4

Ecology of Locomotive Animals

Locomotive animals feed on live biomass of plants and other animals. Small animals exist under conditions of energy abundance. Their consumption of live biomass does not go beyond natural fluctuations of the biomass itself. Large animals face energy shortage. Consumption of live biomass by large animals leads to significant degradation of local ecosystems. To keep the biota and environment stable, population numbers of large animals should be strictly limited.

4.1   DAILY AVERAGE TRAVELLING DISTANCE

Let us now consider the movement of land surface animals. The total metabolic power q of an animal moving at a speed u is usually estimated from the rate of oxygen consumption by the animal. It is convenient to relate the metabolic power q attained by an animal to the basal metabolic power q_0 (see Section 3.1) using a dimensionless total activity A:

$$q(u) \equiv [A(u) + 1]q_0 \tag{4.1.1}$$

At the average metabolic power of existence $\bar{q} = 2q_0$ (Section 3.1) the average total activity $\bar{A}$ is equal to unity.

Numerous experiments have demonstrated that the total activity $A(u)$ of an animal grows linearly with increasing u up to the maximum speeds developed by that animal (Schmidt-Nielsen, 1972, 1984). This relationship holds for all species studied. Another observed fact is that when the animal's speed of movement approaches zero, the value of $A(u)$ approaches a certain non-zero limit $A(0) > 0$, i.e. the total power of movement q does not grade smoothly into the basal power q_0 (Schmidt-Nielsen, 1972, 1984). It is natural to label this limiting value of activity $b \equiv A(0)$ as 'readiness' (for movement) (Gorshkov, 1983a, 1984a). The average value of b is close to unity (see Figure 4.1a). The available empirical data can be represented in the form

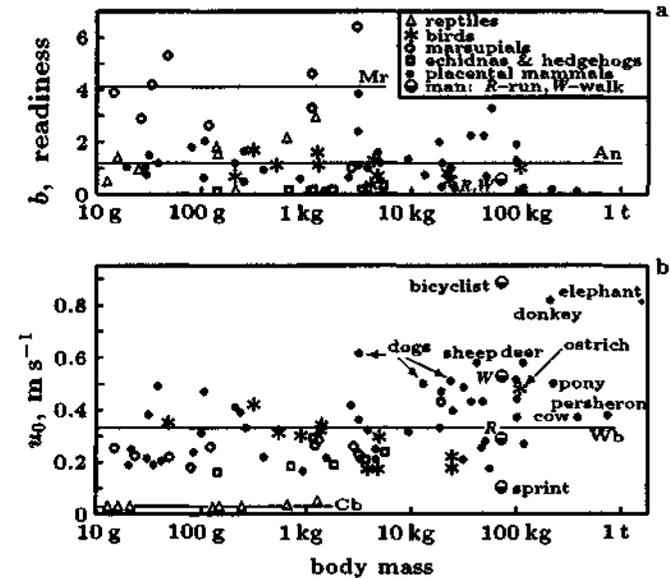$$A(u) = a + b, \qquad a \equiv u/u_0, \tag{4.1.2}$$

Figure 4.1. Readiness for movement, b, and available speed, u_0, for different taxonomic groups of animals (Schmidt-Nielsen, 1972, 1984; Gorshkov, 1983a). Readiness b is equal to the saltatory increment in metabolic power (in units of the basal metabolic power q_0) which corresponds to transition of an animal from the state of rest to movement at almost zero speeds. The available speed u_0 is the average daily speed that can be supported by the animal's metabolism, see also (4.1.2). Lines in the figure denote: An—average readiness for the majority of animals (reptiles, birds, mammals except for marsupials) ($b = 1.0$); Mr—average readiness for marsupials ($b = 4.2$); Wb—average available speed for warm-blooded (endothermic) animals ($u_0 = 0.3$ ms^{-1}); Cb—same for cold-blooded (ectothermic) animals ($u_0 = 0.003$ ms^{-1}). Man is a mediocre long-range runner, the worst sprinter among the warm-blooded animals, but one of the best walkers in the animal world.

where the value of a is the net movement activity, and the fundamental dimensional constant u_0 has the meaning of speed developed by the animal when its net activity a is equal to unity.

Speed u_0 determines the slope of the line presenting the dependence of the measured metabolic power, q, on the speed of movement u, Eqs. (4.1.1) and (4.1.2). Experimental data plotted in Figure 4.1b show that u_0 is a universal characteristic of movement, independent of the animal body size within a given taxonomic group. The average value is $u_0 = 0.3$ m s^{-1} = 26 km day^{-1} for all warm-blooded animals from mouse to elephant. The record belongs to the donkey and elephant, which feature $u_0 = 0.8$ m s^{-1} (Gorshkov, 1983a; Langman et al., 1995).

Let us now analyse the meaning of speed u_0, which acquires considerable significance being a universal fundamental constant. The average daily activity $\bar{A}$ is limited by the average metabolic power of existence. According to the available empirical data, for most animals the average daily activity is close to $\bar{A} \approx 1$. We denote the relative duration of active state for an animal as $x_a \equiv t_a/T$, where t_a is duration of the time interval when the animal remains active during a day, and

$T = 24$ h. The average daily activity can be thus written as

$$\bar{A} = Ax_a = \left(\frac{u}{u_0}b\right)x_a$$

from which we obtain:

$$x_a = \frac{\bar{A}}{\dfrac{u}{u_0} + b} \qquad\qquad (4.1.3)$$

If $\bar{A} = 1$, $u = u_0$, and $b = 1$, we have $x_a = 1/2$ and $t_a = 12$ (a 12-hour working day). More information that can be retrieved from (4.1.3) for $\bar{A} = 1$ and $b = 1$ is that animals cannot move all day long at a speed different from zero (if $x_a \rightarrow 1, u \rightarrow 0$). The distance L_T travelled by an animal in a day is equal to $L_T = ut_a$, i.e. $x_a = L_T/uT$. We then find from Eq. (4.1.3) that:

$$L_T = L_{T_{\max}}\frac{u}{u + bu_0}, \qquad L_{T_{\max}} = \bar{A}u_0 T. \qquad (4.1.4)$$

It follows from Eq. (4.1.4) that the maximum daily travelling distance $L_{T_{\max}}$ is reached at speeds $u \gg u_0$, because the readiness b differs from zero. It means that animals should move quickly but in short bursts. Note that $b \approx 1$ for untrained people, for athletes $b < 1$ (see Figure 4.1). According to Eq. (4.1.4) the maximum distance walked in a day at the daily average activity of $\bar{A} = 1$ is about 26 km (for a donkey it amounts to 70 km day^{-1}). Finally, using Eq. (4.1.3), the average daily speed, $u_a \equiv L_T/T = ux_a$, that the animal's metabolism may support (we may call it the available speed u_a), can be expressed as

$$u_a = \bar{A}u_0\left(1 - \frac{bx_a}{\bar{A}}\right)$$

At $\bar{A} = 1$ and $x_a \ll 1$, the available speed u_a is equal to the speed u_0. Everywhere below we assume that $\bar{A} = 1, x_a \ll 1$ and

$$u_a = u_0. \qquad\qquad (4.1.5)$$

4.2 THE MAXIMUM SPEED OF MOVEMENT FOR ANIMALS

The speed u_0, however, cannot be totally independent of animal body size. We shall demonstrate from the law of energy conservation that, starting from some critical body size, the speed u_0 must start to decrease for larger body sizes l.

Metabolic power is transformed into mechanical power at a certain efficiency level α, which cannot be larger than the observed maximum efficiency of muscles. Within a living individual the latter does not exceed 25% (Hill, 1960; Cavagna and Kaneko, 1977; Heglund et al., 1979). One may therefore assume that $\alpha \leq 0.25$. The mechanical power put out at a constant speed u is spent to compensate for energy dissipated to ground and air friction. The law of energy conservation is then expressed as equality between the mechanical power and the dissipative energy losses.

