

# The body mass allometries as evolutionarily determined by the foraging of mobile organisms

LARS WITTING

Department of Ecology and Genetics, University of Aarhus, Ny Munkegade, DK-8000 Aarhus C, Denmark

**Abstract** It is shown that the exponents of eight across species body mass allometries can evolve from the constraints associated to the foraging process of mobile organisms. The explained exponents include those of metabolic rate, lifespan, population density, home range, population energy use, maximum lifetime reproduction, maximum rate of population increase, and the level of social behavior. Some of the theoretically deduced exponents vary with the dimensionality of the foraging behavior, i.e., they take the values  $\pm 1/2$  when foraging occurs in one dimension,  $\pm 1/4$  and  $\pm 3/4$  when foraging occurs in two dimensions, and  $\pm 1/6$  and  $\pm 5/6$  when foraging occurs in three dimensions. In comparison, the empirically established exponents of terrestrial organisms resemble the theoretical exponents for foraging in two dimensions, whereas the empirical exponents of pelagic organisms resemble the theoretical exponents for foraging in three dimensions.

## 1 Introduction

In 1883 Rubner proposed that the exponent of the allometric relation between the metabolic rate and body mass was explained by the surface rule that was meant to cause thermal homeostasis. However, the surface rule predicts an exponent of  $2/3$  while the observed exponent is  $3/4$  (Kleiber 1932). Blum (1977) pointed out that the surface rule actually predicts  $3/4$  if the world has four spatial dimensions instead of three. But, the fourth dimension remains to be discovered. McMahon (1973, 1975) argues that the metabolic rate is proportional to muscle cross-sectional area and that elastic similarity predicts a muscle cross-sectional area that is proportional to body mass raised to the  $3/4$  power and, consequently, the metabolic rate should scale to the  $3/4$  power of body mass. However, “body support for animals other than the hoofed mammals does not conform to the elastic similarity model” (Calder 1984; p. 85; see also LaBarbera 1986). More theoretical work, including Reiss (1989), Charnov (1993), and related studies reviewed by Calder (1984) and Peters (1983), have been restricted to the deduction of some allometric exponents from other allometric exponents and, thus, this

work does not attempt to explain why  $3/4$ ? As LaBarbera (1986) concludes: “at present there is no general explanation for the  $3/4$  mass exponent for metabolic rate; the most all-encompassing of design generalities in biology must, at present, be treated simply as an empirical fact.”

Besides the  $3/4$  exponent for metabolic rate the body mass exponents across mobile species include  $1/4$  for lifespan (Bonner 1965),  $-1/4$  for the maximal rate of population increase (Fenchel 1974),  $-3/4$  for the population density (Damuth 1981, 1987),  $1$  for home range area (Schoener 1968; Turner et al. 1969; Harestad and Bunnell 1979; Calder 1984),  $0$  for the resource consumed by a population (Damuth 1981, 1987),  $0$  for maximal lifetime reproduction (Charnov 1993), and  $1/4$  for the level of social behavior (Peters 1983; Calder 1984). In this paper I will show that these exponents can evolve from the constraints by which the foraging process generates interference among the foraging individuals when coupled with the constraints by which the exploitation of an individual inhibits the foraging of that individual. These constraints imply that the well-known exponents  $\pm 1/4$  and  $\pm 3/4$  are valid for organisms that forage in two dimensions, while the exponents are  $\pm 1/6$  and  $\pm 5/6$  for organisms that forage in three dimensions, and  $\pm 1/2$  for organisms that forage in one dimension.

I obtain my results by describing the involved processes by the allometric traits (Section 3.1 to 3.2), by optimizing the foraging process (Section 3.3), and by solving the involved equations to obtain the allometric exponents (Sections 4.1 to 4.2). Before this is done, I define some demographic and ecological constraints in Section 2. Although it is not these latter constraints that are the proximate causes for the evolution of the allometric exponents, they are required because they link the different life history traits together and because they link the life history traits to the ecology of resource consumption. A list of the most important symbols is given in Table 1.

$w$	Body mass
$B$	Metabolic rate per unit body mass ( $B \sim w^b$ )
$T$	Lifespan ( $T \sim w^t$ )
$N$	Population density ( $N \sim w^n$ )
$H$	Home range ( $H \sim w^h$ )
$E$	Resource density ( $W \sim w^e$ )
$\alpha$	Exploitation efficiency ( $\alpha \sim w^a$ )
$I$	Level of intra-population interference
$p$	Survival probability
$R_0$	Lifetime reproductive value
$R$	Lifetime reproduction
$\epsilon$	Consumed energy used for reproduction
$f$	Foraging self-inhibition
$g$	Regulation by intra-population interference

Table 1: A list of the most important symbols.

## 2 Demography and ecology

One assumption that is central to my study is the principle of physiological time (Brody 1945). According to this principle the various processes of an organism occur at a timescale that is inversely proportional to the metabolic rate per unit mass of that organism. On empirical grounds this principle is illustrated by the fact that most life-history timings are proportional to the positive 1/4 power of body mass while the metabolic rate per unit mass ( $B$ ) is proportional to the negative 1/4 power of body mass (reviewed in Calder 1984). This is reflected also in Pearl's (1928) notion that the lifespan of an organism is inversely related to the metabolic rate per unit mass, just like the longevity of a machine is inversely related to the rate by which the machine is used. We can formulate this relation between the maximal lifespan ( $T$ ) and the metabolic rate ( $B$ ) as

