meal is integrated into the life cycle of the animal. Similarly, responses are integrated over spatial scales ranging from a few square meters at a feeding site (Parker et al. 1996) to the annual range of the animal (Hobbs 2003; Parker 2003).

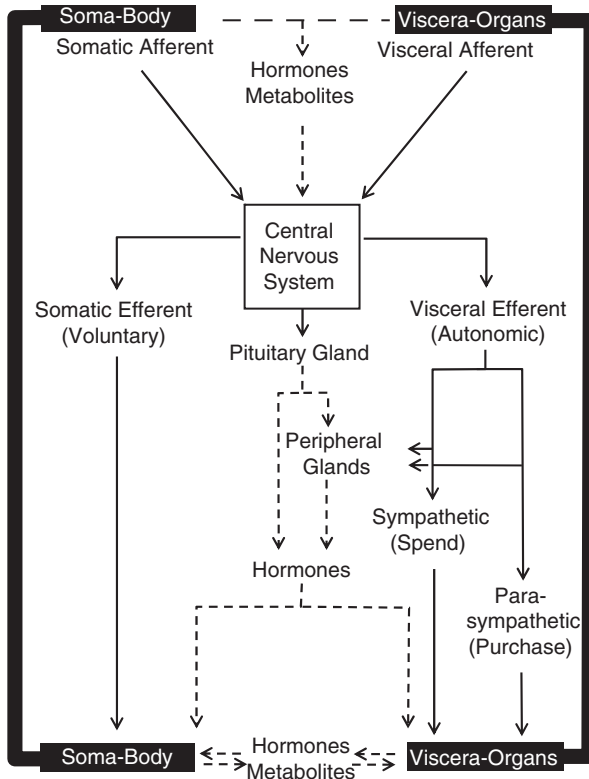
## 11.1 Neuro-Endocrine Integration of Food Intake and Metabolism

Animals consume food, and absorb and metabolize nutrients in an attempt to maintain homeostasis throughout the day. Small changes in the balance between supply and demand for energy and nutrients over many days control changes in body mass and composition during each season. Metabolizable carbon (C) is monitored and regulated through the flows of metabolites such as glucose, SCFA and amino acids, which are key components in the pathways of energy metabolism. The flow of metabolizable C fuels core functions such as thermoregulation and cell turnover to maintain the integrity of the body (Chapter 10; Table 11.1). Similarly, water and electrolytes are monitored and regulated closely to maintain the composition of body fluids within a narrow range (Chapter 9). Coordinated increases in the consumption of both metabolizable C and the components of tissues allow animals to gain body mass for growth and reproduction (Chapter 10).

Nutrient flows within the body are controlled through the actions of nerves, hormones and other cellular signals (Fig. 11.2). Nerves are dedicated connections between cells, whereas hormones and cellular signals rely on the circulation of extracellular fluids to reach target cells that are located either within the same organ or in some other part of the body some distance away. Hormones are typically produced by glands whereas individual cells secrete messenger molecules such as the cytokines from cells in the immune system. Neurotransmitters are small molecules such as acetyl choline and epinephrine that are derived from amino acids. Hormones and cellular signals include a wide variety of molecules, from small lipids such as sterols (e.g., cortisol) to large peptides (e.g., insulin). Nerves transmit the sweet taste of sugar from the mouth to the brain, as well as the response from the brain to the mouth, to continue feeding and produce saliva (Chapter 3). Secretions of the pancreatic hormones insulin and glucagon are carried by the blood to the liver, muscles and fat depots to regulate glucose uptake (Chapter 6).

**Table 11.1** The role of nutrition in homeostatic functions of animals

Homeostatic function	Nutrient group
Temperature, synthesis and work	Energy substrates as fuels (sugars, fatty acids and amino acids)
Hydration and balance of ions and solutes	Water
	Electrolytes (Na <sup>+</sup> , K <sup>+</sup> , Cl <sup>-</sup> , Ca <sup>2+</sup> , Mg <sup>2+</sup> , SO <sub>4</sub> <sup>2-</sup> , PO <sub>4</sub> <sup>2-</sup> )
Structural integrity	Amino acids for proteins
	Essential fatty acids for membranes
	Macrominerals (Ca, P, Mg, S) for bones, membranes, proteins
Functional integrity	Antioxidants (vitamins C and E)
	Trace minerals for enzymes
	Vitamins for metabolic pathways



**Fig. 11.2** The neuro-endocrine system regulates and integrates food intake and metabolism through signals from nerves (arrows with solid lines) and hormones. Extracellular fluids (arrows with broken lines) such as blood plasma and interstitial fluids distribute hormones, other cellular signals (e.g., cytokines) and metabolites among cells. The central nervous system (brain and spinal cord) receives signals along afferent nerves from receptors in skeletal muscles and skin at the mouth (soma or body) and from the visceral organs such as the glands and muscles of the gastric stomach. Efferent nerves return signals from the central nervous system to initiate responses at the soma and the viscera

The neural system is divided between the soma and the viscera (Fig. 11.2). The soma consists of the frame and surface of the body, including the skin, skeletal muscles and mouth. The viscera include internal organs such as the liver, kidney, digestive and reproductive tracts. Somatic sensors in the mouth detect the smell, taste, texture and temperature of food. Visceral sensors monitor distension of the stomach wall and acidification of gastric digesta at the start of the meal, as well as the rise in glucose concentrations in the liver during the meal. Afferent nerves bring information to the CNS whereas efferent nerves transmit impulses to the soma and the viscera for a response. Chewing food is a somatic response from the brain to the muscles of the mouth, but mixing food with acid is a visceral response from the brain to the stomach. Somatic responses are under conscious control; the decision

to stop feeding and start moving to another feeding patch is a voluntary response that is integrated with other information such as the behavior of conspecifics, the ambient temperature and the presence of predators (Chapter 3). Visceral responses are autonomic and controlled by opposing branches of nerves; parasympathetic nerves stimulate actions that 'purchase' energy by consumption of food (e.g., saliva production, gut motility), whereas the sympathetic nerves stimulate actions that 'spend' energy and suppress food intake (e.g., increasing heart rate). In birds that undergo seasonal changes in body mass, parasympathetic signals predominate over sympathetic signals to increase food intake and thus gain fat and lean mass (Kuenzel et al. 1999).

Sensory feedbacks from the soma and viscera modulate neural responses during a meal. Receptors that sense solutes in the mouth and distension of the foregut are used to control food consumption as well as motility and secretion during a meal. Chickens and red grouse slow food consumption as the crop and gizzard fill with food (Savory 1999). Similarly, sheep and cattle slow food consumption and increase ruminal motility as food fills the forestomach (Forbes 2007). Alterations to the set points for these feedbacks lead to increases in the duration of the feeding bout and thus meal size, and finally daily food intake (Savory 1999). Seasonal mass gains of animals are therefore controlled by changes in the sensitivity to sensory (afferent) inputs as well as the pattern of autonomic (efferent) responses.

Sensory inputs also cause the release of hormones from the pituitary gland, which is intimately connected with the hypothalamus at the base of the brain. An increase in the osmolality of blood flowing to the brain causes the secretion of vasopressin from the pituitary, which stimulates water resorption at the kidney (Chapter 9). The brain also stimulates the pituitary to release hormones that activate peripheral glands such as the thyroid, which releases thyroxine that increases metabolic rate during feeding (Chapters 9 and 10). Peripheral glands also receive neural stimulation; changes in blood glucose concentration stimulate the release of insulin and glucagon from the pancreas, which is further modulated by stimuli from autonomic nerves (Chapter 6). Hormones produced in peripheral tissues stimulate other visceral organs and the soma: cholecystokinin (CCK) from the small intestine slows motility of the stomach and increases release of bile from the liver (Chapter 7); vitamin D produced at the skin is activated in the liver and the kidney to stimulate Ca absorption from the intestine (Chapter 9).

Hormones can change food intake and body mass by directly stimulating the brain, by causing the release of other cytokines that enter the circulation of the brain, or by stimulating organs (e.g., the liver) that return afferent neural signals to the brain (Fig. 11.2) (Rhind et al. 2002). Many signal molecules and cells have been implicated in the stimulation and suppression of food intake during a day. The network of signals is like a stage play; many actors with many lines communicate a common theme such as 'increase food intake and body mass for growth'. One signal (one line in the play) from one organ (one actor) provides only a small portion of the total information required to integrate the response across the network.

The diversity of signals reflects the diversity of supplies from food and the demands of the animal. The supply of metabolizable C must be integrated from

foods with different proportions of carbohydrate, protein and lipid to meet the prevailing demands for survival and the anticipated costs of production. For instance, several species of fish, birds and mammals reduce food intake in response to secretion of CCK from the duodenum (Chapters 5 and 7) (De Pedro and Bjornsson 2001; Forbes 2007). Rising concentrations of CCK in the blood indicate to the brain that lipids are being digested. CCK is a good indicator of metabolizable energy supply from most foods because lipids are rich in metabolizable C. CCK is a better indicator of energy intake than the concentrations of fatty acids in the blood because fatty acid concentrations may be slow to increase after a meal and because fatty acids are also mobilized from adipose tissues when food intake is low.