Energy dissipation during movement on the ground is proportional to the product of body weight, mg ($g = 9.8$ m s^{-1} is the free fall acceleration), and the speed of movement u. It may be written as γmgu, where γ is the ground dissipation coefficient analogous to the coefficient of friction. The empirical data available on the maximum velocities of different animals show that the value of γ depends neither on the speed of movement, nor on the body size (i.e. mass) of the animal, and is, on average, equal to 0.04 for most animals (Gorshkov, 1983a).

Dissipation of energy due to air friction is equal to $cl^2\rho_c u^3/2$, where ρ_c is the air density ($\rho_c = 1.2 \cdot 10^{-3}\rho, \rho = 1$ t m^{-3}); $\rho_c u^3/2$ is the energy flux through a unit surface, equal to the product of energy density $\rho_c u^2/2$ and velocity u; cl^2 is the effective streamlined body surface. This value may be treated as the product of the resistance force $cl^2\rho_c u^2/2$ and the velocity u. The air resistance coefficient c may be measured (see references in Gorshkov, 1983a, 1984a). It is equal to 0.4 for the majority of land surface animals.

The body size l of locomotive animals is related to their body mass by the relationship:

$$l = (m/\rho)^{1/3} \qquad\qquad (4.2.1)$$

The mechanical power of movement is equal to αaq_0. Equating it to cumulative dissipative energy losses we have:

$$\alpha aq_0 = \gamma_{\mathrm{tot}}mgu, \qquad\qquad (4.2.2)$$

$$\gamma_{\mathrm{tot}} \equiv \gamma + \gamma_c \equiv \gamma\left(1 + \frac{Fr}{k^2}\right), \qquad\qquad (4.2.3)$$

$$\frac{\gamma_c}{\gamma} \equiv \frac{Fr}{k^2}, \qquad Fr \equiv \frac{u^2}{gl}, \qquad k^2 \equiv \frac{2\rho\gamma}{\rho_c c} \qquad (4.2.4)$$

Here γ_{tot} is the total dissipation coefficient, equal, by definition, to the ratio of resistance force to individual body weight mg; Fr is known as Froude's number, γ_c is the air dissipation coefficient, which is relatively small when $Fr/k^2 \ll 1$.

Using the above relationships one may rewrite the expression for net activity a, Eq. (4.1.2), in the following form (for $Fr/k^2 \ll 1$):

$$u_0 = \frac{\alpha}{\gamma}\lambda_0, \qquad \lambda_0 \equiv \frac{q_0}{mg}. \qquad (4.2.5)$$

Here λ_0 is the metabolic power per unit body weight mg. It has the dimension of velocity and differs from the volume-specific metabolic power used in Chapter 3 (Figure 3.2) by the constant factor $(\rho g)^{-1}$. We have therefore retained the same symbol for denoting it.

Since λ_0 drops for higher body sizes (see Figure 3.2), the observed constancy of u_0 for varying body size l means that either the efficiency α or the dissipation coefficient γ must change with body size l. Using calculations based on the available empirical data we shall demonstrate that the value of γ does not change with body size. Consequently, it is the value of efficiency α that must change.
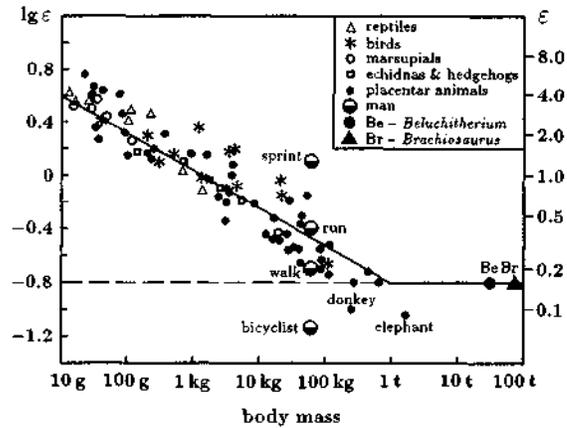
Figure 4.2. Energy cost of movement vs. the animal body size (mass) (Schmidt-Nielsen, 1972, 1984; Gorshkov, 1983a). The dimensionless energy cost of movement ε is equal to net expenditure of metabolic energy (the difference between the total metabolic energy and the metabolic energy put out at the zero speed limit) per unit body weight per unit distance:

$$\varepsilon = [q(u) - q(0)]/(mgu)$$

$q(u)$ is the metabolic movement power at the speed of u; mg is the animal body weight. The solid line is the average value of ε. It does not depend on the absolute animal metabolic power and is identical for mammals, birds and reptiles of equal body size. Due to higher movement efficiency α the value of $\varepsilon = \gamma/\alpha$ decreases at higher body size until the maximum possible value of α is reached. After achieving it, further decrease in ε for larger body sizes should stop. The solid line is numerically extended in the horizontal using values of the observed maximum efficiency α and the average dissipation coefficient γ for the mechanical movement energy (see Figure 4.3). Be—the maximum body mass for an extinct land mammal—Beluchitherium (30 t); Br—the maximum body mass for a terrestrial animal, dinosaur Brachiosaurus (80 t) (Schmidt-Nielsen, 1984).

The ratio

$$\varepsilon \equiv \frac{\lambda_0}{u_0} = \frac{\gamma}{\alpha} \qquad (4.2.6)$$

represents the dimensionless net energy cost of moving a unit weight along a unit distance (it is similar to car mileage): $\lambda_0/u_0 = E/mgL = aq_0/mgu$, where $E = aq_0t$ is the net energy expenditure per travelled distance $L = ut$. The dependence of ε on body size l for animals is presented in Figure 4.2. Due to constancy of u_0 the energy cost ε linearly falls off for larger body sizes proportionally to λ_0 and α^{-1}. This drop goes on until the efficiency α reaches its maximum possible for muscles value. Since then the value of ε must remain constant and independent of body size (Gorshkov, 1983a).

According to observations λ_0, u_0 and hence the ratio α/γ do not depend on the speed of movement. This means that animals move slowly enough, so that one may neglect air resistance, i.e. the second u-dependent term in Eq. (4.2.3). Speeds at which the resistance of air becomes equal to ground friction should be the top limit, because further on energy expenditures (i.e. net activity a) would be mostly due to air
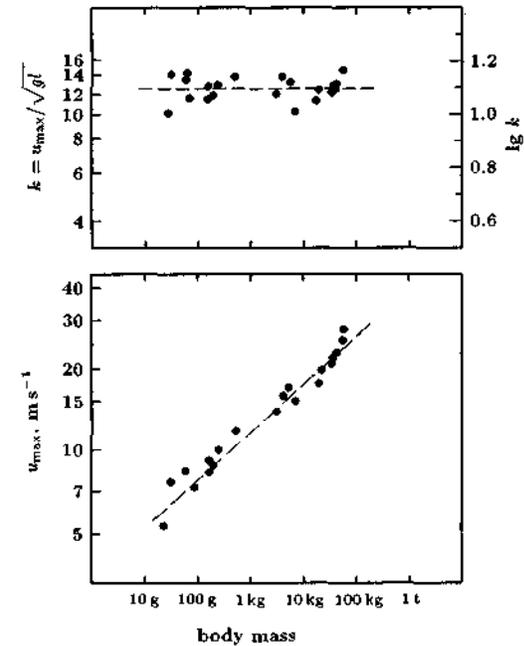
Figure 4.3. Land animals' maximum speeds of movement vs. their body size (mass). The maximum speeds of animal movement correspond to a constant value of Froude's number $k^2 = u_{max}^2/gl$. Equating energy expenditures for ground and air resistance, Eq. (4.2.7), and accounting for the definition of ground resistance, Eq. (4.2.4), the ground resistance, γ, may be retrieved from the known air resistance coefficient $c = 0.4$. It averages $\gamma = 0.04$ (Gorshkov, 1983a, 1984a). At a movement efficiency of $\alpha = 0.25$ we obtain the maximum energy cost of movement $\varepsilon = \gamma/\alpha \approx 0.16$, see Eq. (4.2.6) and Fig. 4.2.

resistance which grows very rapidly as the third power of u making movement at higher speeds extremely inefficient. Therefore the condition

$$\frac{1}{k^2}\frac{u_{max}^2}{gl} = 1, \qquad \text{or} \quad u_{max} = k\sqrt{gl} \qquad (4.2.7)$$

must correspond to maximum speeds recorded for animals of body size l. Empirical data on these speeds (see Figure 4.3) demonstrate that the maximum value of Froude's number u_{max}^2/gl remains constant for all body size intervals, i.e. depends neither on the speed u, nor on the size l. On these grounds one may state that the dissipation coefficient γ entering the definition of k, see (4.2.4), is also constant; as soon as the constancy of the air resistance coefficient c had been repeatedly tested in independent experiments (see references in Gorshkov, 1983a, 1984a).