$$T = \omega/B, \quad (1)$$

where  $\omega$  is a positive constant of senescence that can be modified by selection. Although Pearl's "rate-of-living" has been questioned (Maynard Smith 1958, 1963; Clarke and Maynard Smith 1961a,b; reviewed in Rose 1991) we will find that it is sufficiently accurate in relation to the body mass allometries. To obtain a measure of longevity that includes potentially immortal organisms (i.e.,  $\omega \rightarrow \infty$ ) we can define the average lifespan as

$$\begin{aligned} \bar{T} &= \bar{\omega}/B \\ \bar{\omega} &= \sum_{x=0}^{\infty} x(l_{x-1} - l_x), \end{aligned} \quad (2)$$

where age ( $x$ ) and cumulative survival ( $l_x$ ) are scaled according to the physiological time of the organism, i.e., scaled with  $1/B$ . For those potentially immortal organisms that have constant survival per unit physiological time ( $p_c$ ) the average lifespan of eqn 2 is given as

$$\begin{aligned} \bar{T} &= \frac{\sum_{x=0}^{\infty} xp_c^{x-1} - \sum_{x=0}^{\infty} xp_c^x}{B} \\ &= \frac{1}{B(1-p_c)}. \end{aligned} \quad (3)$$

From eqns 1 to 3 we notice that among the organisms with a similar  $l_x$  function, both the average lifespan and the maximal lifespan are inversely proportional to the metabolic rate per unit body mass. Hence, the theoretical analysis will be restricted to include only maximal lifespan ( $T$ ) knowing that the allometric dependence of this parameter will describe the empirical allometry for average longevity, and the empirical allometries for other life-history timings.

In relation to fitness the relevant survival component is survival to the post-reproductive state whereafter survival is irrelevant (if we assume that post reproductive individuals cannot enhance the fitness of their offspring). This component can be defined as the survival probability

$$p = R_0/R, \quad (4)$$

where  $R_0$  is the expected life-time reproductive value and  $R$  is the lifetime reproduction of an individual if it survives to maximal age. In relation to the definition of  $p$  we can think of a bimodal population in which an individual will die before it reproduces with the probability  $1-p$ , while it will survive with the probability  $p$ , reproduce, and eventually die from senescence. However, we may also think of  $p$  simply as a statistical measure that is defined from age-structured survival and reproduction. For those organisms that are potentially immortal and which, per unit physiological time, have constant reproduction ( $m_c$ ) and constant survival ( $p_c$ ) we have that  $p \rightarrow \infty$  because  $R \rightarrow \infty$  and  $R_0 = m_c \sum p_c^x \rightarrow m_c p_c / (1 - p_c)$ , with  $x \in \{0, 1, 2, \dots\}$ . More generally

$$p = \frac{\sum_{x=0}^{\infty} l_x m_x}{\sum_{x=0}^{\infty} m_x}, \quad (5)$$

because  $R_0 = \sum l_x m_x$  and  $R = \sum m_x$ , with  $x \in \{0, 1, 2, \dots\}$ . Then, if age structured reproduction is

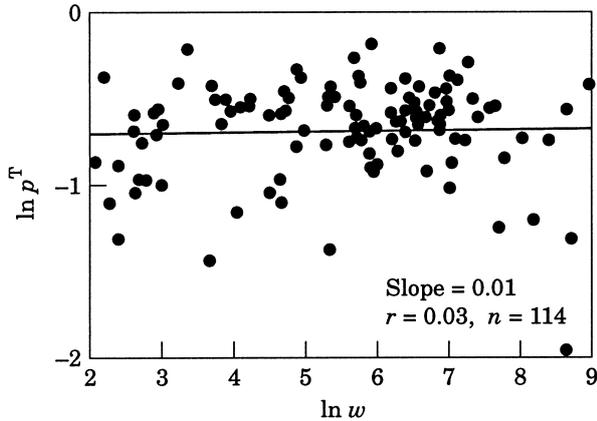


Figure 1: Annual adult survival ( $p$ ) raised to the power of age of first reproduction ( $T$ ) against the body mass ( $w$ ) on double logarithmic scale for 114 species of birds. Data from Cramp & Simmons (1977–1983), Cramp (1985–1992), and Cramp & Perrins (1993).

constant,  $R = \omega m_c$  and eqn 5 reduces to

$$p = \omega^{-1} \sum_{x=0}^{\infty} l_x, \quad (6)$$

From eqn 6 we see that  $p$  is expected to be invariant for organisms with a similar  $\omega$  parameter and similar  $l_x$  (and  $m_x$ ) function(s). As these functions are scaled according to physiological time we expect that  $p$  is invariant among organisms with a similar bauplan. One such group is birds, and in Fig. 1 I show that the invariance of  $p$  is confirmed among 114 species when plotted against body mass. This invariance suggests that mortality is selectively neutral on the body mass axis, i.e., there seems to be no evidence that it is differentiated mortality that has caused the evolutionary differentiation into different body masses. This result opposes the common assumption in life history theory that large organisms that mature later suffer from higher mortality because instantaneous mortality is constant per unit astronomical time (Bell 1980; Roff 1981; Stearns 1992).

I will deal with a non-structured organism with non-overlapping generations in order to simplify the demography. For an unstructured organism reproduction and body mass is age independent and, thus, lifetime reproduction can be given as

$$R(\epsilon) = \epsilon T/w, \quad (7)$$

where  $\epsilon$  is the energy that is allocated to reproduction per unit astronomical time and  $w$  is the energetic mass of an offspring. The inverse relationship (trade-off) between lifetime reproduction ( $R$ ) and body mass

( $w$ ) exists because energy ( $\epsilon$ ) can be used only once. Equation 6 also implies that an organism is assumed to have a fixed body mass, while reproduction is assumed to be phenotypically plastic.