The importance of each signal changes within species with changes in diet and life stage. Sensitivities to insulin and glucagon change with season in hibernating animals; glucagon is more important than insulin during winter because plasma concentrations of glucose are more likely to decline between each bout of torpor (Wang and Lee 1996). Signals have different emphases in different species; evolutionary selection has favored feedbacks between particular organs to ensure homeostasis for survival as well as reproduction. Leptin, a hormone released by adipose cells and liver (Houseknecht and Spurlock 2003), reduces food intake in hibernating rodents such as Arctic ground squirrels and Djungarian hamsters (Ormseth et al. 1996; Klingenspor et al. 2000). High plasma leptin indicates large fat stores in these animals (Florant et al. 2004), but not in all mammals and birds (Speakman et al. 2002); different neuro-endocrine indicators of energy and nutrient status (Rhind et al. 2002) are used in different species to provide similar information for regulating food intake.

Daily patterns of food intake may be regulated by the simple process of filling and emptying the digestive tract, and clearing absorbed nutrients from the blood. This endogenous cycle of feeding is evident in Svalbard reindeer during the continuous night of the polar winter and the continuous day of the polar summer (van Oort et al. 2007). Endogenous cycles of food intake are modulated by internal cues for growth and reproduction. Pituitary hormones that stimulate production include growth hormone that controls development and mass gain, as well as luteinizing hormone (LH) and follicle stimulating hormone (FSH) that promote the production of eggs and sperm. Feeding patterns are also modulated by environmental cues that allow animals to anticipate periods that are favorable for foraging, that is, when risks of predation or thermal stress are lowest and the net gains of nutrients are most likely to be high (Chapter 3). Fish may modify their feeding patterns in relation to regular tides and currents that change the temperature and concentrations of dissolved O<sub>2</sub> and CO<sub>2</sub> in water (Madrid et al. 2001). Daylight is used to schedule feeding in animals that are nocturnal, diurnal or crepuscular (active at dusk and dawn). Changes in the duration of day (photo-period) and night (scotoperiod) may result in seasonal changes in food availability and environmental demands. Daily (circadian) and seasonal (circannual) responses are stimulated by melatonin, a hormone released from the pineal gland. Melatonin is secreted in the dark and suppressed by light exposure; plasma melatonin there-



**Fig. 11.3** Pelage change is one of the metabolic systems affected by photoperiod. The pelage of this snowshoe hare is changing from white to brown as day length increases in spring. The hare will turn back to white again as day length shortens in autumn. Exposure to light suppresses the secretion of the hormone melatonin from the pineal gland. Melatonin regulates the secretion of melanotropin from the pituitary gland, which in turn regulates the production of melanin at the skin and the hair follicle. Decreasing day length in autumn increases melatonin, which suppresses melanotropin and stops melanin synthesis as animals molt into their white pelage for winter (Norris 1997)

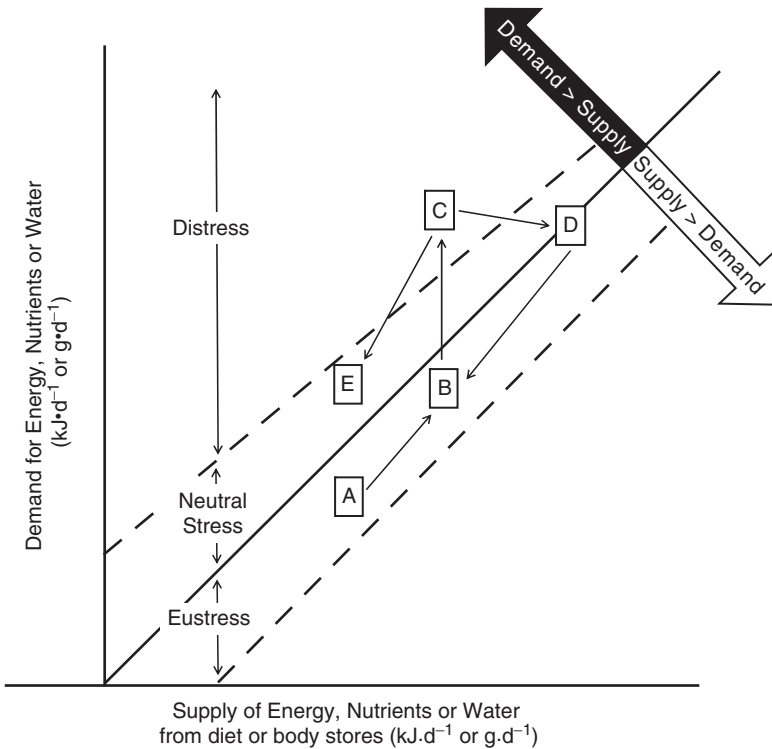
fore signals day length (Norris 1997). Northern ruminants such as red deer increase food intake and gain body mass in the long days of spring and summer (low plasma melatonin) and decrease food intakes in the short days of winter (high plasma melatonin) (Rhind et al. 2002). Day length and melatonin also are used to schedule molt and regrowth of fur and feathers, as well as growth and reproduction in mammals and birds (Fig. 11.3).

## 11.2 Stressors

Any challenge to the homeostasis of an animal may be considered a stressor that requires an integrated response from the neuro-endocrine system (Woebeser 2006). Environmental changes usually present multiple challenges to homeostasis. Droughts challenge animals to regulate their body fluids against declining plasma volume and increasing plasma concentration of Na. Vasopressin and atrial natriuretic hormone (ANH) secretions stimulate responses from the brain to search for water, minimize water loss and eliminate excess Na by changing renal function (Chapter 9). Droughts also cause heat loads that stimulate voluntary responses such as a shift in foraging pattern to minimize exposure to the sun,

autonomic responses such as sweating or panting, and the production of protective agents such as melanin and heat-shock proteins (Chapter 10). Water-stressed animals may reduce food intake, which then limits the supply of energy and nutrients for maintaining the structural and functional integrity of the body (Table 11.1).

Each stressor can be considered as the difference between supply and demand of energy or any nutrient (e.g., water, Na or N) at three different levels: eustress, neutral stress and distress (Breazile 1987) (Fig. 11.4). Eustress is the condition of beneficial stress when supply exceeds demand and the animal is in positive or zero balance. The metabolic load of absorbed nutrients that must be cleared after a meal



**Fig. 11.4** Stress may be considered as positive (eustress), neutral or negative (distress). Stress levels are related to the difference between supply and demand of any nutrient required for homeostasis or integrity of the animal. The *solid line* indicates a complete match between supply and demand. Eustress is a moderate excess of supply over demand (below *solid line*), whereas neutral stress is incurred when animals contend with a moderate deficit of supply (above *solid line*). Animals are distressed as the deficit in supply increases. An animal at maintenance (A) increases its demands as it begins to reproduce (B). A stressor such as a storm or disturbance increases the demands of the animal without changing supply and the animal becomes distressed (C). The animal may alleviate its distress by moving to an area with more food or shelter (D) or by reducing its demands by interrupting breeding (E)



is an example of eustress that maintains the normal range of vascular, liver and kidney functions. Selection of plants that contain plant secondary metabolites (PSMs) is a form of eustress that maintains a complement of detoxification enzymes, which defend the herbivore against toxins; this phenomenon of inoculation or induction by low exposure to stressors is called 'hormesis' (Lindsay 2005).

Neutral stress is incurred when demand begins to exceed supply and animals enter negative balances for some nutrients but can still tolerate the deficit by using body stores (Fig. 11.4). Animals can consume a meal with little N or vitamin A because they can use labile proteins and vitamin A that are stored in the liver. Dietary imbalances in Ca and P are neutral stressors that can be tolerated if stores of Ca and P from bone are available, and if the animal is able to excrete the excess mineral (Chapter 9).

Animals are distressed when demands exceed supplies and the deficit of energy or nutrients exceeds the tolerance threshold provided by body stores (neutral stress). Unpredictable events such as storms force songbirds to mobilize their body stores to either fly away or stay and meet the added demands for thermoregulation when foraging is limited (Fig. 11.4) (Wingfield and Ramenofsky 1999). Animals are more likely to be distressed by these additional demands when their requirements are already elevated for growth or reproduction. Consequently, distressed animals may reduce their demands by slowing or interrupting growth or reproduction so that body stores can be allocated to behavioral and physiological responses that favor survival (Figs. 11.1 and 11.4) (Wingfield 2005). Frequent distresses may prevent reproduction and ultimately debilitate the animal, but reproduction may continue under neutral stress when smaller deficits are met by mobilizing body stores (capital breeders; Chapter 10).