The above leaves efficiency α as the only parameter to change with size l in the relationship (4.2.5). Its changes should be such that the product $\alpha\lambda_0$ remains constant due to the observed constancy of u_0 (Gorshkov, 1983a). As soon as λ_0 decreases with increasing body size l, the efficiency α must accordingly increase with the body size l growing. However, the efficiency α is limited from above by its maximum possible value $\alpha_{max} = 0.25$. After this value is reached, the energetic cost

of movement ε assumes its minimum possible value and does not diminish further with increasing l, while the velocity u_0 begins to decrease with increasing body size l proportionally to λ_0, see (4.2.5). The data available on u_0, γ and λ_0 indicate that this limit is reached for the animal mass of $m \approx 100\text{--}300\,\text{kg}$ (see Figure 4.1). (The observed deviations from the average value of $u_0 = 0.3\,\text{m s}^{-1}$ observed for the elephant and donkey do not go beyond the natural variability of u_0 in warm-blooded animals). Direct measurements made for horse and man showed that their efficiencies are actually close to the top limit (Brody, 1945; Atkins and Nicholson, 1963).

The decrease in efficiency of locomotion α for lower body sizes is only observed when locomotion occurs in the regime of oxygen balance, and energy expenditure is continuously compensated by oxygen consumed from the environment (Gorshkov, 1983a). All animals are capable of short bursts of locomotion in the regime of oxygen debt at maximum efficiency α, independent of their body size. That conclusion follows from the analysis of record jumps by animals of different body sizes (Gorshkov, 1983a, see Figure 3.1).

The observed independence of the mechanical power per unit body weight, $\alpha\lambda_0$, of body size ensures equal conditions for the existence of both small and large animals. Constancy of $\alpha\lambda_0$ means that smaller animals are characterised by a lower muscle efficiency α, because their weight-specific metabolic power λ_0 is greater than that of large animals (see Section 3.2). However, there are no physical reasons that could limit the efficiency of locomotion α of small animals. A possible way of decreasing α at smaller body size could be via reducing the ratio of muscle mass to body mass at still the same maximum efficiency of muscles themselves. However, such a morphological pattern is not actually observed (Gorshkov, 1983a). It means that small animals only use their muscles at the maximum possible efficiency in extreme situations of oxygen debt, e.g. during the highest or longest jumps. With the overwhelming part of their life occurring in conditions of oxygen balance, the efficiency of muscles α apparently drops in animals of smaller body sizes.

In the absence of physical reasons that could bring about such an effect, we thus conclude that the observed constancy of the mechanical power per unit body mass is apparently ecologically caused. It is only due to that feature that the energetic competitiveness of large animals, controlled by their mechanical power, is not inferior to the energetic competitiveness of a congregation of small animals of an equal mass (e.g. an elephant and a hundred thousand mice). Internal correlation of bodies of large animals and their ability to create and maintain a favourable internal milieu optimal for functioning of all cells and organs of the body, contributes additionally to the competitiveness of a large animal as compared to a non-correlated congregation of small animals. As a result, there appear ecological niches where large animals may exist alongside with smaller ones.

However, with body size increasing, the constancy of $\alpha\lambda_0$ is only supported up to a certain critical size, at which the efficiency of locomotion reaches its maximally admissible value $\alpha_{\max}$. Very large animals, with their body size exceeding the critical one, lose energetically to smaller animals and are forced to seek for some additional exotic means of increasing their competitiveness and of gaining an ecological niche

fit for their existence. One such exotic means was the appearance of cultural knowledge in the *Homo sapiens* species.

4.3   MAXIMUM PERMISSIBLE SHARE OF BIOMASS CONSUMPTION BY LOCOMOTIVE ANIMALS

Let us denote here the metabolically-active, short-lived plant biomass per unit land surface as B. We further assume, that while moving across its feeding territory (home range), the animal eats up a part of the plant biomass equal to $B_L \equiv \beta_L B$, where β_L is the consumed share of plant biomass. The effective width of land band across which the animal eats up vegetation is close to that animal's body size l (4.2.1). The vegetation mass consumed in unit time with the animal moving at an average daily speed of u is equal to $B_L l u = \beta_L B l u$. The energy content of the eaten biomass is equal to $K\beta_L B l u$, where K is the energy content of live biomass, see (3.1.2) (we omit the low index 'lb' in this chapter).

Coefficient of food assimilation (digestibility) for an animal may, for simplicity, be assumed equal to unity: for most animals it is actually equal to 0.8 (Gessaman, 1973; Kendeigh, 1974). Energy contained in the food, which is consumed during movement, must be equal to the average metabolic power of existence, i.e. $q = (\overline{A} + 1)q_0 = 2q_0$, where q_0 is the basal metabolic power (see (4.1.1) and Section 3.1):

$$K\beta_L B l u = (\overline{A} + 1)q_0 = 2q_0, \tag{4.3.1}$$

The relationship in Eq. (4.3.1) determines the speed of movement needed to support the animal's existence. It may be called the ecologically necessary speed u_n:

$$u_n = \frac{2q_0}{K\beta_L B l} \tag{4.3.2}$$

The animal may only survive if its available speed $u_a = q_0/(mg\varepsilon)$, see Eqs. (4.1.5), (4.2.5) and (4.2.6), is larger than or equal to u_n, $u_a \geq u_n$. In other words, **the energy provided to the animal by food should not be less than the energy spent by the animal during moving when searching for food and consuming it.**

Using Eqs. (4.1.2), (4.1.5), (4.2.5) and (4.2.6) this inequality may be rewritten as a limitation upon the consumed share of vegetation biomass:

$$\beta_L \geq \beta_{L_{\min}} = \beta_{L0}\varepsilon\left(\frac{l}{l_0}\right)^2, \qquad \varepsilon \equiv \frac{\lambda_0}{u_0} = \frac{\gamma}{\alpha}, \qquad \beta_{L0} \equiv \frac{2g\rho l_0^2}{KB} \sim 10^{-5} \tag{4.3.3}$$

or as a limitation upon the consumed biomass:

$$B_L \geq B_{L_{\min}} = B_{L0}\varepsilon\left(\frac{l}{l_0}\right)^2, \qquad \beta_{L0} \equiv B_{L0}B, \tag{4.3.4}$$

The estimate of the share of consumption β_{L0} of herbivorous animals was made taking the global average metabolically-active (edible) biomass equal to

$B = 4\,\mathrm{kg\,m^{-2}}$ (Gorshkov, 1995). The relationship between scaling values of body size $l_0 = 10\,\mathrm{cm}$, body mass $m_0 \equiv \rho l^3 = 1\,\mathrm{kg}$ and $\varepsilon = 1$ is retrieved from Figure 4.2. All the variables entering the right-hand part of Eqs. (4.3.3) and (4.3.4) are well-known. The available estimates of metabolically-active, short-lived plant biomass B for different ecosystems are presented in Gorshkov (1995).

Note that the basal metabolic rate q_0 has cancelled out from the relationships (4.3.3) and (4.3.4). The energetic cost of locomotion ε is determined by the dissipation coefficient, γ, and the muscle efficiency, α, and hence it cannot depend on the taxonomic group the animal belongs to, being only dependent on body size l. As a result, the limitations (4.3.3) and (4.3.4) are equally justified for all the land surface animals: insects, amphibians, reptiles, mammals and birds.