Given the present assumptions, it follows that the fraction of net assimilated energy allocated to reproduction is body mass invariant. To see this, recall that the body mass is assumed to be constant from birth to death. Hence, net assimilated energy must be allocated to either reproduction or to metabolism, i.e.,  $\epsilon_A = \epsilon + \epsilon_B$  where  $\epsilon_A$  is net assimilated energy,  $\epsilon_B$  is metabolized energy, and  $\epsilon$  is energy allocated to reproduction as previously defined. Furthermore, because a population with stable, or damped, population dynamics will be situated at the population equilibrium an average individual will replace itself by a single individual, i.e.,  $R_0 = p\epsilon T/w = 1$  and, consequently,  $\epsilon = w/pT$ . Then, because the energy that is metabolized is  $\epsilon_B = wB$  and because  $B = \omega/T$ , it follows that the allocation ratio is

$$\begin{aligned} \epsilon/\epsilon_B &= \frac{w/pT}{w\omega/T} = 1/\omega p \\ &= 1/\sum_{x=0}^{\infty} l_x \sim w^0. \end{aligned} \quad (8)$$

Then, as  $\epsilon_A = \epsilon + \epsilon_B$  we have that  $\epsilon_A/\epsilon = 1 + \epsilon_B/\epsilon$  and, thus, that  $\epsilon = c\epsilon_A$  where  $c = \epsilon/(\epsilon + \epsilon_B)$  is a positive constant. We can then simplify the notation by setting  $c = 1$  so that  $\epsilon$  denote both net assimilation and the amount of energy that is allocated to reproduction.

If we assume that an individual assimilates all the energy that it consumes, net assimilation is equal to

$$\epsilon = \kappa E, \quad (9)$$

where  $\kappa$  is the realized resource consumption efficiency and  $E$  is the resource density at the population dynamic equilibrium. This resource density is defined also by the following growth equation

$$dE/dt = E(r_e - \gamma_e E - \kappa N), \quad (10)$$

where  $r_e$  is the maximal rate of increase in resource density,  $-\gamma_e$  is the density regulation in the resource,  $N$  is the density of the consumer organism, and the superscript dots denote arbitrary densities. The resource density at the population equilibrium is then

$$E = E_m - \kappa N/\gamma_e, \quad (11)$$

where  $N$  is the consumer density at the equilibrium and  $E \rightarrow E_m = r_e/\gamma_e$  at the limit  $N \rightarrow 0$ .

In the present study I will partition the realized resource consumption efficiency ( $\kappa$ ) into three multiplicative components. The first component is the exploitation efficiency ( $\alpha$ ) that describes the ecological potential of  $\kappa$  which occurs when competition is purely exploitative and the resource is exploited evenly. The second component ( $g$ ) is the regulation of  $\kappa$  as it is caused by the interactions among the foraging individuals. The third component ( $f$ ) is the self-inhibition of  $\kappa$  as it occurs when an individual exploits its own fraction of the resource more heavily than the population exploits the total resource. The energy that is consumed by an individual is then given as

$$\epsilon = \alpha f g E. \quad (12)$$

In the following sections we will see that the exponents of the body mass allometries are explained by the constraints that are associated with the two functions  $f$  and  $g$ .

### 3 The foraging process

#### 3.1 Self-inhibition

To formulate self-inhibition consider foraging as it occurs within a home range. In this instance the organism is likely to forage along some more or less well defined foraging tracks, and the length ( $L$ ) of these tracks is expected to be proportional to the  $d$ -th root of the  $d$  dimensional home range ( $H$ ), i.e.,  $L \sim H^{1/d}$  with  $d \in \{1, 2, 3\}$ . At least for mammals this expectation is not falsified because the length of their foraging bouts scale to the square root of their home range area (Garland 1983; Calder 1984). The time interval between track reuse ( $T_V$ ) is the track distance ( $L$ ) divided by the foraging speed ( $V$ ), i.e.,

$$T_V = L/V \sim H^{1/d}/V. \quad (13)$$

As the foraging speed is proportional to lifespan (Garland 1983; Calder 1984), the time interval between track reuse scales as

$$T_V \sim H^{1/d}/T. \quad (14)$$

The availability of food along the foraging track can be considered to be proportional to the time interval between track reuse, as the longer the time period between foraging events, the more time there is available for the resource to regrow or to disperse into the foraged area. Because of this regrowth/dispersal delay, the frequency of track reuse ( $1/T_V$ ) will describe the degree to which an individual will inhibit its own foraging.

The time interval between reforaging as described by eqn 14 is measured in astronomical time. This implies that self-inhibition as described by the frequency  $1/T_V$  is given as an absolute measure. However, self-inhibition is a relative term; relative to the situation where no individual reuses its foraging tracks, i.e., relative to the situation with infinitely large home ranges. In this default case with no self-inhibition the resource is reharvested by a given frequency and thus, in order to describe self-inhibition by the time interval between track reuse ( $T_V$ ), we need to scale this interval by the interval between resource reharvesting in the situation with infinitely large home ranges. From the principle of physiological time we expect that the time available for regrowth/dispersal in the default situation is inversely proportional to the metabolic rate per unit body mass, i.e., proportional to lifespan ( $T$ ). That is, smaller organisms are expected to reharvest an area at a faster pace than larger organisms are. Accepting this scaling, the scaled  $T_v$  is

$$T_{V,S} \sim H^{1/d}/T^2. \quad (15)$$

The foraging efficiency in the presence of self-inhibition can then be described as

$$\kappa = \alpha f(H^{1/d}/T^2), \quad (16)$$

where  $f$  is the self-inhibition function that is expected to be convex and to increase monotonically from zero to unity as the size of the home range increases from zero to infinity. According to eqn 16, we have that, in the absence of intra-population interference, optimal foraging will occur at infinitely large home ranges where self-inhibition is absent.