Distress responses are integrated at the brain by both hormonal and neural pathways. Sympathetic autonomic nerves activate the distress response from organs and fat depots as well as the adrenal gland, which releases epinephrine to the blood (Fig. 11.2). The neural path is fast acting and part of the 'fight or flight response' that increases blood flow and O<sub>2</sub> delivery to the brain and muscle, and suppresses the blood supply and activity of the digestive tract, kidney and skin (Breazile 1987). The CNS also initiates the hormonal pathway for distress by secreting hormones from the hypothalamus and pituitary gland that stimulate the adrenal gland to release the glucocorticoid (GCORT) hormones cortisol or corticosterone. GCORTs are longer acting than epinephrine and more likely to be detected in blood and hair and as excretory conjugates in urine and feces (Parker et al. 1993a; Wasser et al. 2000; Washburn et al. 2002; Davenport et al. 2006). GCORTs increase the concentration of glucose in plasma by suppressing insulin responses, increasing gluconeogenesis in the liver and mobilizing protein and lipid from muscle and fat. GCORTs mobilize stored energy to prepare the animal for the sudden demands of intense activity that may be required to survive an external threat to the body or to flee the area to alleviate a challenge to homeostasis.

Food intake is both stimulated and suppressed by GCORTs. Mild distress at low concentrations of GCORTs stimulates food intake and increases energy supply to meet the anticipated demand; chronic low elevations of GCORTs may be associated

with overfeeding and obesity in some mammals, including humans (Wingfield 2005). Small rises in plasma GCORT may serve as a signal to resume feeding in fasting animals that also use body stores for reproduction. In lactating Antarctic fur seals, for example, plasma GCORT increases before they return to sea to forage (Guinet et al. 2004). High concentrations of GCORTs suppress food intake as well as immune responses and wound healing, which diverts energy away from maintenance of the body. High concentrations of cortisol in breeding males impair renal function, and increase the incidence of mortality from wounds and infection among reindeer, Arctic ground squirrels and the semelparous marsupial brown antechinus (Barboza et al. 2004; Boonstra 2005; Naylor et al. 2008). Interactions between GCORTs and other hormones may alleviate some adverse effects. Testosterone reduces the effect of cortisol on renal function in brown antechinus, so that the dominant males with the highest concentrations of testosterone survive and breed for the longest period, but still eventually die from the consequences of impaired body maintenance (Naylor et al. 2008).

High concentrations of GCORTs also impair development and may suppress reproduction (Sapolsky 2001). The adverse effects of GCORTs are ameliorated by binding the hormones to proteins (corticosteroid binding globulins) in the plasma, which reduces the concentration of unbound hormone (Reeder and Kramer 2005). Alternatively, the release of GCORT may be suppressed by increasing the threshold for distress. Cortisol levels, for example, are not related to changes in body fat or food intake of pregnant females among Sitka black-tailed deer or reindeer during winter (Parker et al. 1993a). The beneficial effects of GCORTs are only realized when the animal has sufficient stores to escape the stressor or when increased activity can increase the supply of energy (Wingfield and Ramenofsky 1999). Plasma corticosterone in small, food-deprived Magellanic penguin chicks increases in response to the stress of handling during early development, but not when birds are handled at fledging. Small chicks therefore avoid the adverse effects of corticosterone when body stores must be conserved at fledging (Walker et al. 2005). Adult king penguins and common eiders do not use corticosterone but rather other hormones such as prolactin from the pituitary to stimulate resumption of feeding and mass regain (Cherel et al. 1994b; Criscuolo et al. 2006).

Distress responses are not always due to deficits in energy (Walsberg 2003). Secretion of GCORT is stimulated by behaviors that perceive immediate threats such as pursuit by a predator, and perceived threats such as the sight, smell or sound of a predator. Plasma concentrations of cortisol in wild snowshoe hares increase with predation risk (Boonstra 2005). These reactions may be altered by experience; flight responses of caribou are reduced after one generation following the elimination of predators (Berger 2007a). GCORT concentrations are affected further by dominance interactions among social animals such as baboons and wolves. That is, social rank and breeding status affect the apparent distress of animals within a group or population (Sapolsky 2001; Creel 2005).

Population cycles are correlated with GCORT concentrations in some species. Cyclical declines in a population of water voles, for example, are accompanied by elevated fecal metabolites of cortisol that indicate distress as animals respond to

overcrowding and to shortages of food or water (Charbonnel et al. 2008). Concentrations of GCORTs vary with season in many species of amphibians, reptiles, birds and mammals. These seasonal changes in the distress response may be associated with changes in the sensitivity of animals to energy demands (e.g., locomotor activity and field metabolic rate (FMR)) and behavioral cues (e.g. predation, mating) that ultimately prepare the animal for each stage of its life history (e.g., growth, pregnancy) (Romero 2002).

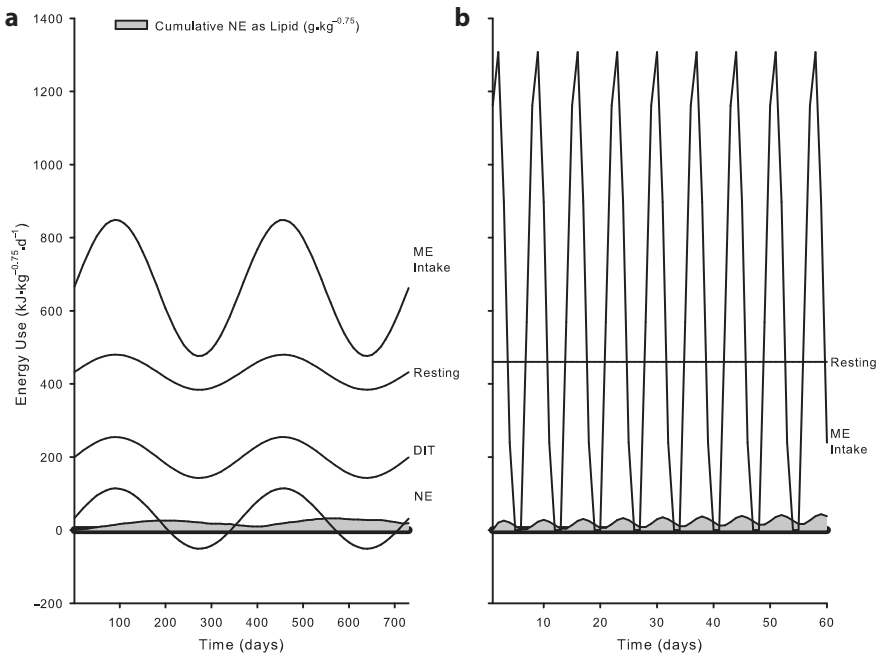
Distress responses therefore may indicate the net outcome of multiple stressors on a population and must be considered in the context of the species and season. The procedures for handling wild or domestic animals often include behavioral stressors of unfamiliar sounds, smells and sights in confined spaces close to other animals, and physiological stressors of fasting, dehydration and increased exposure to infection (Spraker 1993; Hogan et al. 2007). Consequently, a true evaluation of stressors may require multiple indices combined with measures of body condition. Indicators that integrate responses over longer time frames should be more useful for evaluating neutral stress as well as the frequency of distress. Extraction of GCORTs from excreta rather than blood samples provides a longer integration of distress responses and can be collected with little or no disturbance to the animal (Berger et al. 1999; Wasser et al. 2000). Extraction of N metabolites from urine and feces for isotope measures of nutritional stress can also provide a 'hands off' estimate of body protein loss in wintering reindeer (Barboza and Parker 2006). Antibodies and cytokines such as tumor necrosis factors, interleukins and haptoglobins can provide additional indices of exposure to stressors such as toxins or disease that may ultimately lead to more specific indicators for the species and population under study (Ditchkoff et al. 2001b; Bowyer et al. 2003; Wobeser 2006).

### 11.3 Plasticity of Food Intake and Production

The patterns of feeding in animals are ultimately determined by variation in their environments. In terrestrial animals, seasonal variations in light, temperature and water affect the abundance and distribution of food, and circadian variations in light and temperature affect the animal's ability to consume that food in a foraging window with minimum risk (Chapter 3). Consequently, environmental variations in food abundance and quality often affect seasonal food intakes of some herbivores more than the endogenous cues for feeding (Iason et al. 2000). The ability to tolerate variation in food supply depends on the physiological plasticity of the species. Fluctuating food supplies require integrated responses of digestion, intermediary metabolism, body mass regulation and reproduction.

Variation in food supplies and thus food intakes can be considered as an oscillating pattern of energy intake based on calculations in Chapter 10. The pattern of metabolizable energy (ME) intake oscillates around a mean (ordinate) with varying amplitude and frequency. In Fig. 11.5a, seasonal food intakes are modeled on a frequency of

365 days for one annual cycle. Large herbivores such as Arctic muskoxen increase food intakes by 28% above the mean in summer when plant biomass is greatest, and decrease intakes to 56% of the peak intake in winter at the nadir of food abundance (Fig. 11.5a) (Peltier et al. 2003). The model includes two costs of maintenance: energy demands at rest (resting metabolic rate, RMR) and the energy lost when metabolizing food (diet-induced thermogenesis, DIT). These costs follow the pattern of food intake because muskoxen and other northern herbivores decrease RMR from summer to winter (Lawler and White 1997) and because DIT is proportional to ME intake (Blaxter 1989; Lawler and White 2006).