4.4   SETTLED AND NOMADIC LIFESTYLE OF LOCOMOTIVE ANIMALS

There is another way of interpreting of the necessary speed of movement u_n determined by Eq.(4.3.1). The metabolically-active biomass of vegetation per unit surface area $B = \rho L$ (L is the thickness of the layer of metabolically-active biomass when evenly spread over the considered territory, $\rho = 1\,\mathrm{t\,m^{-2}}$, $B \sim 4\,\mathrm{kg\,m^{-2}}$, $L \sim 4\,\mathrm{mm}$) may be expressed as $B = P^+\tau$, where τ is the turnover time for the metabolically-active (short-lived) biomass; P^+ is the net primary productivity in units of live biomass $\mathrm{kg\,m^{-2}year^{-1}}$. The area of feeding territory S of a single animal, approximately equal to its 'home range' (Harestad and Bunnell, 1979; Damuth, 1981a, 1981b), may be expressed as $S \equiv N^{-1}$, where N is the population density of animals of a particular species per unit surface area.

The distance travelled by an animal across its feeding territory is of the order of S/l (l is body size). Denote the time in which the animal makes a round of the whole feeding territory as τ_S. (The band of width l must scan the whole territory of area S in time τ_S.) Then the necessary speed of movement u_n may be expressed as $u_n = S/(l\tau_S)$.

The rate of food consumption $Q \equiv (\bar{A} + 1)q_0/K$ by animals of a given species and a given body size l may be written using the value of consumed species-specific share β_l of plant production P^+ over the total feeding territory S, $Q = \beta_l P^+ S$. Substituting these values into Eq. (4.3.1) and cancelling identical terms in both parts of the equation we obtain the relationship between the species consumption share of vegetation biomass β_L and the species consumption share of the net primary production β_l:

$$\beta_L = \beta_l \tau_S/\tau \tag{4.4.1}$$

The share of consumption of net primary production $\beta_l = Q/(P^+S)$ may be expressed using the value of cumulative biomass B_l of animals of a given species of body size l, $B_l = \rho L_l$ (L_l is the layer thickness for animal biomass). Feeding territory S is related to biomass B_l by relationship $SB_l = m$, ($SL_l = l^3, m = \rho l^3$), where m is the average body mass of a single animal. We thus obtain for a species
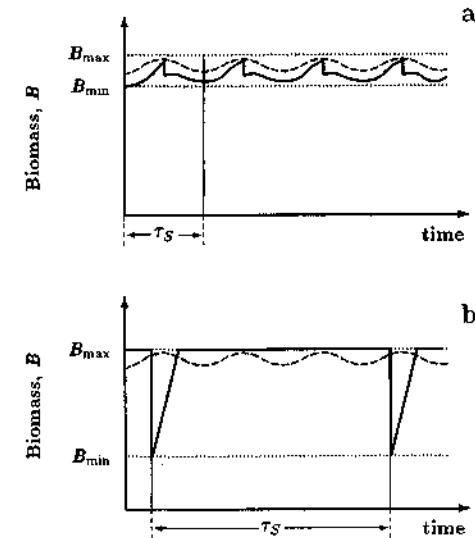
Figure 4.4. Oscillations of the natural community biomass caused by small settled (a) and large nomadic (b) animals. The dashed line indicates the range of natural fluctuations of plant biomass independent of the presence or absence of animals. τ_S is the time in which the animal makes a round of the whole of its territory. Note that consumption of biomass by small settled animals does not go beyond natural biomass fluctuations. In contrast, large nomadic animals substantially destroy the community's biomass and do not return to the same community until the biomass of all the parts of the community is completely restored. Note, however, that in both cases the community spends most time in the nonperturbed state. This is ensured by ecological limitations imposed on population densities of both large and small animals (cf. Figure 6.19 in Section 6.8.5).

consumption share of net primary production β_l:

$$\beta_l = \Lambda L_l/P^+, \tag{4.4.2}$$

where $\Lambda \equiv Q/l^3$ is the rate of food consumption per unit volume of the animal's body.

The relationship in Eq. (4.4.1) makes possible quantitative differentiation between settled and nomadic life styles. If an animal traverses its feeding territory in time τ_S equal to vegetation reproduction period τ, it would return to a given area within its feeding territory in exactly the time needed for the vegetation to reproduce the part of biomass eaten by that animal during the previous attendance of that area. In that case the share of consumed plant biomass and the plant production would coincide with each other: $\beta_L = \beta_l$.

In reality, most small-sized animals go round their feeding territories in a shorter time $(\tau_S \ll \tau)$, each time eating away an amount of biomass significantly smaller than the permissible share $(\beta_L \ll \beta_l)$. This permits the animal to visit any part of its feeding territory at practically any time and also reduces fluctuations of vegetation biomass on that territory. Small-sized animals may therefore exist in conditions of abundance of food and metabolic energy. Fluctuations of vegetation biomass due to its consumption by small animals do not exceed the natural fluctuations of that

biomass in the absence of animals (Figure 4.4a). The presence of such animals does not leave any noticeable trace and does not disturb the natural distribution of the vegetation.

A large animal has to consume a very substantial part of vegetation biomass ($\beta_L \gg \beta_l$). Vegetation and the whole community around the animal are then destroyed, and the closed matter cycle in a local range where consumption took place is disrupted. Then the animal leaves the destroyed area and returns to it only after a time τ_S, when the steady state distribution of vegetation, community structure and the closed character of matter cycles are restored. During that succession time (which is much longer than the vegetation reproduction period, $\tau_S \gg \tau$) the net primary production is consumed by different species (species-repairers, see Sections 4.7 and 6.7) which act to close the matter cycle again. As a result, the effective share of net primary production consumed by large animals remains within the ecologically permissible norm when averaged over large time period of the order of τ_S (see Figure 3.3). However, large animals leave a noticeable trace in the observable distribution of vegetation, visible, e.g. from on board an aircraft (Figure 4.4b). At any given moment of time, only a tiny part of the enormous feeding territory appears to be fit for life of a large animal. This part is equal to the ratio $\tau/\tau_S = \beta_l/\beta_L \ll 1$, see Eq. (4.4.1). All the rest of the territory must be closely guarded against the intervention of competitors. A large animal remains constantly in a state of food and energy deficit (see Figure 4.5).

The strategy of existence following which a round of the feeding territory is completed during a time shorter than that of reproduction of vegetation, so that it does not leave any traces in the natural distribution of vegetation, corresponds to a *settled* lifestyle. The strategy following which such a round takes more time than the reproduction period for vegetation, and leaves a noticeable trace in the natural distribution of vegetation, corresponds to the *nomadic* lifestyle.

If the consumption share of vegetation production β_l is fixed, all the large animals, having $\beta_{L_{min}} > \beta_l$, may only exist in the nomadic regime (Figure 4.5). At anomalously low values of β_l even small animals may fall into an obligatory nomadic lifestyle, if their $\beta_{L_{min}} > \beta_l$. Small animals may also turn sporadically to a nomadic lifestyle if they reach extremely high population density numbers and consume an extremely high share of vegetation biomass, while the relationship $\beta_L > \beta_l > \beta_{L_{min}}$ holds (Figure 4.5). Such facultative nomadic behaviour apparently arises in communities disturbed by man (e.g. arable lands invaded by locusts, managed forests destroyed by insect pests, see Section 6.8.3).