#### 3.2 Intra-population interference

If the home ranges of two individuals are non-overlapping, clearly the two individuals cannot meet and the probability that they will encounter each other is zero. In general, the probability of an encounter between two individuals is expected to be proportional to the relative overlap of their home ranges. At the population equilibrium the home ranges are expected to be evenly distributed as shown in Fig. 2 for the two-dimensional system. Then the home ranges are partitioned into zones that are utilized by a variable number of individuals, and the number of interference encounters experienced per individual is proportional to the total degree of home range overlap. This total degree of overlap ( $O$ ) can be described as the average home range ( $H$ ) divided by the per capita availability of space

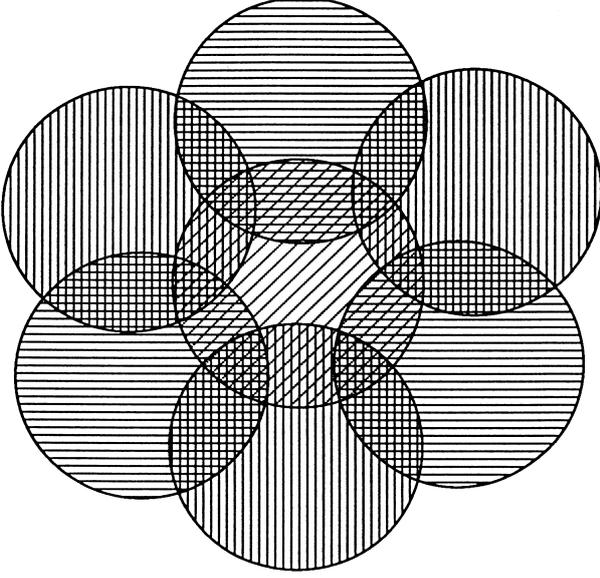


Figure 2: An illustration of home range overlap and levels of intra-population interference for a two-dimensional system. Hatched areas resemble zones of no interference because they are used by one individual only. Double-hatched areas resemble zones of interference between two individuals. Triple-hatched areas resemble zones with interference among three individuals.

$(1/N)$ , i.e., as

$$O \sim HN, \quad (17)$$

where both the home range and the population density ( $N$ ) is measured in  $d$  dimensions.

The level of interference depends also upon the rate of foraging, i.e., the faster the foraging tracks are covered the more often the individuals will encounter each other. Thus, the number of interference encounters per individual per unit astronomical time is proportional to the frequency by which the tracks are reused, i.e., proportional to the home range overlap [eqn 17] divided by the time interval between track reuse [eqn 14]. Hence,

$$I \sim TH^{(d-1)/d}N, \quad (18)$$

when the level of interference ( $I$ ) is proportional to the number of interference encounters experienced per individual per unit astronomical time.

The number of encounters depends also upon the density of the resource. If the resource density is low the individual will have to cover its foraging tracks at a fast rate to find sufficient resource, whereas if the resource density is high the individual need hardly move in order to find sufficient resource. The level of interference is then expected to be inversely proportional to

the resource density and we obtain

$$I = TH^{(d-1)/d}N/E. \quad (19)$$

The inhibition of foraging that is caused by intra-population interference is given by the function  $g(I)$ . Contrary to self-inhibition ( $f$ ), inhibition by interference is absent ( $g = 1$ ) when the home ranges are infinitely small and non-overlapping, and it is at its maximum ( $0 \leq g \leq 1$ ) when the home ranges are infinitely large and completely overlapping.

### 3.3 The foraging optimum

From the previous two sub-sections we have that the foraging efficiency is given as

$$\kappa = \alpha f(H^{1/d}/T^2)g(TH^{(d-1)/d}N/E). \quad (20)$$

As  $f$  increases and  $g$  decreases monotonically with  $H$  we might expect that the realized exploitation ( $\kappa$ ) has an optimum on the home range axis. We can determine this optimum by differentiating the foraging eqn 20 with respect to the home range, and by setting the derivative equal to zero. Let

$$f(X) = f(H^{1/d}/T^2), \quad (21)$$

then, we obtain

$$\begin{aligned} d\kappa/dH &= (\alpha/d)H^{(1-d)/d}T^{-2}f'(X)g(I) \\ &+ [\alpha(d-1)/d]H^{-1/d}TNE^{-1}f(X)g'(I), \end{aligned} \quad (22)$$

where  $f'$  and  $g'$  are the derivatives of  $f$  and  $g$  with respect to  $X$  and  $I$ . Setting  $d\kappa/dH = 0$  we can reduce eqn 22 and obtain

$$\frac{f(X)}{f'(X)} + \frac{g(I)}{g'(I)} \frac{1}{d-1} \frac{EH^{(2-d)/d}}{T^3N} = 0. \quad (23)$$

In another unpublished study I have shown that  $I \sim w^0$  when the body masses of the different species are in evolutionary equilibria. The allometric scaling of the fraction  $EH^{(2-d)/d}/T^3N$  in eqn 23 will then remain the same if it is multiplied by  $I = TH^{(d-1)/d}N/E$ . For  $T \sim w^t$ ,  $H \sim w^h$ ,  $N \sim w^n$ , and  $E \sim w^e$ , the exponent of this product ( $I \cdot EH^{(2-d)/d}/T^3N$ ) is

$$\begin{aligned} t + h(d-1)/d + n - e + e \\ + h(2-d)/d - 3t - n = h/d - 2t. \end{aligned} \quad (24)$$

This exponent is equal to the exponent of  $X$  [eqn 21] and, thus,

$$X \sim EH^{(2-d)/d}/T^3N. \quad (25)$$

Because  $I \sim w^0$  it follows that  $g(I)/g'(I)$  is body mass invariant and, thus, we can combine eqn 23 and eqn 25 in order to reduce eqn 23 to

$$\frac{f(X)}{f'(X)} - kX = 0, \quad (26)$$

where  $k$  is a positive constant. Recall now that  $f$  is a convex and monotonically increasing function of  $X$ . Consequently,  $f/f'$  is monotonically increasing with  $X$ . Then, at the most, eqn 26 can have two roots and, thus, only one optimum with a limited home range. As individual selection will optimize the foraging efficiency it will maintain the individuals at the home range optimum which implies that there is selection for a body mass invariant  $X$ .