**Fig. 11.5** Two models of variable food intake. **a** Annual variation in food intake of a northern ungulate such as muskoxen. **b** Weekly variation in food intake of a carnivore (e.g., mountain lion) or migratory bird on wintering grounds (e.g., black duck). Oscillations in metabolizable energy (ME) intake ( $Y$ ) were modeled with the equation  $Y = Y_0 + a \cdot \sin\left(\frac{2\pi X}{b}\right)$ , where  $Y_0$  is the ordinate of the oscillation,  $X$  is time in days,  $a$  is the amplitude of the oscillation and  $b$  is frequency (Barboza and Hume 2006). The seasonal intake of muskoxen for model **a** was calculated as:  $Y_0 = 662.4 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $a = 186.5 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $b = 365 \text{ d}$  (Peltier et al. 2003). Feeding responses of intermittently fasted black ducks for model **b** were calculated as:  $Y_0 = 568.5 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $a = 758.6 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $b = 7 \text{ d}$  (Barboza and Jorde 2001). Diet-induced thermogenesis ( $DIT$ ) was calculated at  $0.3 \cdot \text{ME}$  intake in model **a** and at  $0.15 \cdot \text{ME}$  intake in model **b** (Blaxter 1989). Seasonal resting metabolic rate (RMR) for model **a** was estimated as:  $Y_0 = 432.0 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $a = 48.0 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $b = 365 \text{ d}$  (Lawler and White 2006). RMR was fixed at  $460.8 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$  for model **b** (Kaselloo and Lovvorn 2003). Net energy ( $NE$ ) is the energy remaining from ME intake after deducting RMR and DIT. The available NE was converted to a change in body lipid (*shaded areas*) with the calculations described in Table 10.1 and summed over the duration of each model

The net energy (NE) available for production of fat increases in autumn but declines during winter when ME intakes are insufficient to meet the combined costs of RMR and DIT (Fig. 11.5a).

Slow oscillations of food intake and mass gain in seasonal herbivores do not include regular periods of fasting (Fig. 11.5a). Many animals, however, feed and fast intermittently in much shorter cycles with greater amplitudes (Fig. 11.5b). Intermittent feeders include predators such as lions and pythons that fast between large kills, and shorebirds or waterfowl that are restricted to foraging between tides or migratory flights (Barboza and Hume 2006). Mean energy intake and the frequency of feeding increase with metabolic demands of endotherms and ectotherms. Endothermic lions feed every few days, whereas ectothermic pythons may feed at intervals of several weeks, depending on ambient temperatures (Chapter 10). Black ducks can tolerate fasting for 4–5 days and feeding for 2–3 days in a weekly cycle that mimics frequent interruptions of feeding by winter storms and tides (Barboza and Jorde 2001). These birds resume feeding at 233% of their mean intake to compensate for each fast (Fig. 11.5b). Other birds respond in a similar manner to increased energy demands during exposure to cold temperatures (McWilliams and Karasov 1998).

Each oscillation in the pattern of food intake switches between hyperphagia and hypophagia. Hyperphagia presents a load on both digestive and metabolic systems because intakes of ME and other nutrients exceed requirements. Hypophagia is a deficit that must be met from body stores because intakes are insufficient for requirements. Large changes in the abundance of foods select for hyperphagic responses in animals because the subsequent ability to tolerate food shortages is dependent on prior accumulation of nutrients. Highly variable environments that frequently alter food abundance for animals select for rapid adjustments to both hyperphagia and hypophagia. These responses are quickly integrated by the neuro-endocrine system, but more time and nutrients may be required to alter the activities of tissues and metabolic pathways.

The time to respond to a sudden change in energy demands and food intake is met by 'spare capacity', which is a safety margin for increasing supply in response to a sudden demand. Spare capacities can be measured as the increase in daily digestible intake of animals switched from low to high demands for thermoregulation or reproduction. Spare capacity varies widely from 9–50% in small endotherms such as yellow-rumped warblers, white-crowned sparrows and prairie voles that were switched from mild to cold temperatures (Karasov and McWilliams 2005). Enzyme induction is the first response to a shift in diet and food intake (Fig. 11.1). Endogenous enzymes are induced within a day by synthesis at the surface of the intestinal mucosa and the pancreas in response to changes in carbohydrate and protein intake (Karasov and Hume 1997). Dietary induction of exogenous enzymes that are produced by fermentative microbes may require more than a week, depending on the composition and turnover rate of the microbial community (Chapter 6). Similarly, enzymes and transporters that oxidize and eliminate PSMs may also require longer periods of induction, depending on the frequency of exposure to the toxin (Chapter 3).

Structural changes in organs follow enzymatic changes as dietary shifts and intakes are sustained (Fig. 11.1). Morphological changes in the digestive tract and liver are observed within 1–2 days of a change in diet for birds such as Japanese quail, red grouse and red knots (Battley and Piersma 2005; Starck 2005). Food composition affects the sequence of changes by stimulating different organs: abrasive diets stimulate mass gains of the gizzard, high lipid loads promote increases in liver mass, and solute loads promote enlargement of salt glands and kidneys (Chapters 5 and 9).

The time available to process increasing amounts of food depends on rates of digesta flow and digestion and the volume of the digestive tract (Chapter 5) (Fig. 11.1). Foods that are quickly degraded by endogenous enzymes can be processed in a tubular gut system (midgut plug flow reactor, PFR). This allows migratory shorebirds, eagles and bears to attain high food intakes and utilize brief periods of food abundance, such as spawning salmon and horseshoe crabs. Slowly digested substrates such as lipids are most affected by high flow rates and high food intakes. In harbor seals, high intakes of lipid in herring reduced lipid digestibility from 90% to 50%, but protein digestibility was maintained over a wide range of protein intakes (Trumble et al. 2003). The maximum capacity to process lipids, proteins and carbohydrates varies with the composition of the diet and with the secretory and absorptive capacity of the species. Carnivores such as seals and cats have very high capacities to process proteins, whereas the ability to handle sugars is greatest among nectarivores and frugivores (Chapters 5, 6 and 8).

Slow flow rates and large digestive volumes are required to utilize structural carbohydrates. Fermentation is a slow, multi-step process that is best suited to large mixing chambers in either the foregut (e.g., rumen continuous-flow, stirred-tank reactor, CSTR) or the hindgut (e.g., colonic modified plug flow reactor, MPFR; Chapter 5). High food intakes and flow rates may limit fiber digestion to the hemicellulose fraction of the cell wall in waterfowl (Dawson et al. 2000). Intermittent feeding by black ducks decreases the digestibility of cellulose but does not affect hemicellulose digestion (Barboza and Jorde 2001). Herbivores such as ruminants and equids that utilize cellulose are poorly suited to rapid increases in food intake and sudden changes in diet composition because those changes may exceed the capacity to maintain homeostasis. Captive ruminants that are quickly switched to diets with high concentrations of soluble carbohydrates are vulnerable to bloat and acidosis because one portion of the microbial community can dominate the fermentation (Owens et al. 1998). Conversely, alligators consume large meals (10% of body mass), which are mixed in a muscular stomach that produces large amounts of acid through adaptations of the vascular system and the pathways for acid–base balance (Wang et al. 2005; Farmer et al. 2008). The large digestive capacities of herbivores allow animals to increase food intake, especially as food quality declines (Chapter 5), but those increases in food intake are usually achieved over several days or weeks (Bunnell and Gillingham 1985; Barboza and Parker 2008). Muskoxen increase total digesta fill by 58% when food intakes increase by 73% over several weeks between spring and autumn (Barboza et al. 2006).

Declines in food intake are associated with a reduction in the mass of intestine, liver and kidney. Herbivores such as alpine marmots reduce the digestive tract as food intakes decline before hibernation but quickly restore those tissues when feeding resumes in spring (Hume et al. 2002). Reductions in the mass of nutritional organs are associated with reduction in the basal metabolic rate (BMR) of migratory shorebirds. These reductions reduce their wing loading and increase their flight range (Battley and Piersma 2005). Conversely, migratory garden warblers restore digestive function as food intake increases during the first 3 days after arriving at their destination (Hume and Biebach 1996). Frequent cycles of feeding and fasting, however, may not allow animals to reduce their digestive tissues and their BMR during a fast because they must maintain the capacity for digestion when feeding resumes. The high BMR of seals and dolphins is related to the high costs of maintaining a long intestine (Williams et al. 2001, 2004a). The energy required for maintenance of the body may therefore increase with the frequency of intermittent feeding and fasting.