In a settled regime any animal in its natural community consumes less than 20% of all the eatable biomass in any given spot of its feeding territory (Golley, 1973), which guarantees sustainability of the whole community under any fluctuations. In a nomadic regime the share of biomass consumption may even reach unity (all the edible biomass is completely destroyed), and, consequently, the whole community perishes. Following that, a long restoration period is needed during which the biomass and the community as a whole are generated anew and then regain their most competitive steady state. Such rare cases of nomadic behaviour are only encountered in the human population (slash-and-burn agriculture and modern
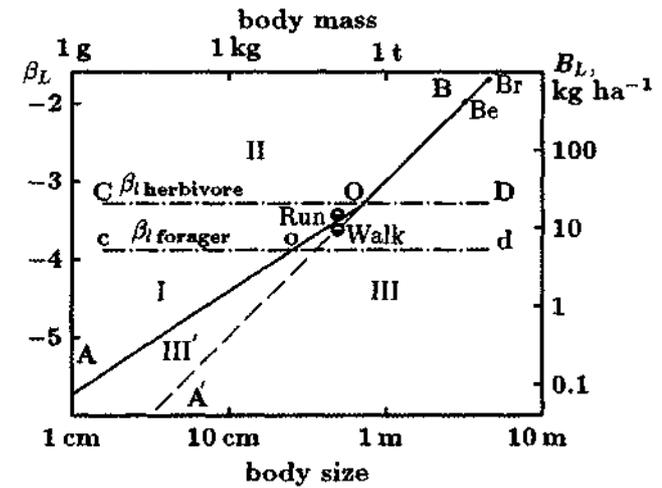
Figure 4.5. The share of vegetation biomass consumption by herbivores and foragers vs. their body size (mass). The solid line shows the minimum value of edible biomass $B_{l_{min}}$ (and the corresponding share of the total edible plant biomass consumption $B_{l_{min}}$) which still covers energy expenditure of animals of a given body size associated with their movement across their feeding ground. The circles Run and Walk correspond to Ho—*Homo sapiens*, Be—*Beluchitherium*, Br—*Brachiosaurus*. The breaking point of the solid line corresponds to the breaking point in Figure 4.2, which corresponds to the efficiency of movement reaching its maximum. Movement efficiency is at maximum to the right of point O (line OB). Line AO describes the observed decrease in efficiency for lower body sizes (see Figure 4.2). The dash-dot line CD corresponds to the share β_l of consumption of net primary *production* by herbivorous mammals in natural terrestrial ecosystems (see Figure 3.5b). Note that line COD crosses line AOB at the latter's breaking point, which is presumably not a random coincidence. Line cod gives the admissible share of consumption of plant production by foraging mammals (four times less than the herbivores' share). Range III to the right of line A'OB is prohibited energetically. Range III' limited by lines A'OA is prohibited physiologically. Range I, limited by lines AOC for herbivores (Aoc—for foragers) is open for them in a settled regime, $\beta_L/\beta_l < 1$. Range II, limited by lines COB (coOB—for foragers) is open for nomadic animals, $\beta_L/\beta_l > 1$. Existence of animals of body size falling to the right of point O for herbivores (and to right of point o for foragers) is possible only in a nomadic regime.

clear cutting of wood) and also in certain insects in human-disturbed ecological communities (Holing, 1978; Isayev *et al.*, 1984).

Under pressure of anthropogenic activities, natural ecological communities are permanently destroyed every few tens of years ($\tau_S/\tau \sim 10$) in the majority of the continental areas, so that they are never able to reach their steady state corresponding to the maximum stability of community and ecosystem as a whole. The steady state of most natural communities might only be restored if the frequency of anthropogenic disturbances were reduced by at least an order of magnitude on a global scale.

4.5 CARNIVORES

As we have seen above, the stability of organisation of ecological communities is mainly dictated by the character of interaction between autotrophic plants and

heterotrophic herbivores. Let us now consider the internal structure of the heterotrophic part of the ecological community in more detail, subdividing it into herbivores and carnivores.

Animal biomass production by herbivorous animals is 10 times less than the production of vegetation they consume, i.e. it is less by more than an order of magnitude than the net primary production of the ecosystem. Therefore, in order to be able to live on animal biomass, a carnivore must be locomotive. Their feeding territory must be 10 times larger than the feeding territory of their prey and, respectively, their population density number should be 10 times lower (given a metabolism level similar to that of their prey).

Predators should not only be locomotive animals themselves, but they may only feed off locomotive prey. Live biomass produced by locomotive prey is concentrated into their projection area and presents a 'source' of productivity with characteristic density exceeding net primary plant productivity by several orders of magnitude. In contrast to a herbivore, a carnivore does not need to collect the evenly-spread food products by moving over the whole feeding territory. For carnivores, it is enough to move from one 'source' (prey) to another or to keep attached to the 'source' itself (the phenomenon of parasitism). All the carnivores, despite their enormous feeding territories, always remain in the state of energy abundance.

Herbivores consume only a small part of the net primary production of plants. Due to this fact herbivores could, in principle, increase their population number at constant biomass and productivity of feeding plants. However, this is ecologically forbidden, being incompatible with the stable existence of the community (see Section 3.7). By contrast, predators consume a major part of the 'net' production of their prey. It follows that under natural conditions, predators cannot increase their population number if the population number of their prey remains constant. Therefore, natural predators of any body size are incapable of disrupting the ecological equilibrium in the community. (However, under the artificial conditions of suburban areas, dogs and cats living off man may completely extinguish their natural prey.)

The most important ecological function of predators in the community is to eliminate decay (weak, ill, injured, etc.) individuals from the prey species of the same community (see, e.g. Vorisek *et al.*, 1998). In strongly disturbed external conditions, such decay polymorphism of all individuals sharply increases (see Chapter 9). This brings about a sharp increase in the population number of the respective predator species. On the contrary, when the decay polymorphism of the prey species tends to zero, the predator species becomes less important and its population number diminishes. The same reasoning is valid for the correlation between plants and herbivorous consumers, mainly insects. A sharp increase of the decay polymorphism in plants precipitates a respective sharp increase in the population number of herbivorous insects. Such processes are observed after fires, forest clear cutting and other strong perturbations of natural communities (Holing, 1978; Isayev *et al.*, 1984; Morneau and Payette, 1989). Under stable natural conditions when the decay polymorphism in all the plant species of the community is kept at its minimum, population numbers of all the plant consumers

are also very low, leaving plant biomass to be decomposed by reducers in the form of dead bodies of plants.

Correlated associations of the type of 'predator–prey', as well as all the diverse forms of symbiosis between various species, may only propagate and be further supported if ecological communities which include such associations become more competitive than communities without them. If one considers the interaction between the predator and its prey at a species level, it appears extremely difficult to reach even a dynamic stability of the system, and remains absolutely impossible to explain the sustained genetic stability of correlation of such kind.

One may similarly treat the presence of parasites in the bodies of higher living beings. Naturally, the malfunctioning individual that contains parasites in its body features lower competitive capacity as compared to the healthy one. Thus, decay of the level of organisation in parasites, and decrease of their functional activity, should have led to higher competitive capacity of their hosts and, hence, to their higher numbers. However, that is not actually the case, and no on-going degradation and extinction of parasites is observed. Even when losing some of their inner organisation, parasites only do so in the direction of increasing the efficiency of their functioning in the host body. The loss of their own respiration and distribution systems by some parasites only works to increase their competitive capacity within the host body, as compared to those parasite species that have retained such morphological features.

If a sufficiently large population of competitively-interacting parasites exists either within the host body or on its surface, their functional organisation may be supported due to stabilising selection among them, taking place within the body limits of each separate host. However, the inevitable loss of competitive capacity of a host affected by parasites should result in decreasing the number of such deficient individuals, and in their further exclusion from the population together with their parasites. In the opposite case, when the body of a single host is not large enough for a population of parasites to live in, the process of expulsion of the host affected by parasites from its own population might only be retarded via the decay of the organisation of parasites, that is via the extinction of the phenomenon of parasitism itself. In both cases, one appears unable to explain the observed stability of the phenomenon of parasitism, considering it at the level of host–parasite interactions.

The only possible way to explain the phenomenon of parasitism is to tackle the problem at the level of the ecological community to which the host species belongs. The complex nature of correlation between individuals of different species in the community results in that the community, in which a sufficient number of individuals from a given species contain parasites, appears to be more competitive than communities in which the individuals from the same species host no such parasites. Competitive interaction between communities in a population of communities results in the support of those communities which favour parasites.