## 4 The body mass allometries

### 4.1 The allometric deduction

We have now enough information to deduce the allometric exponents. From the body mass invariant level of interference ( $I = TH^{(d-1)/d}N/E \sim w^0$ ) we have that

$$t + h(d-1)/d + n - e = 0. \quad (27)$$

From the body mass invariant level of self-inhibition ( $X = H^{1/d}/T^2 \sim w^0$ ) we have that

$$h/d - 2t = 0. \quad (28)$$

From eqn 11 we have that the resource density at the equilibrium is  $E = E_m - \kappa N/\gamma_e$ . Then, as  $E_m \sim w^0$ , and  $\gamma_e \sim w^0$  we have that  $E \sim \kappa N$ , from which it follows that  $E/\kappa N \sim w^0$ . If we insert into this equation  $\kappa = \alpha fg$ , with  $f \sim w^0$ ,  $g \sim w^0$ , and  $\alpha \sim w^a$ , we find that

$$e - a - n = 0. \quad (29)$$

Then, let  $I = 1/ZE$  with  $Z = 1/TH^{(d-1)/d}N$ . We can then insert  $E = E_m - \alpha fgN/\gamma_e$  into  $I^{-1} = EZ \sim w^0$  and obtain  $E_m Z - \alpha fgNZ/\gamma_e \sim w^0$ , from which it follows that  $E_m \sim \alpha fgN/\gamma_e$ . If we insert  $E_m \sim w^0$ ,  $\gamma_e \sim w^0$ ,  $f \sim w^0$ , and  $g \sim w^0$  into this equation we obtain the scaling  $\alpha N \sim w^0$ , from which it follows that

$$n = -1. \quad (30)$$

Since the population is in equilibrium we have that  $pT\alpha fgE/w = 1$  and, as  $p \sim w^0$  [eqn 6] and  $f \sim g \sim w^0$  the scaling of this expression reduces to  $T\alpha E/w \sim w^0$ . Then, from  $T\alpha E/w \sim w^0$  we have

$$t + a + e = 1. \quad (31)$$

Trait	1D	2D	3D	dD
$B$	-1/2	-1/4	-1/6	-1/2d
$T$	1/2	1/4	1/6	1/2d
$N$	-1/2	-3/4	-5/6	(1-2d)/2d
$H$	1	1	1	1
$U$	0	0	0	0
$BM$	1/2	1/4	1/6	1/2d
$S$	1/2	1/4	1/6	1/2d
$R_m$	0	0	0	0
$r_m$	-1/2	-1/4	-1/6	-1/2d

Table 2: The exponents of the body mass allometries as theoretically deduced for mobile organisms that forage in one (1D), two (2D), three (3D), or  $d$  ( $dD$ ) spatial dimensions.  $B$ : metabolic rate per unit body mass.  $T$ : lifespan.  $N$ : population density measured in  $d$ -dimensions ( $d \in [1, 2, 3, d]$ ).  $H$ : home range size measured in  $d$ -dimensions.  $U$ : population energy use ( $U = NBw$ ).  $BM$ : biomass ( $BM = Nw$ ).  $S$ : Armitage's sociality index.  $R_m$ : maximal lifetime reproduction.  $r_m$ : maximal rate of population increase.

We then have five equations (27 to 31) from which we can deduce the five unknown allometric exponents:  $e$ ,  $t$ ,  $h$ ,  $n$  and  $a$ .

To deduce the allometric exponents, from  $n = -a$  [eqn 30] and  $e - a - n = 0$  [eqn 29] we have

$$e = 0. \quad (32)$$

From  $h/d - 2t = 0$  [eqn 28] it follows that

$$h = 2td. \quad (33)$$

When this  $h = 2td$  is inserted into eqn 27 together with  $e = 0$  [eqn 32] we get  $t + 2t(d-1) + n = 0$  and, thus,

$$t = n/(1-2d). \quad (34)$$

Inserting this  $t = n/(1-2d)$ ,  $a = -n$  [eqn 30], and  $e = 0$  [eqn 32] into eqn 31 we have

$$n/(1-2d) - n = 1, \quad (35)$$

which can be solved for  $n$

$$n = \frac{1-2d}{2d}. \quad (36)$$

Then, from eqns 30 and 36

$$a = \frac{2d-1}{2d}. \quad (37)$$

From eqns 34 and 36 we have

$$t = 1/2d. \quad (38)$$

From  $B \sim w^b$ ,  $B \sim 1/T$ , and eqn 38

$$b = -1/2d. \quad (39)$$

From eqns 33 and 38

$$h = 1. \quad (40)$$

## 4.2 Additional allometries

The results from eqns 32 and 36 to 40 provide us with the basic allometric exponents from which we can obtain the exponents of other body mass allometries. Because the population density scale as  $N \sim w^{(1-2d)/2d}$  [eqn 36], and because the metabolic rate per unit body mass scale as  $B \sim w^{-1/2d}$  [eqn 39], we have that the energy that is metabolized per population ( $U$ ) is body mass invariant, i.e.