Frequent oscillations between deposition and mobilization of energy stores may further increase food intakes because energy is lost in converting body tissue to metabolic demand (e.g., 80%) and restoring that body tissue with food (e.g., 50%; Chapter 10) (Blaxter 1989). For example, if an animal requires  $1 \text{ MJ}\cdot\text{d}^{-1}$  of ME for maintenance, it would use  $2 \text{ MJ}\cdot\text{d}^{-1}$  from the diet (50% efficiency) or  $1.25 \text{ MJ}\cdot\text{d}^{-1}$  from body tissue (80% efficiency). For an animal meeting its maintenance energy requirement from body stores, it must replenish the lost body energy by consuming an additional  $2.5 \text{ MJ}\cdot\text{d}^{-1}$  ( $1.25 \text{ MJ}\cdot\text{d}^{-1}$  at 50% efficiency) during refeeding. That is, each day of fasting increases the subsequent food intake from  $4.0$  to  $4.5 \text{ MJ}\cdot\text{d}^{-1}$  ( $2.0$  for current maintenance +  $2.5$  for regain). Frequent fluctuations in food abundance can increase energy costs for animals, which may reduce the number of animals that can use the same amount of food, and increase the time required to regain mass. Daily interruptions to feeding may extend the time required for waterfowl to regain mass at migratory stopover sites and reduce the number of birds that can be sustained on a wintering ground.

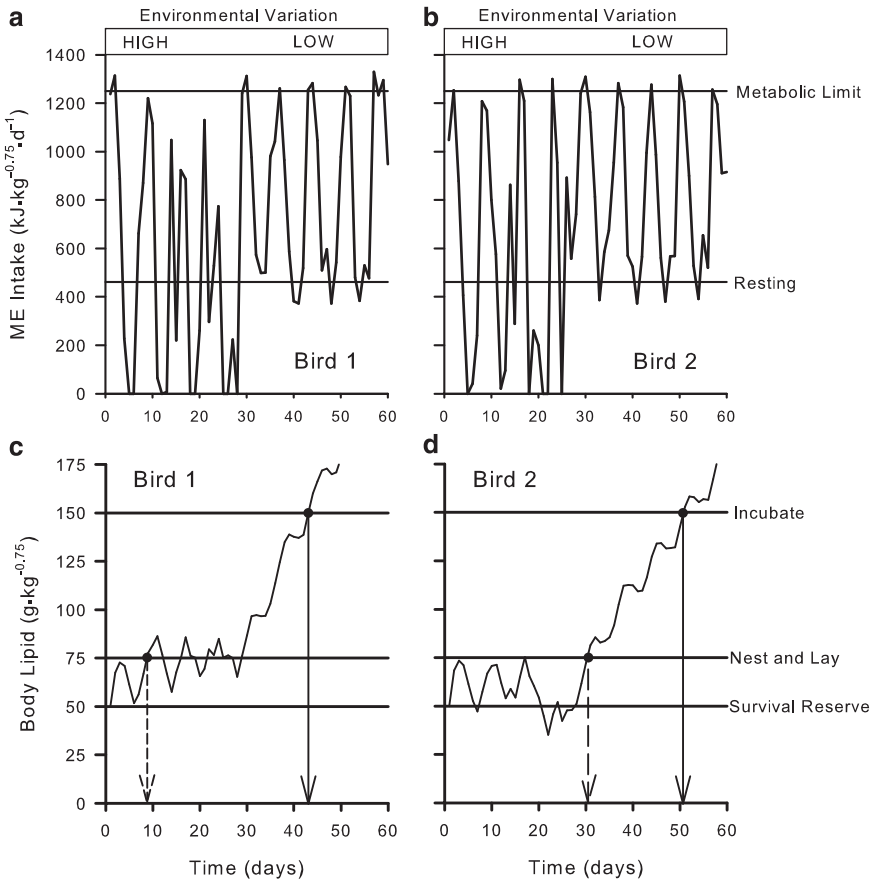
Energy expenditures of small mammals and birds during a fast may be reduced by entering torpor, especially in winter when reductions in food abundance are combined with increased thermoregulatory demands (Chapter 10). Torpor, however, interrupts the development of gametes and embryos in mammals (Wang and Lee 1996; Naylor et al. 2008). Male Arctic ground squirrels arouse from hibernation earlier than females and consume cached food to maintain body temperatures that are needed for sperm production. Reproduction can therefore continue during hypophagia only if body stores are used to maintain parental homeostasis and to synthesize gametes or new tissues of the offspring. Female bears can give birth and suckle cubs during winter dormancy because the mother uses body fat and protein to sustain the cubs and maintain body temperatures at only a few degrees below the active body temperature in summer (Farley and Robbins 1995). Similarly, female reindeer can give birth and commence lactation before peak food abundance because they use body stores of fat and protein deposited in autumn for the production of the fetus as well as the synthesis of milk in the first 4 weeks after birth in spring (Barboza

and Parker 2008). Increasing body size may be associated with a greater tolerance of hypophagia during reproduction. In comparison with small species, large animals have proportionately larger fat stores (scalar  $>1$ ) but smaller BMRs (scalar  $<1$ ) that allow them to survive on the same proportion of body fat for longer periods of time (Chapter 10). Large species also require a longer period to develop, which may allow offspring more opportunities to compensate for brief interruptions in growth (Chapter 10) (Barboza and Hume 2006).

Some animals may be unable to dampen dietary fluctuations in all nutrients, especially when demands for synthesis are high and body stores are small. Thus intermittent feeding impairs the synthesis of red colors in male house finches and three-spined sticklebacks because the skin cells require a constant supply of carotenoids, energy and amino acids for these changes in pelage and skin (Chapter 9) (Frischknecht 1993; Hill 2000). Fluctuations in food supply may also alter the response to stressors such as infections, parasites, disease and toxins (Krasnov et al. 2005; Smith et al. 2005). Lower food availability reduces immune function in deer mice even though body mass is not affected (Martin et al. 2008). Consequently, intermittent fasts may increase the requirements of some nutrients even though animals may be able to achieve the same ME intake during refeeding. Intermittent fasts may be a neutral stress that could be alleviated by altering food selection to enhance the intake of some nutrients (Fig. 11.4). Migratory songbirds rely on a diversity of fruits and insects at staging grounds to meet demands for energy, protein and trace nutrients depleted during hypophagia (Smith et al. 2007).

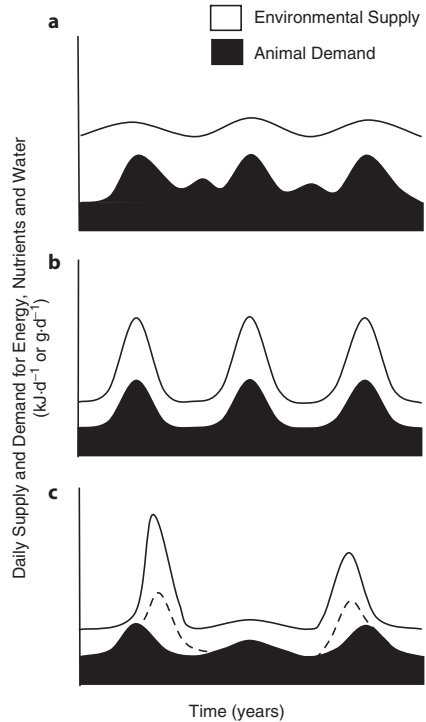
The timing of productive events that increase demands for energy and nutrients depends on environmental conditions that regularly provide adequate supplies. The transition from low food abundance in winter to high food abundance in spring also may be accompanied by a shift from high to low variance in weather conditions and thus environmental demands. Environmental variation in feeding cycles affects the rate at which animals can gain mass for production. High variation in feeding conditions increases the variation in body condition among animals and the time at which they attain sufficient stores to begin reproduction (Fig. 11.6). Timing of body stores may be one of many factors that affect the reproduction of migratory ducks such as lesser scaup (Anteau and Afton 2004). Changes in the availability and species of invertebrate prey affect foraging times for scaup (Poulton et al. 2002) and the body composition of birds as they migrate to their breeding grounds in the prairies and boreal forests (Vest et al. 2006). Variation in the quality and abundance of foods in breeding areas may influence reproduction of ducks by affecting the supplies of energy and nutrients for replenishing body stores (capital) as well as those nutrients that are required from the diet each day (income) for production of eggs and feathers. Stressors associated with variable foraging conditions may therefore impair reproductive development and behavior with regard to nesting and laying eggs. Black ducks that were intermittently fasted did not complete egg laying until food was available each day even though birds had sufficient body mass and lipid stores to complete the clutch of eggs when food was provided intermittently (Barboza and Jorde 2002). Diversity of foods and feeding areas may minimize variation between sites for reproducing females. Birthing windows for red deer are





**Fig. 11.6** Environmental variations that affect food intake and survival costs ultimately affect timing of productive events such as mass regain for migration, reproduction and growth in waterfowl. The model for black ducks from Fig. 11.5b was used to simulate high variation in late winter and lower variation in spring. Two model runs (*Bird 1* and *Bird 2*) are plotted for ME intake and the corresponding cumulative change in body lipid. Birds consistently gain body lipid when variation in food intakes decline from winter to spring. High environmental variation in winter increases the variation in condition between birds during both periods. Bird 1 experienced slightly better conditions during the period of high environmental variation. Consequently, it could begin nesting and laying earlier than Bird 2; body fat first exceeded the threshold for nesting in Bird 1 at 9 days whereas Bird 2 only initiated nesting at 31 days (*broken lines*). Bird 1 also met the incubation threshold for body fat 8 days earlier than Bird 2 (43 vs. 51 days) (*solid lines*). Model parameters for high variation:  $Y_0 = 568.5 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $a = 758.6 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $b = 7 \text{ d}$ , with 10% variation on all parameters. Model parameters for low variation:  $Y_0 = 852.7 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $a = 474.38 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ;  $b = 7 \text{ d}$ , with 2% variation on all parameters. RMR was fixed at  $460.8 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ . An upper limit for ME intake was set at  $1,250 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ , so no NE for production was available when ME intake exceeded this limit

**Fig. 11.7** Annual patterns of food availability for a population of animals. Demands for energy, nutrients and water for the population are highest during periods of growth and reproduction. **a** Low variation in food abundance allows animals to grow and reproduce through most of the year. **b** Regular patterns of food abundance select for a similar pattern in animal production. **c** Irregular patterns of food abundance prevent reproduction in some years, especially when animals follow a regular pattern of reproduction and growth. The *dotted line* indicates a shift in timing of reproduction to follow immediate cues of food abundance such as rainfall and primary plant growth in deserts



wider in Norway than in France even though the window for plant growth is much narrower at the higher latitude; alpine terrain in Norway provides a wider window of plant emergence and a greater diversity of feeding areas for reproducing females (Loe et al. 2005).

