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Density-dependent invariance, dimensionless life histories and the energy-equivalence rule

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ABSTRACT

It is suggested that Damuth's 'energy-equivalence rule' for mammal populations follows from a particular population dynamics invariance rule, one which leads to similar population dynamics when various species are viewed in a particular density and rate-of-change space.

Keywords: allometry, density independence, juvenile survival, macroecology, mammals.

Across mammal species, mean *adult* population densities (N_i) decline with *adult* body mass (W_i), while energy use by an individual scales as $W^{0.75}$, so that the rate of energy use per unit area by the *adult* population ($N \cdot W^{0.75} = C$) is independent of species body mass (Damuth, 1981, 1987, 1993; Fig. 1); this has been referred to as the 'energy-equivalence rule'. Although log plots of N versus W show substantial variation in log C , the slope approximates -0.75 and the range in log W is two to three times the range in log C (Fig. 1). We think it important that the energy-equivalence rule refers to *adult population density*; this suggests that, across mammal species, there exists an even more basic 'population dynamics' invariance rule. We hypothesize that survival of immatures to adulthood is negatively related to *adult* density, so that plots of juvenile survival versus $N_i \cdot W_i^{0.75}$ are *similar for all mammal species*. In this note, we show how this density-dependence-invariance across species leads easily to a limited range of C values that do not show any trend with body size (Fig. 1). Birds may obey a slightly different energy-equivalence rule (Maurer and Brown, 1988) and the theory developed here uses *that* rule to suggest how mammals and birds (may) differ in the operation of density dependence.

Although we have not been able to test the theory, the elegance of the scheme and the universal meaning it attaches to $N \cdot W^{0.75}$ are reason enough to take it seriously and we hope to stimulate further investigations.

Consider a life history characterized by age-independent fecundity of b daughters per year and an average adult lifespan of E . Alpha (a) is the age of first birth, measured with respect to age zero at independence from the mother; S proportion of these independent offspring survive to breed. This life history (Charnov, 1991) approximates that of mammals

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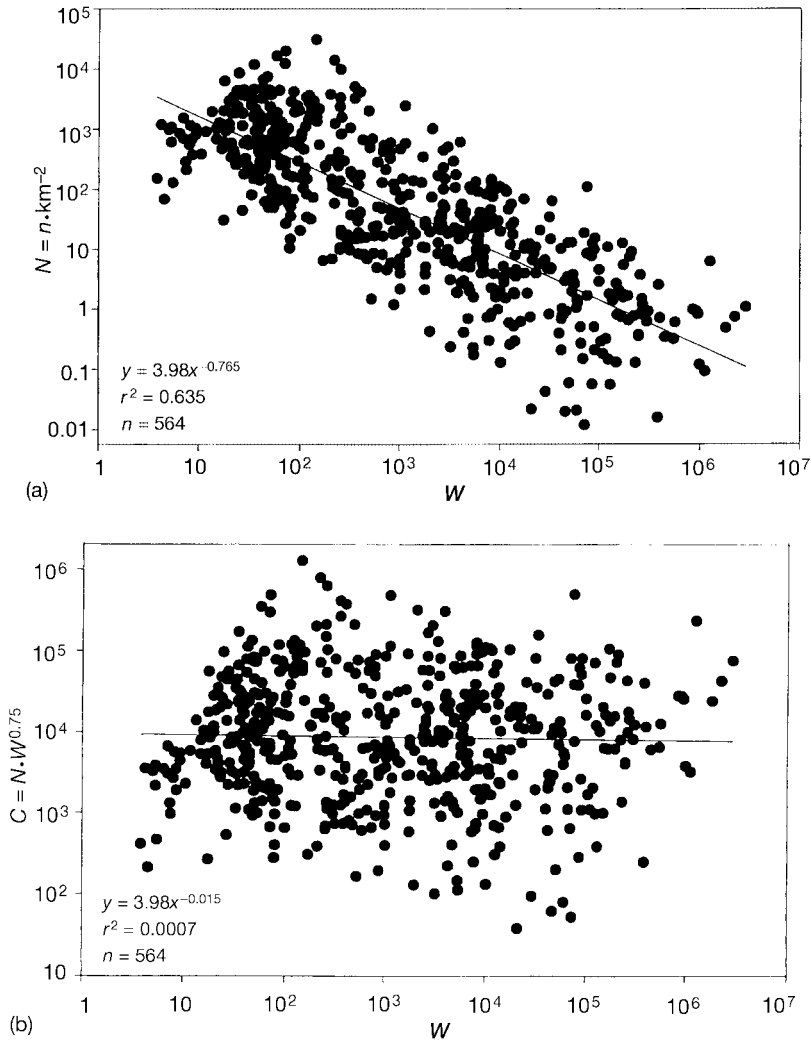