$$U = NBw \sim w^{(1-2d)/2d} w^{-1/2d} w^1 \sim w^0, \quad (41)$$

and that the biomass ( $BM$ ) of the consumer organism will scale as

$$BM = Nw \sim w^{(1-2d)/2d} w^1 \sim w^{1/2d}. \quad (42)$$

Lifetime reproduction is maximal (i.e.,  $R = R_m$ ) at the limit  $E \rightarrow E_m$ ,  $f \rightarrow 1$ , and  $g \rightarrow 1$ . This implies that  $R_m = T\alpha E_m/w$  and that it will scale as

$$R_m \sim T\alpha/w \sim w^{1/2d+(2d-1)/2d-1} \sim w^0. \quad (43)$$

Then, the maximal rate of increase in the population density will scale as

$$r_m = \ln(pR_m)/T \sim w^{-1/2d}. \quad (44)$$

Sociality has been defined as the “state of group formation when members of a population . . . have markedly overlapping home ranges” (Armitage 1981). Hence, Armitage’s sociality index ( $S$ ) is given by the home range overlap

$$S \sim HN \sim w^1 w^{(1-2d)/2d} \sim w^{1/2d}. \quad (45)$$

In Table 2 the deduced exponents are summarized for organisms that forage in 1, 2, 3 and  $d$  spatial dimensions.

## 5 Empirical evidence

Empirically, it is the allometric relationship between the metabolic rate and body mass that has been studied in most detail. Table 3 lists the empirical exponents for

Group	2D	3D
Deduced	0.75	0.83
Mammals <sup>1</sup>	0.74 ± 0.01	
Bats <sup>2</sup>	0.74	
Birds <sup>3</sup>	0.74 ± 0.01	
Reptiles <sup>4</sup>	0.76 ± 0.02	
Snakes <sup>5</sup>	0.74 ± 0.04	
Lizards <sup>6</sup>		0.82 ± 0.02
Turtles <sup>7</sup>		0.86 ± 0.03
Amphibians <sup>8</sup>	0.77	
Frogs <sup>9</sup>	0.71	
Salamanders <sup>10</sup>		0.82 ± 0.02
Freshwater fishes <sup>11</sup>		0.81 ± 0.01
Marine fishes <sup>11</sup>		0.79 ± 0.01
Lampreys <sup>8</sup>		0.81
Lancelets <sup>8</sup>		0.91

Table 3: The exponents for the allometric relation between the metabolic rate and body mass as estimated for mobile chordates by linear regression on double logarithm scale. The estimated exponents are grouped according to whether they resemble the exponent deduced for organisms that forage in two (2D) or three (3D) dimensions.<sup>1</sup>Stahl (1967).<sup>2</sup>McNab (1969) and Konoplev et al. (1978).<sup>3</sup>Calder (1974).<sup>4</sup>Kayser & Heusner (1964), Bennett & Dawson (1976), and Zotin & Konoplev (1978).<sup>5</sup>Bennett & Dawson (1976).<sup>6</sup>Bennett & Dawson (1976) and Bartholomew & Tucker (1964).<sup>7</sup>Bennett & Dawson (1976) and Kayser & Heusner (1964).<sup>8</sup>Zotin & Konoplev (1978).<sup>9</sup>Hutchinson et al. (1968).<sup>10</sup>Whitford & Hutchinson (1967) and Feder (1976).<sup>11</sup>Winberg (1960).

total metabolic rate ( $wB$ ) for a variety of mobile chordates, as estimated by linear regression in double logarithmic scale. The estimated exponents are grouped according to whether they resemble the exponent deduced for organisms that forage in two or three dimensions. The metabolic exponents for almost all terrestrial taxa resemble the theoretic deduction for foraging in two dimensions. To the contrary, the metabolic exponents for all pelagic taxa resemble the theoretic deduction for foraging in three dimensions. This overall separation is likely to reflect the fact that for most terrestrial vertebrates foraging and intra-population interference are constrained to occur in the two horizontal dimensions, while pelagic organisms have an extra vertical dimension in which to forage and interact. This partitioning is present also between the terrestrial versus pelagic mammals. Among 40 species of pelagic mammals (taxa *Cetacea*, *Pinnipedia*, and *Sirenia*) the exponent for maximal lifespan is  $0.16 \pm 0.02$  while the same exponent is  $0.25 \pm 0.04$  among 195 species of terrestrial mammals (data from Nowak 1991).

From Table 3 we notice that the metabolic exponents

for bats and birds, which move freely in the vertical dimension, resemble the theoretic deduction for foraging in two dimensions. This resemblance is probably because of the fact that the foraging of most birds, and probably also of most bats, occurs in a relatively thin vertical layer where the movements in the two horizontal dimensions is considerably larger than the movements in the vertical dimension. Furthermore, intrapopulation interference in form of territorial behavior is predominately horizontal in birds. Thus, the true dimensionality of these systems may be close to two, although the organisms can move in three dimensions.

The metabolic exponent for frogs resembles the theoretical exponent for foraging in two dimensions, while the metabolic exponent for salamanders resembles the theoretical exponent for foraging in three dimensions. This separation may arise because many salamanders are more dependent upon ponds and lakes than are many frogs. Likewise, many turtles are more dependent upon ponds, lakes and rivers than are snakes. The observed exponent for turtles resembles three dimensions while the observed exponent for snakes resembles two dimensions. At present it remains unclear why the metabolic exponent of lizards apparently conforms to a three dimensional system.