Timing of reproduction and growth in a population may be aseasonal when plants or prey are abundant throughout the year, as they are in some tropical habitats and in captivity (Fig. 11.7a). Pulses of births in primates from these largely aseasonal environments are mostly due to the variation among individuals in the time required to grow and establish sufficient condition to reproduce (Brockman and van Schaik 2005). Synchrony of births in herbivores is also affected by risks of predation and thus the density of predators. In African ungulates, species that form large herds (e.g., wildebeest) birth in narrow windows that overwhelm the predator response, whereas species that form small herds (e.g., impala) have a wider window of births that presumably reduces the attraction of predators (Sinclair et al. 2000).

Seasonal plant production favors some form of synchrony between environmental supply and animal demands (Fig. 11.7b). Births of African ungulates are timed in relation to the emergence of new plant growth and peak protein availability or to the subsequent peak in plant biomass (Sinclair et al. 2000). The correspondence between food production and animal reproduction is closest for income breeders. Capital breeders such as sheep are less sensitive to the timing of plant production because body stores are used for reproductive demands (Durant et al. 2005). Food abundance affects

the supply of nutrients for current reproduction of income breeders as well as stores for the subsequent commitments of capital breeders. Thus high metabolic demands make populations of endotherms (e.g., Atlantic puffins) more sensitive to seasonal food abundance than those of ectotherms (e.g., Atlantic cod) (Durant et al. 2005).

The cues for timing reproduction may be immediate indicators of food availability (e.g., number of meals, delays between meals) or correlative cues such as day length, water temperature and lunar cycles. Animals that use correlative cues to anticipate seasonal food availability for reproduction may mismatch supply and demand (trophic mismatch) when they change habitat or when the habitat changes around them (Fig. 11.7c). Blue tits that breed long before the peak abundance of insect prey expend more energy to feed their offspring than birds that breed close to the peak in prey (Thomas et al. 2001). Trophic mismatches may increase as animals move further between seasonal ranges, as the seasonal window for food production narrows, and as species rely on food rather than body stores for reproduction (income vs. capital breeding). Birds that migrate long distances may be more vulnerable to trophic mismatches than resident birds because environmental cues for departing the wintering grounds may not reflect the changes in food at their destination hundreds of kilometers away. For example, photoperiodic changes for songbirds in Mexico may not reflect changes in air temperature and insect abundance at their breeding grounds in Canada. Narrow windows of plant and insect abundance at high latitudes increase the likelihood of trophic mismatches for Arctic and Antarctic animals, many of which are also long-distance migrants. Small, income breeders such as Arctic-nesting shore birds (Klaassen et al. 2001) are probably more vulnerable to trophic mismatches than large-bodied birds such as trumpeter swans or snow geese that can rely on body capital to breed in the Arctic (Ankney and MacInnes 1978).

Correlative cues such as photoperiod become less informative as food availability becomes less seasonal or more unpredictable. Consequently, birds from less predictable habitats (e.g., hot deserts) and species that breed opportunistically when adequate conditions arise use immediate indicators of food availability to time breeding (Wingfield et al. 1992; Hahn et al. 1997). Zebra finches initiate breeding when rains break a drought in their desert habitat. Commitments to reproduction are further modulated by the emergence of grass seeds and insects that are required for feeding nestlings in the weeks that follow rainfall (Hahn et al. 1997). The immediate cues of food abundance and food quality (e.g., metabolizable energy or protein content) also stimulate ovulation in domestic sheep, pigs and chickens (Torrell et al. 1972; Hocking 1987; Downing and Scaramuzzi 1991; Johnson 2000).

## 11.4 Global Climate Change

Climate is the description of weather patterns at large scales of space (national, continental, global) and time (decadal, millennial, epochal) that affect food supplies and the environmental demands for wildlife at multiple levels, from habitats to ecosys-

tems. The longest scale of changes in global climate are associated with Milankovitch cycles of solar radiation that reflect changes in the orbit of the earth around the sun in periods of 23,000–100,000 years, which correspond with changes in the size of the polar ice caps and continental glaciers (Chapin et al. 2002; van Schaik and Brockman 2005). These changes in ice cover altered sea levels that opened and subsequently closed land bridges, which allowed wildlife to disperse between continents. Low sea levels allowed moose to spread from Europe to Alaska across the Bering land bridge whereas high seas isolated kangaroos in Australia and kiwis in New Zealand.

Interactions between the atmosphere, ocean, land and ice drive currents of air and water. Albatross use the strong winds of the Southern Ocean to forage across large areas where upwellings of cold water bring nutrients to the surface for their prey of invertebrates and fish (Weimerskirch et al. 2005). Atmospheric interactions vary widely between decades and result in contrasting weather across oceans and regions. The El Nino Southern Oscillation (ENSO) intensifies droughts and fires in Australia but enhances rainfall on the other side of the Pacific Ocean in Peru. However, El Nino also slows the cold, nutrient-rich Humboldt current that supports schools of anchovy and other prey for seals and seabirds in South America (Chapin et al. 2002). The North Atlantic Oscillation (NAO) causes warm winters that result in rain on the coast and snow in the mountains of Norway when the NAO index is high. Norwegian red deer use coastal habitat in winter and mountain pastures in summer where longer periods of snow melt increase the window for plant growth. A series of winters with high NAO indices allow female red deer to produce proportionately more male calves that are larger than female calves at birth and continue to grow more than young females in the subsequent summers (Post et al. 1999; Mysterud et al. 2000).

Small changes in temperature have profound effects on air and water currents that affect the distribution of rainfall and nutrients in both terrestrial and aquatic systems. The global climate has warmed by 0.6°C over the last 100 years (Root et al. 2003; Parmesan 2007) and is projected to increase in the northern hemisphere by another 1–4°C over the next 100 years (Bertheaux et al. 2004). Warming has increased changes in precipitation over many areas of the globe, resulting in drier sub-tropical regions in Africa and wetter north-temperate regions of North America and Central Asia (Walther et al. 2002). Temperature also affects the metabolic rates of bacteria, plants and ectothermic animals such as invertebrates, fish, amphibians and reptiles; a rise of 10°C can double energy expenditures in these organisms and enhance their rates of growth and reproduction ( $Q_{10} = 2$ ; Chapter 10). Consequently, global warming has advanced the seasonal window for production of plants and ectotherms in several areas (Parmesan 2006). In the northern hemisphere, the window for plant growth has advanced at an average rate of 2.8 days·decade<sup>-1</sup> and is now increasing by up to 4.9 days·decade<sup>-1</sup> (Parmesan 2007). Some animals such as yellow-bellied marmots are advancing their annual cycles of feeding by emerging earlier from hibernation (Inouye et al. 2000). Many birds that migrate short distances in Europe have likewise advanced their arrival and nesting dates, presumably to match the emergence of insect prey (Walther et al. 2002; Both et al. 2004).

Global warming is also shifting the distribution of many plants and animals to higher latitudes at an average rate of 6.1 km·decade<sup>-1</sup>, and to higher altitudes at an

average rate of  $6.1 \text{ m} \cdot \text{decade}^{-1}$  (Parmesan and Yohe 2003). Expansion of shrubs and trees into Arctic tundra enhances the rate of snow melt and warming of the land, which favors a progression to habitats that are more suited to browsing moose than to grazing muskoxen (Chapin et al. 2006). Conversely, global warming is shrinking mountain cloud forests used by frogs and neotropical rainforests used by migrant songbirds (Norris et al. 2004; Parmesan 2006).