The cause for higher competitive capacity of communities with parasites may be related to resulting limitations upon and control of population densities of host species in these communities. For example, an uncontrolled growth of the population density of large animals could disrupt the closed biochemical cycles of matter

within the community, that are a prerequisite of environmental stability (see Section 3.7). A spontaneous increase in population density of hosts accelerates the spread of parasites, that in most cases, entails an epidemic and subsequent fall in population density down to the initial optimal value. Higher degree of correlation between the host and its parasites should also work to improve the competitive capacity of a community. That may be the reason for the observed complicated patterns of successive changes of hosts during the life cycle of many parasites (Raven and Johnson, 1988).

4.6 DIFFUSION OF EXCRETA

Let us now consider an additional, very peculiar, limitation on consumption by locomotive animals.

Fall-off of dead parts of plants provides for stability of concentration of nutrients in a local ecosystem, only if these nutrients, randomly distributed in the fall-off, have time to diffuse back to their initial position before they are again used by autotrophs. This may happen in two ways: short-lived leaves are small enough to be distributed evenly after falling off, while large tree trunks grow slowly and just as slowly decompose after falling.

Locomotive herbivores collect nutrients from their feeding territories, transport biogenic elements within their bodies and concentrate them in their excreta, of which 80% fall to urine and 20% to faeces (Kleiber, 1961; Kendeigh, 1974). As follows from the data presented in Figure 3.3, small locomotive animals (like dungbeetles) feeding off the faeces consume no more than 10% of them. The principal part of the excreta is destroyed by bacteria and fungi. Therefore, a stationary state is only possible when the nutrients, transported and concentrated in the excreta, spread again over the territory they had been collected from in the course of diffusion or with help of external matter fluxes; this process should not be longer than the period of vegetation reproduction τ.

Let L_{ex} be the average distance between two separate excreta of an animal (Figure 4.6). The average amount of excreta, proportional to the animal's body size l, may be denoted as δl^3, where $\delta \approx 0.001$ (Kleiber, 1961). Moving along the distance L_{ex} the animal scans a band of width l and eats the amount (volume) of vegetation equal to $\beta_L L_{ex} l L$, where $L = B/\rho$ is the average thickness of the layer of edible biomass. The excretion distance L_{ex} is determined from the equality $\delta l^3 = \beta_L L_{ex} l L$, from which we deduce, assuming that $\beta_L \sim \delta \sim 10^{-3} \div 10^{-4}$:

$$L_{ex} = l^2/L$$

The time τ_D that excreted nutrients take to diffuse along the distance from which they had been concentrated is of the order of:

$$\tau_D = L_{ex}^2/D = \left(\frac{1}{DL^2}\right)l^4, \qquad (4.6.1)$$

where D is the diffusion coefficient with dimension cm^2 s^{-1} (that is why the term
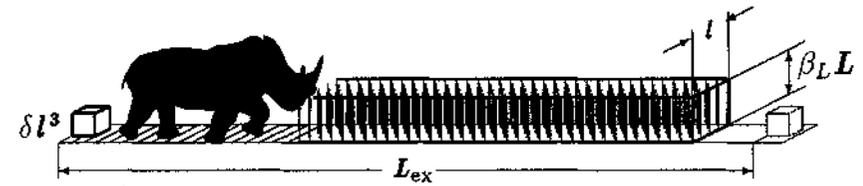
Figure 4.6. Diffusion of excreta of animals. A moving animal eats away biomass inside a band of approximate width l (l is the body size). The effective thickness of the layer of consumed biomass is equal to $\beta_L L$, where β_L is the share of biomass consumption by that animal, L is the thickness of edible plant biomass. The average distance between two excreta is equal to L_{ex}. The average volume of excreta is δl^3, where δ is a small constant coefficient of the order of β_L. In a stationary case the biogens contained in the excreta should spread over the territory where they have been collected. The time of diffusive spread $\tau_D = (l/l_D)^4 \tau$, where $\tau \sim 1$ year is the time of vegetation reproduction, $l_D = (\tau DL^2)^{1/4} \approx 1$ cm, see (4.6.2). A stationary state on the basis of diffusion is only possible at $l \leq l_D$. At $l \sim 1$ m the time of diffusion spread of excreta exceeds the time of vegetation reproduction by a factor of 10^8.

L_{ex}^2/D has the dimension of time). Spreading of excreta occurs mostly due to their molecular diffusion in water solutions (including molecular diffusion in plant roots). The molecular diffusion coefficient in water is of the order of magnitude $D \approx 10^5$ cm^2 s^{-1} = 10^{-2} m^2 year^{-1}. The condition $\tau_D \leq \tau \approx 1$ year imposes a limit on the value of l:

$$l \leq l_D \equiv (\tau D)^{1/4}L^{1/2} \qquad (4.6.2)$$

Assuming the average thickness of the metabolically-active edible live biomass layer of vegetation $L \approx 4$ mm (Section 4.3) we obtain $l_D \approx 1$ cm. As seen from Eq. (4.6.2) this value is hardly sensitive to even significant variations in any of the input variables.

Therefore, there is no problem of the excreta spread for very small animals with $l \leq l_D \approx 1$ cm. Even if this spread occurs by means of the slowest possible process, i.e. molecular diffusion in liquid, it takes less time than reproduction of vegetation. In contrast, for animals with body sizes $l \geq l_D$ the time of diffusive spread of excreta τ_D sharply increases with growing body size l, see Eq. (4.6.1). The time τ_D increases by four orders of magnitude, while body size l increases by only one. At $l \approx 10^{-1}$ m, the time τ_D is already equal to 10^4 years, while at $l \approx 1$ m we have $\tau_D \approx 10^8$ years. These estimates do not change considerably even if the diffusion coefficient D changes by a few orders of magnitude. Therefore, nutrients excreted from the bodies of large animals cannot be returned by the process of diffusion to those places from which they had been collected. Thus, processes of diffusion cannot account for the observed sustainable distribution of nutrients within natural undisturbed ecosystems.

Ecosystems inhabited by large animals may only remain stable due to external natural fluxes of matter, which mix and transport the animal excreta across the land surface. The principal role in mixing the excreta of large animals is played by the surface runoff of precipitated water. The amount of nutrients mixed by surface water runoff may be assessed from the level of ionic runoff of carbon, which amounts to about 10^{-3} of the organic carbon production (Watts, 1982; Schlesinger, 1990). In a

stationary case, the amount of nutrients concentrated in the excreta of large animals must not exceed the amount of nutrients returned on average to their initial location by the surface ionic runoff. **Consequently, the global average share of consumption by all the large animals must not exceed several tenths of a percent of net primary production,** which corresponds to the distribution presented in Figure 3.3. In the areas of low surface runoff large animals may comparatively quickly turn the land surface into desert. Note that this conclusion represents an independent estimate of the large animals' share of consumption of net primary production of the biosphere compatible with environmental stability.

In coastal areas, estuaries, river floodlands and also in rivers and lakes themselves, where the ionic runoff locally approaches the level of net primary production, the share of consumption by large animals may be significantly larger than the global average. In such areas, large animals (both predators and prey) may develop very high population densities as compared to those on land.

After a substantial disturbance of an ecosystem that entails destruction of soil cover and of the natural homogeneous distribution of biogens (e.g. fire, volcanic eruption, etc.), locomotive animals may play a significant role as species-repairers in spreading biogens across the affected territory and transporting them to places where physical water fluxes are of no help (e.g. transporting biogens up a hill). Therefore, the structure of the pioneer vegetation during the early stages of a community's recovery after perturbations offers a larger share of consumption of its production to locomotive animals than in a stationary case (Section 6.7.2).

4.7 CONCLUSIONS

We will now sum up the results for the energetics of ecological communities obtained in Chapters 3 and 4.