Fig. 1. The relationships between mass (W) and (a) population density (N) and (b) population energy use per unit area ($N \cdot W^{0.75} = C$) as shown by Damuth (1981, 1987, 1993). Redrawn using the data from Damuth (1993), available at http://eteweb.lscf.ucsb.edu/pub_datasets/Damuth.Nature.93.html.

and birds, and has the average number of surviving daughters produced over the mother's life (R_0) equal to the number of daughters (b) times average adult lifespan times the proportion of daughters surviving to age a (S); or $R_0 = b \cdot E \cdot S$ (eqn 1 in Charnov, 1997). $R_0 > 1$ for growing populations and $R_0 = 1$ at the equilibrium population size when a female just replaces herself.

R_0 can be rewritten as $R_0 = (S)(a \cdot b)(E/a)$ (eqn 2). Interestingly, the three dimensionless numbers (S , $a \cdot b$ and E/a) are independent of adult body size (W_i) in mammals (presumably measured in equilibrium populations; Charnov, 1993; Purvis and Harvey, 1995). Two of them ($a \cdot b$, E/a) are also probably independent of population density; this claim is

supported by studies of density dependence in mammals that suggest increasing population density negatively impacts S the most strongly (and consistently) of all life-history parameters (Fowler, 1981, 1988). Suppose, as suggested elsewhere (Charnov, 1993), *only* S is affected by population density; we assume that the survival of an immature to adulthood declines with the amount of production already captured by the adults (i.e. $N_i \cdot W_i^{0.75}$). Figure 2a has S_i declining with $N_i \cdot W_i^{0.75}$ and assumes that $b \cdot E$ is independent of population density (N) and adult body mass (W). $S = 1/(b \cdot E)$ at equilibrium, when $R_0 = 1$; it is clear that similar $N \cdot W^{0.75}$ across species follows from similar S versus $N_i \cdot W_i^{0.75}$ curves among the species. The equilibrium ($S = (a \cdot b \cdot E/a)^{-1}$) is displayed in a different way in Fig. 2b, where we plot $S \cdot a \cdot b$ versus $N \cdot W^{0.75}$ and find where it intersects the (a/E) line, again taken to be independent of $N \cdot W^{0.75}$ (as discussed above). This plot would be useful if density dependence affects b as well as S , since here $b \cdot E$ would not be independent of population density. In Appendix 1, we show how Fig. 2 implies a general rule for how the intrinsic rate of increase is expected to change with $N \cdot W^{0.75}$ within a species. In Appendix 2, we review data from small mammals that suggest how we may begin to estimate the dependence of S on population density.

Figure 3 results if the species differ somewhat in S curves and in $b \cdot E$ numbers (or the $a \cdot b \cdot S$ curves and a/E numbers); note that this variation generates variation in the equilibrium $N_i \cdot W_i^{0.75}$ ($= C$) values. Figure 3 may be used to derive predictions as to how C

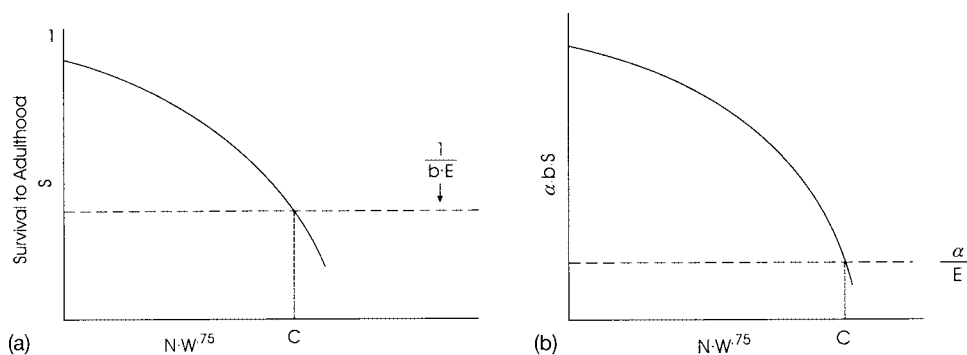


Fig. 2a. The survival (S) of a female offspring from independence to the age of first reproduction (a) is assumed to be negatively related to adult density measured as the ‘production captured’ by the adult population ($N \cdot W^{0.75}$). The equilibrium is C , where S crosses the $1/(b \cdot E)$ line; $b \cdot E$ is the average number of female offspring produced over a mother’s reproductive life. $b \cdot E$ is independent of adult body size in mammals and is most probably independent of population density (see citations in text). Equal C values among species follows from the same $b \cdot E$ number, and the same decline of S with $N \cdot W^{0.75}$. Since $\partial S/\partial(N \cdot W^{0.75})$ is the same for all species, $\partial S/\partial N \propto W^{0.75}$, where S and N are at the equilibrium.