The effects of climate warming vary widely because animals and their habitats respond differently to changes in temperature and precipitation. Warm temperatures that reduce snowfall may improve mobility for moose but increase the exposure of voles to cold temperatures and predators by reducing the sub-nivean space (Guthrie 1990). The shift from snow to rain is not always beneficial for large mammals; freezing rain increases thermoregulatory costs of reindeer by reducing insulation of the pelage (Chapter 10) and impedes feeding by covering the tundra with ice (Tyler et al. 2007). Warming may also alter the spread of diseases in wildlife. Mild winters increase the survival of ectotherms that include both external parasites (e.g., ticks) and internal parasites (e.g., nematodes) and their intermediate hosts (e.g., snails and insects). Warm summers allow these parasites to develop more rapidly and to increase rates of infection of their endothermic hosts (reindeer, muskoxen, moose and elk) (Kutz et al. 2005). Furthermore, changes in the distribution of a host will alter the dispersal of the disease it transmits to other populations and other species (Crowl et al. 2008). The effect of climate warming on a population is therefore the outcome of several responses and interactions among species to changes in temperature and the availability of food and water.

Climatic changes that rapidly alter habitats are likely to affect many species. Warming of the Antarctic affects the entire trophic chain, from zooplankton to penguins, because reductions in sea ice are accompanied by declines in production of phytoplankton and algae that are the base of the food web (Parmesan 2006). Consequently, extinctions of populations have been correlated with climate warming, especially in communities that are restricted to a narrow range of conditions, such as the shallow coastal areas colonized by corals and also the species that live in the reef. Populations may avoid extinction if animals have enough time to change their behavior or physiology in response to habitat changes. Female red squirrels advanced the timing of births by 6 days each generation as their diet of white spruce cones increased in abundance with increasing spring temperatures and decreasing precipitation over 10 years. However, most of the variation in timing of birth was attributed to phenotypic plasticity rather than evolution by natural selection (Berteaux et al. 2004). Long-term changes in the morphology of mammals probably reflect both phenotypic and evolutionary changes. Bushy-tailed woodrats declined in body size as climate warmed over a period of 25,000 years, which indicates that either growth was limited by food and water supply or natural selection favored smaller body sizes and absolute requirements for energy and water in dry climates (Smith et al. 1995) (Chapters 1, 9 and 10). Evolutionary changes in response to recent climate change have been observed in insects because those animals usually have higher intrinsic growth rates and shorter generation times than mammals and birds (Parmesan 2006). However, phenotypic plasticity may be the principal response to recent changes in climate for

large, long-lived species of wildlife. Pacific black brant use the same physiological plasticity in body lipid stores to migrate to Mexico in autumn or to overwinter in Alaska (Mason et al. 2007). The growing population of brant that overwinter in Alaska probably reflects abundant supplies of their principal food (sea grass) as well as higher winter temperatures that allow the geese to survive to spring and start reproduction with minimum delay and cost for migration (Mason et al. 2006).

## 11.5 Resilience and Wildlife

The concept of resilience is an approach to understanding the sustainability of human societies in ecosystems by considering multiple levels of responses to environmental change (Walker and Salt 2006). Our societies value wildlife for a wide variety of consumptive and aesthetic purposes, from wildlife watching to subsistence harvest and trophy hunting. Populations of fish and wildlife are therefore an important source of food and commerce for our society. Societies have long observed animals for indications of change because wildlife populations integrate environmental stressors. Movements of wildlife have marked our seasons of food supply for centuries; the arrival of migrant songbirds indicates the start of our season for plant cultivation and their departure indicates the times for harvest and hunting (Leopold 1949). We now look to arrivals of migrant songbirds as one indicator of a changing climate (Walther et al. 2002). Furthermore, wildlife populations are being monitored for diseases, toxins and variation in productivity because they integrate many of the stressors that challenge human societies (Crowl et al. 2008). Measures of radioactive isotopes in the food web of lichen, reindeer and wolves, for example, have been used to monitor the fallout from nuclear tests and accidents and to indicate the risks for human consumption of reindeer in northern Europe (Staaland et al. 1991). Similarly, selenium and mercury are monitored in salmon, seals and bowhead whales in order to evaluate the health of the animals and the quality of their tissues for subsistence hunters (Dehn et al. 2006).

Wildlife populations are resilient to environmental change if they can recover from the stressors that accompany the change. Stressors cause a deficit in the available energy, nutrients, space or time required to complete the life cycles of individuals in the population. A population is resilient to the change when enough individuals can complete their life cycle for the population to persist (Chapter 2). Resistance of the stressor may lead to distress, which may prompt individuals to avoid the stressor by moving to find more food and space (e.g., change in distribution). Natural selection for individuals that tolerate the stressor expands the region of neutral stress and may lead to an adaptive change in the species (e.g., changes in kidney function for water resorption). Resilient populations have multiple routes of response to avoid and tolerate stressors. Behavioral plasticity, physiological plasticity, genetic diversity and demography all contribute to the resilience of a population.

Boreal forests are disturbed by fire, logging and roads which present a variety of stressors to wildlife. Moose are often resilient to these changes because they are large enough to avoid the initial disturbance by moving out of the area (Fig. 11.8)



**Fig. 11.8** Moose populations often are favored by early stages of plant succession in boreal forests. Fires provide abundant food for moose within 25 years. Land management practices that limit the cover of large trees also increase forage for moose. Consequently, moose are often seen foraging in clearings adjacent to roads. Vehicle collisions and other conflicts with moose increase as the moose population grows and continues to exploit areas that provide abundant food near human developments

(Osko et al. 2004). Large body size also allows moose to tolerate the initial deficit in food supply by using their body stores (Schwartz 1992). Moose are able to utilize a wide variety of plants throughout the year and quickly adapt to consuming new species that emerge after fires and along roads (Franzmann and Schwartz 1998). Fires improve forage quality for moose as plants colonize the area; plants consumed by moose are higher in N content at 10 years than 30 years after fire (Regelin et al. 1987). In addition, moose have relatively high rates of intrinsic growth for ungulates, which allow populations to recover quickly from a decline or disturbance. Males can begin breeding as yearlings; females can begin reproduction at 2 years of age and are able to produce two calves per year when body fat stores are high (Schwartz et al. 1982; Franzmann and Schwartz 1985; Keech et al. 2000). However, no species is resilient to all stressors or their combined effects. Persistent declines in a population of moose in north-central USA have been related to multiple stressors associated with poor nutrition, disease and climate warming (Murray et al. 2006).

The interactions between populations may result in positive, neutral or negative effects on one or more species; that is, one population can become a stressor for another population. The microbial community in the digestive tract includes all three of these effects among microbes as well as between microbes and host; the microbial community includes potentially pathogenic bacteria, protozoa that have little effect on the host, and bacteria that degrade cellulose or provide vitamins to the host (Chapter 5). Resilient balances are those that allow populations to persist

by both tolerating and resisting stressors. Mice use their immune system to resist an infection by destroying a parasite or tolerate the infection through replacement of infected cells. Energy and nutrients are expended by the mouse in both responses, but the parasite is exposed to different processes that select for either greater ability to evade detection during resistance, or faster replication to persist against tolerance. Responses of tolerance and resistance may have different and unexpected outcomes as each species evolves in response to changes in the prevailing environment (Raberg et al. 2007). Gradual changes in a habitat result in the replacement of species as one population is replaced or displaced. The succession of plant communities after a fire provides food for moose in the first 25 years, but as the forest develops and matures resources become available over a longer period for flying squirrels, owls and caribou. The ecosystem may be most resilient when the largest number of species and trophic levels are supported; this provides the whole system with the greatest number of options to respond to changes (Chapter 2).

Resilience of wildlife is further influenced by numbers of individuals. As populations of wildlife grow, they can have large impacts on the structure of their habitat. Large species such as elephants can alter woodlands by breaking trees that are used by a wide variety of other animals (Owen-Smith 1988). Similarly, growing populations of moose can alter their habitat and reduce the abundance of migrant songbirds (Berger et al. 2001a). Populations of white-tailed deer attain high densities when acorns and other foods are abundant and when deaths from winter exposure and predation are low. Dense populations of animals include distressed individuals that are vulnerable to disease. White-tailed deer are hosts for a brain-worm (*Paraelaphostrongylus tenuis*) that can spread with the population and quickly infect other ungulates including moose, elk, mule deer, caribou, bighorn sheep and pronghorns (Woebeser 2006). Acorn production also affects the number and movements of white-tailed deer that carry ticks infected with *Borrelia burgdorferi*, which causes Lyme disease in humans. A large acorn production increases the risk of human Lyme disease within 2 years because it increases the production and transfer of the pathogens from ticks that live on both white-tailed deer and deer mice (Woebeser 2006).

Harvest and predation can have both positive and negative effects on populations of herbivores and thus their resilience to change. Hunting can quickly reduce a population from a high density and improve the body condition of individuals by alleviating competition for food (Swihart et al. 1998; Boertje et al. 2007). Predation may have a greater impact on animal condition than hunting because weaker individuals are preferred as prey. The average age of female elk selected by gray wolves in the Yellowstone ecosystem (13.9 years) was much greater than that selected by hunters (6.5 years) (Wright et al. 2006). Low levels of wolf predation therefore had less effect on the potential production of the elk herds because wolves removed females that were at or near the end of their reproductive lives.