The source of external energy supporting the life of communities of the Earth's biota is solar radiation. Due to the zero mass of photons, solar energy cannot be stored in the environment in the form of short-wave radiation. The Earth's plants, for which solar radiation is the primary source of energy, are therefore incapable of increasing their energy consumption by locomotion. That is why green plants are immobile and form a continuous vegetation cover. A continuous cover of immobile vegetation is typical for all the land ecosystems and the oceanic shelf.[1]

The fact that plants do not need to move results in the possibility of their existence in the form of weakly-correlated (modular) multicellular individuals of large size. The mode of functioning of plants is similar to that of the functioning of a completely non-correlated set of single-cell individuals of equal metabolically-active mass. That feature provides for lowering the fluctuations of photosynthesis

[1] Mobility of single-cell individuals in certain species of oceanic phytoplankton is not related to an increased energy consumption. Rather, it is determined by the fact that phytoplankton biomass follows a certain non-random distribution with depth and that a vertical movement is needed to keep that phytoplankton within the euphotic layer (Sieburth, 1976; Gorshkov, 1980).

of organic matter within the local ecosystem, as based on the action of the law of large numbers.

Destruction of synthesised organic matter in the community is also performed by the immobile, weakly-correlated individuals—bacteria and fungi. (Mobility of certain forms of bacteria, similar to that of certain forms of phytoplankton, pursues the aim of vertical movement through soil layers, but not the increase of energy consumption.) Taking into account the respiration of plants themselves, immobile weakly-correlated individuals account for decomposition of more than 95% of the photosynthesised organic matter (Section 3.7). Similar to the synthesis of organic matter, such organisation of the destruction process makes it possible to reduce fluctuations in the destruction of organic matter within the local ecosystem, as based on the action of the law of large numbers.

Organisation of the community on the basis of a large number of completely uncorrelated or modular, weakly-correlated parts, makes it possible to control both the rate of synthesis and of destruction of organic matter to a high degree of accuracy. That, in its turn, makes it possible to keep the matter cycles strictly closed, and the environment steady provided there are no external disturbances. Also, such organisation enables the community to perform an adequate reaction directed towards compensation of any external disturbances of the ecosystem. Epilithic lichens represent an example of a simplest type of community composed solely of immobile individuals (of algae and fungi).

The existence of a universal minimum admissible value of energy consumption per unit volume (or mass) in all the living beings results in a strict limitation upon the admissible effective vertical size of an individual, provided the flux of energy incident upon the unit projection area of that individual upon the Earth's surface is constant. That size is controlled by the flux of solar radiation and by the photosynthesis efficiency. For the biosphere, on average, the solid cover of the metabolically-active biomass for both synthesisers of the organic matter (green plants), and their reducers, heterotrophs (bacteria and fungi), may only reach a thickness of no more than 3 mm. The observed extremely large body size of woody plants is explained by the fact that the overwhelming part of space occupied by those plants is empty and most of the biomass of such plants is metabolically inactive (effectively dead).

In order to support life of large individuals with a metabolically-active layer much thicker than that formed by plants and other immobile organisms, it is necessary to employ energy fluxes, which by far exceed the flux of solar energy, even in the hypothetical case when the biochemical efficiency of the solar energy consumption is equal to unity. Hence, large individuals cannot form a solid continuous cover (a 'stationary crowd'). The feeding energy for these individuals should be collected from a large surface, significantly exceeding the projection area of such individuals upon the Earth's surface. Since, apart solar radiation, there are no other forms of primary energy available, while solar radiation cannot be accumulated, such individuals cannot feed off the solar energy immediately. Hence, large individuals may only feed off the secondary energy of synthesised organic matter which, unlike solar photons, has non-zero mass and can be accumulated locally. In other words,

large individuals may only be heterotrophic, and have to participate in destroying organic matter.

Feeding off the locally accumulated plant biomass is only possible via movement of large individuals over their feeding territory. Movement, on the other hand, demands that the body of a large individual is a rigidly-correlated formation (unlike weakly-correlated bodies of immobile plants).

The community consisting of immobile and, hence, of effectively small-sized modular individuals can afford strict equality between the synthesis and destruction over any arbitrarily small time interval, i.e. of strict constancy of the organic and inorganic mass in each local ecosystem. This may be assured due to small relative fluctuations characterising any system comprising a large number of uncorrelated components.

The introduction of large mobile animals into the community results in a drastic change in the way of functioning of that community. Mobile animals feeding off the accumulated biomass inevitably bring about sharp fluctuations of that biomass in any local area of the community. The animal very quickly eats away that biomass, after which it is regenerated very slowly. That, in its turn, results in fluctuations of inorganic matter excreted by the animal into the environment after consumption of organic matter. Hence, the state of the environment ceases to be stationary, and suffers significant perturbations. Stationary state of the environment may only be reached after averaging over a long enough time period. That result imposes strict limitations upon the possible species composition and the behaviour of the animals entering that community.

Random oscillations of biomass and of destruction rate of organic matter in a community being strong, it becomes impossible to close matter cycles and to ensure the long-term stability of the ecosystem. Therefore, the average consumption quota of plant products by mobile animals should not exceed the natural fluctuations of plant production. When that condition is met, the presence of animals in the community does not leave any apparent traces in plant biomass. Fluctuations in plant biomass introduced by large animals grow with the body size of those animals. Hence the quota of consumption of plant production by those animals should drop for larger body size of the consumers. That conclusion agrees with the observed distribution of plant production over consumers of different body size (Figure 3.3). Reducing the number of species of large animals slows down the rate at which that consumption quota drops for a separate species with their body size increasing.

The ubiquity of large animals (i.e. the fact that they are present in the overwhelming majority of ecosystems) means that the net impact of large animals to the community's stability is positive. Communities where large animals are present appear to be more stable and competitive than communities without them. There may be several reasons for that.

After external perturbations the population density of species-repairers reaches its maximum value, while where no external disturbances are present, the ecosystem contains very few individuals of species-repairers (Sections 6.7 and 6.8.2). For example, in a climax spruce, forest birch and aspen (species-repairers) are present in very low numbers and may not even form a population. The genome of every

species-repairer should contain information about optimal population density and behaviour of its individuals that corresponds best to the task of rapid recovery of the ecosystem after external disturbances. That information is only put into operation in a disturbed ecosystem. Therefore, the appropriateness of that information can be tested and maintained only in a disturbed environment, when species-repairers form large populations and there opens a possibility for stabilising selection to operate.

Under normal environmental conditions that information is continuously decaying. Natural disturbances are of a rare and non-regular nature. If the time interval between two successive disturbances becomes too long, the genetic information of species-repairers may substantially degrade. As a result, natural communities would not be able to cope with natural disturbances and the stability of their organisation would be undermined.

There are two ways to settle the problem. Firstly, stabilising selection of the normal genome of the species-repairers can be performed by the dominant species in the community. In that sense it is a kind of artificial selection: as soon as individuals of one species are unable to form its own population, they are selected by individuals of another species. The mechanisms of such artificial selection may be very complex and difficult to reveal. One may only speculate about it. For example, the dominant plant species (e.g. spruce) may modify the biochemical composition of soil in such a way that only normal birches will grow best in the ecosystem, while birches with decay genetic information will lose the competition. Also, dominant plant species may support the existence of locomotive animals that would eat up decay individuals of species-repairers (e.g. eliminate young birches that grow too slowly or too rapidly, etc.). The same function can also be performed by large animals under disturbed conditions, the efficiency of intraspecific stabilising selection of species-repairers. The observed increase in population numbers of large animals (e.g. elks) during processes of forest succession after fires, clear cutting and other disturbances testifies for such a role of large animals (Section 6.8.2).

Secondly, it is possible to introduce regular disturbances of biotic nature into the ecosystem in order to 'train' species-repairers. This task can be also performed by large animals. For example, elephants are known to make big clearings in the forest, where pioneer plant-repairers (herbs, shrubs) are given a possibility of forming relatively dense populations.

The described ecological functions of large animals (we have not mentioned here the previously discussed stabilising function of carnivores, see Section 4.5) contribute to the stability of ecological communities and thus allow large animals themselves to continue.