Fig. 2b. The input to the adult population ($a \cdot b \cdot S$) is negatively related to the production captured by the adults ($N \cdot W^{0.75}$); the equilibrium (C) will be where the descending curve ($a \cdot b \cdot S$) crosses the a/E lines (see equation 2). $a \cdot b \cdot S$ is the recruitment to the adult population in a units of time, while a/E is the adult ‘mortality rate’ in a units of time. a/E is likely body size and density-independent within mammals; $a \cdot b \cdot S$ is independent of body size. This plot is particularly useful when density dependence affects b as well as S . Since equation (2) is true for *any* age-structured life history (Charnov, 1997), this plot is also useful for species (other than birds and mammals) where $b \cdot E$ is not an invariant with body size but a/E is (Charnov, 1993).

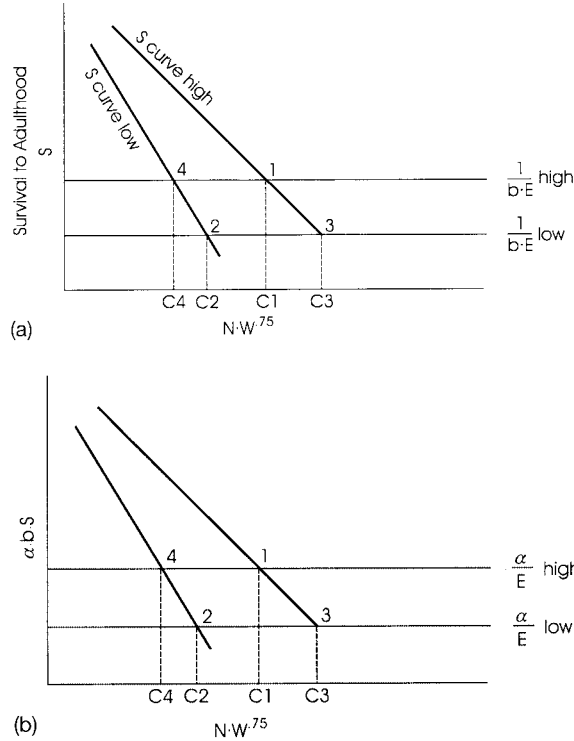


Fig. 3a. If mammal species vary in $b \cdot E$ and/or the declining S curves, there will be variation in the C values; if the height of the S curve is negatively correlated with the height of the $1/(b \cdot E)$ line, the highest (lowest) C values will be associated with the lowest (highest) $1/(b \cdot E)$ numbers, and the equilibria will be at 3 and 4. In this case, C will correlate positively with $b \cdot E$. However, if high (low) S curves are always associated with high (low) $1/(b \cdot E)$ lines, the equilibria will be at 1 and 2 and C will correlate negatively with $b \cdot E$.

Fig. 3b. Variation in a/E and/or the declining $a \cdot b \cdot S$ curves will lead to variation in C among species. See discussion to Fig. 3a for when C is expected to correlate positively, or negatively, with the a/E numbers.

will correlate with $b \cdot E$ and E/a across species. To illustrate, consider Fig. 3a and assume we cannot observe the declining S curves and can only measure the $b \cdot E$ numbers and the C values across species. If the high S curve is associated with the high $1/(b \cdot E)$, the equilibrium C will be at C_1 . And if the low S curve is associated with the low $1/(b \cdot E)$ number, the equilibrium for that species will be at C_2 . For this situation, a plot of C versus $b \cdot E$ will be *negative*; high C_1 will go with low $b \cdot E$, low C_2 will go with high $b \cdot E$. But suppose the high S curve is associated with the low $1/(b \cdot E)$ number and the low S curve is associated with the high $1/(b \cdot E)$ number. Then the two equilibria will be at C_3 and C_4 . For this case, a plot of C versus $b \cdot E$ will be *positive*; high C_3 with high $b \cdot E$ and low C_4 with low $b \cdot E$, just the reverse of the previous situation. Of course, the same logic applies to Fig. 3b and the expected correlation between C and E/a . We have been unable to decide which of these cases appears more likely; in the absence of independent knowledge of how the heights of the S curves correlate across species with the values of the $b \cdot E$ (or E/a) numbers, we cannot say how

C is expected to correlate with $b \cdot E$ or E/a across species. (Of course, the absence of a correlation is also plausible!)

Although the theory seems difficult to test, we consider it worthwhile to ask how C correlates with $b \cdot E$ and E/a across mammal species. Figure 4 displays the Purvis and Harvey (1995) life table estimates of $b \cdot E$ (and E/a) combined with the data used in Damuth (1993; available from the Internet, see caption to Fig. 1) and Silva (from Brown, 1995), which give estimates of C for the 40 or so species where the three data sets overlap (Purvis and Harvey have life table data for about 65 species, while C values are available for several hundred species). The species and data are shown in Table 1. Unfortunately, the data set of Purvis and Harvey (1995) lacks species with low C values.