Most of the metabolic exponents that have been estimated for invertebrates lie between 0.71 and 0.85 (reviewed in Peters 1983) as expected for organisms that forage in either two or three dimensions. Metabolic exponents that resemble a two dimensional system have been found for terrestrial taxa such as insects (0.76 by Zotin and Konoplev 1978), moths (0.78 by Bartholomew and Casey 1978) and spiders (0.71 by Greenstone and Bennett 1980), while metabolic exponents that resemble the three dimensional picture have been found for pelagic taxa such as unicells ( $0.83 \pm 0.06$  by Robinson et al. 1983) and unicellular algae ( $0.90 \pm 0.06$  by Banse 1976).

Of any group of organisms it is the terrestrial vertebrates that have been subjected to the far most detailed allometric studies. The estimated exponents from some of these studies are listed in Table 4 together with the deduced exponents for a two-dimensional system. From this table it can be concluded that for all studied allometric traits a reasonable resemblance exist between the deduced and the observed allometric exponents.

The deduced exponents are based on the assumption that interactions among the individuals of the involved species are insignificant. This assumption is expected to be fulfilled for the empirical exponents in the present study, because these exponents have been estimated at geographic scales above communities and

Trait	2D	Mammals	Reptiles	Birds
<i>B</i>	-0.25	-0.26 <sup>1</sup> 349	-0.24 <sup>4</sup> 128	-0.26 <sup>7</sup> 130
<i>T</i>	0.25	0.25 <sup>2</sup> 235	- -	0.18 <sup>8</sup> 242
<i>N</i>	-0.75	-0.78 <sup>3</sup> 467	-0.7 <sup>5</sup> 11	-0.75 <sup>9</sup> 147
<i>H</i>	1	0.99 <sup>2</sup> 125	0.95 <sup>6</sup> 29	1.16 <sup>10</sup> 75
<i>U</i>	0	-0.08 <sup>3</sup> 63	- -	- -
<i>S</i>	0.25	0.22 <sup>2</sup> 210	- -	- -
<i>R<sub>m</sub></i>	0	-0.03 <sup>2</sup> 96	- -	0.00 <sup>8</sup> 221
<i>r<sub>m</sub></i>	-0.25	-0.27 <sup>2</sup> 174	- -	-0.14 <sup>8</sup> 221

Table 4: The deduced (2D) and estimated exponents for the body mass allometries for terrestrial vertebrates. *B*: metabolic rate per unit body mass. *T*: lifespan. *N*: population density. *H*: home range area. *U*: population energy use. *S*: Armitage's sociality index. *R<sub>m</sub>*: maximal lifetime reproduction. *r<sub>m</sub>*: maximal rate of population increase. The empirical exponents are estimated by linear regression on double logarithmic scale, and the numbers below the exponents are the number species considered. <sup>1</sup>Stahl (1967). <sup>2</sup>Data from Nowak (1991). <sup>3</sup>Damuth (1987). <sup>4</sup>Kayser & Heusner (1964), Bennett & Dawson (1976), and Zotin & Konoplev (1978). <sup>5</sup>Peters (1983). <sup>6</sup>Turner et al. (1969). <sup>7</sup>Zar (1969). <sup>8</sup>Data from Cramp & Simmons (1977–1983), Cramp (1985–1992), and Cramp & Perrins (1993). <sup>9</sup>Nee et al. (1991). <sup>10</sup>Schoener (1968).

among species independently of competitive guilds. In comparison, when the allometric exponents are empirically established at smaller scales, as within competitive guilds, deviations have been found from the exponents listed in the present study. For example, within the genera and tribes of British birds Nee et al. (1991) found a positive exponent for the population density allometry, whereas the exponent decreased to the expected  $-3/4$  when the same species were compared across larger taxonomic units.

**Acknowledgements** I am grateful to Lev R. Ginzburg for stimulating discussions and to Volker Loeschke, Koos Boomsma and anonymous referees for helpful comments on various manuscripts. The study was first submitted for publication on the 2 February 1994, and it was financed by a Ph.D. stipend from the Faculty of Natural Science, University of Aarhus.