The obtained estimates of size of local ecosystems, that were based on the condition of low fluctuations of the community's major characteristics (Section 3.5), show that local ecosystems are much smaller in size than typical feeding territories of large animals. However, the biological community of the local ecosystem is able to control population density of large animals, e.g. by changing production of edible parts of plants. Communities that maintain population density of large animals at an optimal level become most competitive and force out all other communities. As a result, optimal population density of large animals is maintained

on large territories covered by a population of local ecosystems with the most competitive communities. In that sense, large animals represent a certain component of the environment, which is kept, similarly to concentrations of the important nutrients, at a certain optimal level by the population of communities consisting of plants and microorganisms (see also Section 5.8).

Note that it is erroneously assumed sometimes that the community should include whole populations of all the species of large animals present in the ecosystem. In that case, the size of the community could not be less than the largest territory occupied by a population of large animals, and there would be no populations of communities possible at all, leaving unsolvable the task of preventing the internal correlation of communities from decay (Section 2.8). The estimated size of the community appears to be of the order of several metres (Section 3.5). We consider this result as one of the most important statements made in Chapters 3 and 4.

Easily noticeable disturbances produced by large animals in the ecosystem may be misinterpreted as the principal managing role of large animals in the community. However, as we have seen, in natural communities large animals are only allowed to consume a tiny part of the net primary production of plants, which is achieved via regulating population density of large animals by other species of the community. Thus, the community controls the large animals, but not vice versa, as it is sometimes asserted (Sher, 1990). Substantial destabilisation of ecological communities following artificial elimination of large animals (e.g. due to hunting) does not contradict this statement. There are no unnecessary species in the community, so that elimination of any of them (including large animals) would impair the community's wellbeing. However, the effect of elimination of dominant species of the community (plants, bacteria and fungi, see Figure 3.3) by far overrides disturbances that may be introduced by elimination of large animals. Elimination of dominant species leads to rapid complete degradation rather than to gradual destabilisation of the community. Thus, it is reasonable to think that during evolutionary process as well, changes in the dominant species impose on average by far a more drastic effect on the community structure than evolutionary changes in large animals.

Under natural conditions, the population density of large animals is determined not by the availability of food (the latter is always present in excess to the needs of the animals, see Section 4.3), but by the condition of maximum stability of the ecological community or its rapid recovery after disturbances. Information about the optimal population density should be written in the normal genome of a species, as well as the programme of correct interaction with all the other species in the community.

An increase of the population density of large animals above the optimal value presents a serious danger to the community's integrity due to their ability to rapidly destroy the community's biomass. Thus, most behavioural traits the animal displays are aimed at preventing excessive growth of population density of large animals, rather than to stimulate increase of population density to the limit the food resources can stand. That aim is reached via strict control of the size of the feeding territory per single individual (McNab, 1983). Such control is based on various interactions of

individuals at all levels of the community organisation (voice signals of neighbours, migration of individuals with too high population density (McFarland, 1985), control of population density by parasites and carnivores, etc.). All these correlated interactions of individuals, often perceived as 'altruistic', are aimed at ensuring the maximum possible stability of the community. Communities that are able to stabilise their optimal environment in the most efficient way, survive. Species unable to perform correlated ('altruistic') interactions with other species in the community may increase their population density until resources permit, disrupt correlated organisation of the community, disturb the community's environment and finally perish together with all the communities that favoured their existence. This is what is now going on with the global environment under anthropogenic impact.

Energy spent by an animal for making the rounds of its feeding territory quickly increases with the animal's body size due to purely physical reasons (Section 4.2). According to the ecological reasons outlined above, the energy of food consumed by the animal per unit of the distance covered should reduce with the increasing body size of the animal (Sections 3.6 and 3.7). The life of an animal is physically possible when the energy spent to traverse that territory is regained with food the animal collects on that territory. This ecological condition is only met for small enough animals, their size not exceeding a certain critical value (Section 4.3). The body size of man coincides with that critical body size in its order of magnitude. With the animal body size exceeding that critical limit, the share of plant food it consumes inevitably grows. To support the ecological equilibrium, such animals may only exist in nomadic mode, at a very low average density of their population number, while at the same time saving an enormous feeding territory from intervention by competitors.

Biotic regulation of the environment is determined by a strictly specified relation between the synthesis and destruction of organic matter, which should be dependent on the current environmental situation. Possible forms of such a relationship are limited by the above enumerated strictly described laws of nature. Within the limitations set by those laws, biological relations may assume any forms, however complex. One of those forms is the trophic structure of the destruction of organic matter, that is, the way the heterotrophs are divided into reducers, destroying dead organic matter, and the consumers, who devour live individuals. Herbivores, carnivores of the first order eating away the herbivores, carnivores of the second order which feed off the carnivores of the first order, etc. are identified in natural ecosystems. Such a division into different levels forms a well-known ecological pyramid of energy fluxes, which is often envisaged as the basis of ecology (Odum, 1983). However, the pyramidal organisation of energy fluxes is only observed on condition of low ratio of production to consumption in a population of species at each level of the pyramid. For reducers like bacteria and fungi that consume the most part of the net primary production (see Figure 3.3), and for which that ratio is not low, such a pyramid loses sense as soon as the energy flux practically does not change from one species to another (Gorshkov and Dolnik, 1980; Gorshkov, 1982b).

Carnivores feature certain peculiarities (discussed in Section 4.5), that are based on the general physical laws of nature. Details of interaction between the carnivores

and their prey are controlled by the correlated nature of interaction between all the species in a natural community which, in principle, may be considered as one of the forms of symbiotic interaction. Dividing the interaction between the species in the community, such as commensalism, amensalism, predation, parasitism, symbiosis, etc. (Begon *et al.*, 1986) is quite artificial and arbitrary, and in no way defines the actual sense and diversity of these interactions. All such interactions are but different forms of correlation between the species in a natural community and are similar to correlation between the different organs in a body or organelles and biological macromolecules in a cell, being aimed at maintenance of stable organisation of the ecological community.

The enormous power of information fluxes processed by the molecular structures of living beings in a natural community exceeds by many orders of magnitude the maximum achievable fluxes of information flowing through all the computers of modern civilisation (Chapter 7). This indicates that it is hopeless to try to construct any mathematical models pretending to describe the actual processes within the natural ecological communities. These processes are many orders of magnitude more complex than the processes taking place within a separate living individual, in particular those evolving within the brains of large animals and man, and will apparently never fall subject to detailed modelling. (That comment does not refer to artificial communities, devoid of a programme of stabilisation of the environment, the only aim of their construction being to provide enough food for humans.) Meanwhile, studying the physical limitations upon the processes taking place in the community yields reliable results and opens the way to unequivocal conclusions.

5

Ecological Principles of Biotic Regulation

5.1   ECOLOGICAL LIMITATIONS ON EXPANSION OF SPECIES

As noted in Section 2.1, expansion is one the most important properties of life, ensuring its stability. It is a most general characteristic of life, observed in every species; it even covers such advanced forms of claiming new territories as space ventures by man.

Expansion in its general sense may occur in two ways. First, population density of individuals may increase within the boundaries of a given territory. This type of expansion may be called 'intensive'. Second, population may expand into as yet unoccupied areas ('extensive' expansion). Genetic evolutionary changes accompanied by an increase in competitiveness become fixed in the population in the course of expansion.

The most important feature of the expansion process is that, during expansion, competitive interaction and, consequently, stabilising selection in the population weaken or even cease altogether. Individuals spend their efforts in occupying new positions instead of competing with each other. This implies that a new progressive evolutionary trait only has a chance to persist in the population if the process of expansion of its carriers takes a shorter time than it takes such a trait to decay in the absence of stabilising selection.

Were infinite territories and fluxes of energy available for life, expansion (either 'intensive' or 'extensive') would have been infinite as well. Competitive interaction would be totally switched off, so that stabilisation of the existing level of organisation of biological objects would be impossible. Therefore, life may exist sustainably only in the absence of energy and territory abundance, i.e. when all available energy fluxes are already claimed by the biota. Presence of energy or territory abundance entails biological expansion that undermines the process of competitive interaction, which is the only guarantee for the stability of life organisation (Chapter 2). Hence, evolutionary processes necessarily accompanied by expansion may only occur very infrequently, so that species spend the majority of their time in a state of evolutionary stasis (Haldane, 1954).