Many predators select young animals because they are easier to catch than adults. Predation of neonatal and growing animals directly reduces the annual production of a population. Wolves, bears, wolverines and mountain lions prey on the calves of various ungulates including caribou, moose, bighorn sheep and mule deer. Consequently, female ungulates may select birth sites with the lowest predation



risks for their young even though food abundance may be inadequate for the demands of lactation (Bleich et al. 1997; Gustine et al. 2006; Poole et al. 2007). Behavioral plasticity allows females to choose birthing sites and subsequent foraging areas that balance the risks of predation with other stressors such as impaired calf growth and exhaustion of maternal body stores. In the Yellowstone ecosystem, female moose selected birth sites closer to roads because grizzly bears avoided these disturbed areas (Berger 2007b).

High rates of predation can limit populations and even extirpate small populations. Predators with high intrinsic growth rates such as wolves are able to respond quickly to changes in the populations of their prey. Predators that use multiple prey items can have a dramatic effect on one prey population, especially when they select young animals in a small population of prey. Grizzly bears consume both prey and plants during the year (Fig. 11.9). Grizzly bear predation on moose calves during the spring can have a large effect on the moose population. However, the



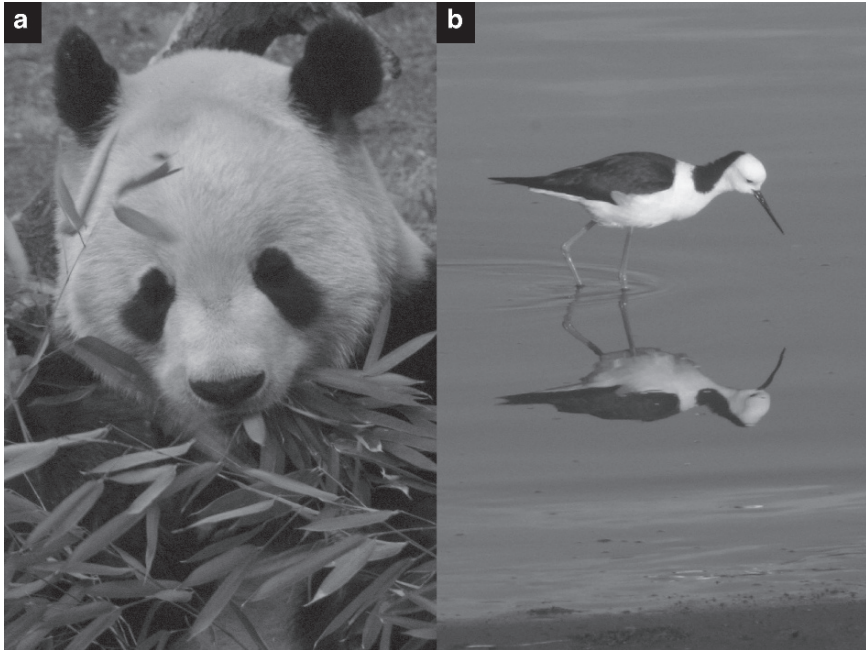
**Fig. 11.9** Grizzly bears in Alaska prey on the calves of moose, caribou and muskoxen as well as on adult ground squirrels and salmon. The effects of a population of bears on any one of these prey species depend on the relative availability of each prey and on the growth rates of the populations of both predator and prey. Bears have low intrinsic growth rates in comparison with other predators such as wolves; that is, bears cannot reproduce and recruit young into the population as quickly as can wolves. Populations of bears and wolves often switch among prey items. The persistence of large populations of bears and wolves can maintain populations of caribou and moose at levels below the limit of available forage. Populations of prey with low intrinsic growth rates are more vulnerable to high densities of predators. Moose are more fecund than caribou, and therefore the same number of predated calves has less of an effect on a moose population than on a caribou population. A population of moose may sustain enough bears and wolves in an area to keep a caribou population from increasing because some caribou are predated when predator numbers are high. Complete removal of bears and wolves from the area could allow caribou and moose populations to increase. However, high populations of these herbivores affect the populations of plants they consume and can eventually alter the habitats they share with other species

bear population is less affected by changes in the availability of moose calves because other sources of energy and nutrients contribute to the maintenance of female bears and the growth of their cubs. Populations of bears and wolves must be suppressed over several years to increase the production of moose in an area (National Research Council 1997) because these populations of predators are resilient and have sufficient behavioral and physiological plasticity to recover from translocations and hunting.

Enormous efforts also are required to remove introduced predators (e.g., red foxes) and rodents (e.g., brown rats) from islands where they prey on seabirds and their nests. Predator reductions often attempt to displace the predator so that human society can improve their harvest of the prey (e.g., moose) or prevent local extirpation of the prey (e.g., woodland caribou). These reductions are usually based on the assumption that the population of the native predator is resilient and is able to recover by reproduction and immigration from other areas. Small populations of predators that are isolated by barriers such as mountains or seas, however, may be vulnerable to outbreaks of disease and genetic bottlenecks. Canine distemper virus from large populations of coyotes, skunks and dogs has caused large mortalities in small populations of Ethiopian wolf, African wild dogs, African lions, Baikal seals and American black-footed ferrets (Woebeser 2006). The point at which a predator becomes vulnerable to extirpation is difficult to judge and often only recognized when efforts to suppress the predator are no longer required because the population is no longer resilient to change. Californian grizzly bears and Tasmanian tigers were both abundant populations of predators that were suppressed and failed to recover.

Extirpation of a natural predator may reduce the resilience of an ecosystem because predators reduce the adverse effects of high herbivore density such as habitat degradation and disease transmission. Alternatively, extirpation of an introduced predator or herbivore may allow an ecosystem to return to a more stable state that is more resilient to stressors. Introductions of predators such as Indian mongoose to the Hawaiian Islands and herbivores such as domestic goats to the Galapagos Islands threaten to extirpate a diverse range of native animals. Control and restoration of native predators or introduced species are extremely controversial because of the enormous amounts of public money and time that may be required to address the problem and because each sector of society may have a different value for the predator, prey or habitat in question (Lessard et al. 2005). Approaches that attempt to maximize the number of trophic levels and species for the financial and human resources available may be the most sustainable and thus most resilient to unexpected changes (Walker and Salt 2006).

Wildlife populations are part of complex systems with properties that result from interactions among species and between each species and the environment at multiple levels (Fig. 11.10). For example, conditions associated with global climate change in Australia, such as increased atmospheric CO<sub>2</sub> concentrations and average temperature, could lead to increases in the concentration of PSMs such as phenolics and a reduction in the concentration of N in the leaves of *Eucalyptus* spp. These reductions in leaf nutritional quality have been shown to adversely affect the growth of an invertebrate herbivore (Christmas beetle). It is possible that they may also



**Fig. 11.10** Species that rely on foods in complex habitats include the giant panda and migratory shorebirds. **a** Bamboo, which comprises most of the diet of pandas, flowers in cycles of decades. These flowering events cause sudden reductions in food abundance for giant pandas, which must then use alternative patches of bamboo over large areas. **b** Intertidal marshes and mangroves are sustained by complex patterns of water flow that are affected by sediments from nearby rivers as well as ocean currents and tides. Translocation of nutrients from the ocean to freshwater and intertidal communities supports production of many invertebrates, fish, mammals and birds such as the black-winged stilt. The eggs of spawning horseshoe crabs in Chesapeake Bay in northeastern USA feed a variety of shorebirds, including red knots that migrate from the southernmost parts of South America to the Canadian Arctic

have a negative impact on the intake of energy and nutrients by folivorous marsupials such as koalas. As a result, a large proportion of forests presently suitable for folivorous marsupials could become unsuitable. The potential for substantial reductions in population densities and ranges is such that local extinctions may well be widespread. The effects of projected increases in atmospheric  $\text{CO}_2$  concentrations over the next century will be most pronounced in forests growing on poor soils; it is these forests that dominate conservation reserves in Australia (Hume 1999).

We cannot anticipate the effects on our society of perturbations such as these to such complex communities. We can, however, look closely at wildlife populations for the cumulative effects of changes in the environment. Body condition, health and productivity of wildlife are measures of the health of the ecosystems that sustain both their populations and our society.

## 11.6 Conclusion

Wildlife nutrition informs management of the condition of habitats and populations because changes in supplies and demands for one population may affect the entire food web and the structure of animal and plant communities. This book began with two questions that confront wildlife biologists:

- What does a population need?
- Will that population grow or decline, and why?

The approaches used in the book emphasize the importance of the energy and nutrient requirements of a species to complete its life cycle, and therefore of a population of individuals from each class of age and sex of this species to survive. An understanding of nutritional requirements and linkages is essential to understand the likely range of responses that will sustain a population or increase its resilience to anticipated and unexpected environmental changes. Wildlife biologists are therefore tasked with answering a third question for societies:

- What is the risk of changes to a population and its ecosystem?

The answers to this question will improve our stewardship of wildlife populations and the ecosystems we share with them.