## References

- Armitage K. B. (1981). Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–49.
- Banse K. (1976). Rates of growth, respiration, and photosynthesis of unicellular algae as related to cell size - a review. *Journal of Phycology* 12:135–140.
- Bartholomew G. A. Casey T. M. (1978). Oxygen consumption of moths during rest, pre-flight warm up, and flight in relation to body size and wing morphology. *Journal of Experimental Biology* 76:11–25.
- Bartholomew G. A. Tucker V. A. (1964). Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Physiological Zoology* 27:341–354.
- Bell G. (1980). The cost of reproduction and their consequences. *The American Naturalist* 110:57–77.
- Bennett A. F. Dawson W. R. (1976). Metabolism. In: Gans V. C. Dawson W. R. (eds). *Biology of the Reptilia*: Academic Press, New York, volume V, pp 127–223.
- Blum J. J. (1977). On the geometry of four-dimensions and the relationship between metabolism and body mass. *Journal of Theoretical Biology* 64:599–601.
- Bonner J. T. (1965). *Size and cycle*. Princeton University Press, Princeton.
- Brody S. (1945). *Bioenergetics and growth*. Hafner, New York.
- Calder W. A. I. (1974). Consequences of body size for avian energetics. In: Paynter R. A. (ed). *Avian Energetics*: Nuttall Ornithological Club, Cambridge, pp 86–151.
- Calder W. A. I. (1984). *Size, function, and life history*. Harvard University Press, Cambridge.
- Charnov E. L. (1993). *Life history invariants. Some explorations of symmetry in evolutionary ecology*. Oxford University Press, New York.
- Clarke J. M. Maynard Smith J. (1961a). Independence of temperature of the rate of aging in *Drosophila subobscura*. *Nature* 190:1027–1028.
- Clarke J. M. Maynard Smith J. (1961b). Two phases of aging in *Drosophila subobscura*. *Journal of Experimental Biology* 38:679–684.
- Cramp S. (1985, 1988, & 1992). *Handbook of the birds of Europe the middle east and north africa. The birds of the western palearctic volume IV-VI*. Oxford University Press, Oxford.
- Cramp S. Perrins C. M. (1993). *Handbook of the birds of Europe the middle east and north africa. The birds of the western palearctic volume VII*. Oxford University Press, Oxford.
- Cramp S. Simmons K. E. L. (1977, 1980, & 1983). *Handbook of the birds of Europe the middle east and north africa. The birds of the western palearctic volume I-III*. Oxford University Press, Oxford.
- Damuth J. (1981). Population density and body size in mammals. *Nature* 290:699–700.
- Damuth J. (1987). Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biological Journal of the Linnean Society* 31:193–246.
- Feder M. E. (1976). Oxygen consumption and body temperature in neotropical and temperature zone lungless salamanders (*Amphibia: Plethodontidae*). *Journal of Comparative Physiology* 110:197–208.
- Fenchel T. (1974). Intrinsic rate of natural increase: The relationship with body size. *Oecologia* 14:317–326.
- Garland T. (1983). Scaling the ecological cost of transport to body mass in terrestrial mammals. *The American Naturalist* 121:571–587.
- Greenstone M. H. Bennett A. F. (1980). Foraging strategy and metabolic rate in spiders. *Ecology* 61:1255–1259.
- Harestad A. S. Bunnell F. L. (1979). Home range and body weight - a re-evaluation. *Ecology* 60:389–402.
- Hutchinson V. H., Whitford W. G., Kohl M. (1968). Relation of body size and surface area to gas exchange in anurans. *Physiological Zoology* 41:65–85.
- Kayser C. Heusner A. (1964). Etude comparative du métabolisme énergétique dans la série animale. *Journal of Physiology (Paris)* 56:489–524.
- Kleiber M. (1932). Body size and metabolism. *Hilgardia* 6:315–353.
- Konoplev V. A., Sokolov V. E., Zotin A. L. (1978). Criterion of orderliness and some problems of taxonomy. In: Lamprecht I. Zotin A. L. (eds). *Thermodynamics of Biological Processes*: deGruyter, Berlin, pp 349–359.
- LaBarbera M. (1986). The evolution and ecology of body size. In: Raup D. M. Jablonski D. (eds). *Patterns and processes in the history of life*: Springer-Verlag, Berlin, pp 69–98.
- Maynard Smith J. (1958). The effects of temperature and of egg-laying on the longevity of *Drosophila subobscura*. *Journal of Experimental Biology* 35:832–842.
- Maynard Smith J. (1963). Temperature and the rate of aging in poikilotherms. *Nature* 199:400–402.
- McMahon T. A. (1973). Size and shape in biology. *Science* 179:1201–1204.
- McMahon T. A. (1975). Allometry and biomechanics: limb bones in adult ungulates. *The American Naturalist* 109:547–563.
- McNab B. K. (1969). The economics of temperature regulation in neotropical bats. *Comparative Biochemical Physiology* 32:227–348.
- Nee S., Read A. F., Greenwood J. J. D., Harvey P. H. (1991). The relationship between abundance and body size in British birds. *Nature* 351:312–313.
- Nowak R. M. (1991). *Walker's mammals of the world volume I-II*. 5th edn. The Johns Hopkins University Press, Baltimore.
- Pearl R. (1928). *The rate of living*. Alfred A. Knopf, New York.
- Peters R. H. (1983). The ecological implication of body size.

- Cambridge University Press, Cambridge.
- Reiss M. J. (1989). *The allometry of growth and reproduction*. Cambridge University Press, Cambridge.
- Robinson W. R., Peters R. H., Zimmermann J. (1983). The effects of body size and temperature on metabolic rate of organisms. *Canadian Journal of Zoology* 61:281–288.
- Roff D. A. (1981). On being the right size. *The American Naturalist* 118:405–422.
- Rose M. R. (1991). *Evolutionary biology of aging*. Oxford University Press, New York.
- Rubner M. (1883). Über den einfluss der körper grosse auf stoff-und kraft-wechsel. *Z. Biol.* 19:535–562.
- Schoener T. W. (1968). Sizes of feeding territories among birds. *Ecology* 49:123–131.
- Stahl W. R. (1967). Scaling of respiratory variables in mammals. *J. A. Physiol.* 22:453–460.
- Stearns S. C. (1992). *The evolution of life histories*. Oxford University Press, Oxford.
- Turner F. B., Jennrich R. I., Weintraub J. D. (1969). Home range and body size of lizards. *Ecology* 50:1076–1081.
- Whitford W. G., Hutchinson V. H. (1967). Body size and metabolic rate in salamanders. *Physiological Zoology* 40:127–133.
- Winberg G. G. (1960). Rate of metabolism and food requirement of fishes. Fisheries Research Board Translation Services 194.
- Zar J. H. (1969). The use of the allometric model for avian standard metabolism-body weight relationships. *Comparative Biochemical Physiology* 29:227–234.
- Zotin A. I., Konoplev V. A. (1978). Direction of the evolutionary progress of organisms. In: Lamprecht I., Zotin A. I. (eds). *Thermodynamics of Biological Processes*: deGruyter, Berlin, pp 341–347.