Figure 4a plots $b \cdot E$ versus C and finds no correlation for all the data; if we drop the one outlier in the top right-hand corner, the correlation is significant at the 0.02 level (two-tailed test), but r^2 is only 0.12. This is weak evidence for the equilibria being C_1 and C_2 in Fig. 3a. Figure 4b plots E/a versus C and finds a weak ($r^2 = 0.09$), if significant ($P \approx 0.06$), positive relation. If the theory is correct, plot 4b rules out a strong, positive correlation between the height of the $a \cdot b \cdot S$ curve and the height of the a/E line. Clearly, Fig. 4 does not provide strong support for any particular correlation structure between the S curves and the $b \cdot E$ or E/a numbers.

The mammal energy-equivalence rule is one of macroecology's most enduring yet least explored patterns (Brown, 1995). This paper proposes that it results from a deeper symmetry for mammalian population dynamics; adult mammals impact their own offspring survival (S) (or offspring production, $a \cdot b \cdot S$) in the same density-dependent way, when adult density is measured in units of adult energy use, $N \cdot W^{0.75}$. The declining S functions may well vary somewhat with factors such as energy availability to the organism and other features of natural history; in this way, the C values could similarly be correlated with the same factors. For example, C values are higher for herbivores than carnivores (Damuth, 1987). It is probably worthwhile to note that sharing the same S and $b \cdot E$ relations leads to a new between-species life-history allometry (Fig. 2a); $\partial S / \partial N \propto W^{0.75}$ at the population equilibrium. $\partial S / \partial N$ may be called the 'strength of density dependence'.

After its original presentation by Damuth (1981, 1987), the empirical pattern of the energy-equivalence rule relationship between body size and population energy use (Fig. 1)

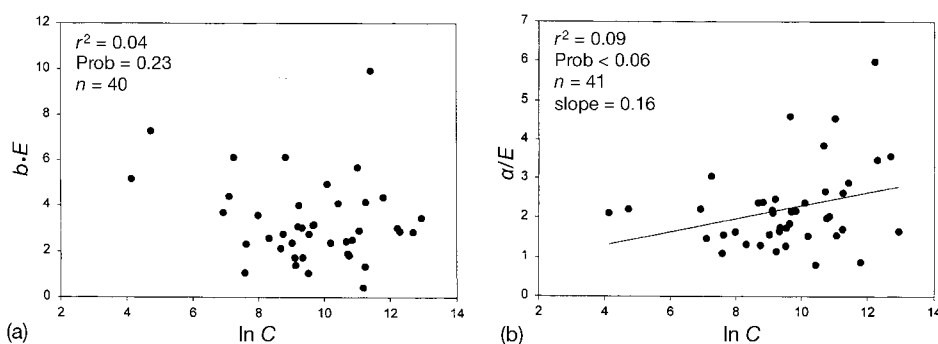


Fig. 4. The relationships between (a) $b \cdot E$ and C and (b) a/E and C . Life-history data obtained from Purvis and Harvey (1995). Energy values are from Damuth (1993), available at http://eteweb.lscf.ucsb.edu/pub_datasets/Damuth.Nature.93.html, and Silva (from Brown, 1995).

Table 1. Data used in Fig. 4 obtained from Purvis and Harvey (1995). Energy values were provided by Damuth (see Fig. 1) and Silva (from Brown, 1995)

	<i>b</i>	<i>E</i>	Alpha	<i>C</i>
<i>Aepyceros melampus</i>	0.45	4.17	1.58	10.72
<i>Ailuropoda melanoleuca</i>	0.55	4.17	2.7	7.62
<i>Alces alces</i>	0.47	3.62	2.1	9.35
<i>Alopex lagopus</i>	4.68	1.52	0.71	4.72
<i>Apodemus flavicollis</i>	8.59	0.28	0.18	9.54
<i>Canis lupus</i>	2.79	1.81	0.88	4.13
<i>Capreolus capreolus</i>		2.98	1.63	9.64
<i>Cervus elaphus</i>	0.41	4.39	2.24	10.76
<i>Clethrionomys glareolus</i>	8.24	0.3	0.1	12.29
<i>Damaliscus lunatus</i>	0.28	1.49		11.18
<i>Equus burchelli</i>	0.29	8.33	2.18	10.67
<i>Erinaceus europaeus</i>	3.87	2.53	0.89	11.42
<i>Felis catus</i>	3.52	1.21	0.85	7.1
<i>Hippopotamus amphibius</i>	0.17	16.67	4.68	12.69
<i>Kobus ellipsiprymnus</i>	0.56	5.56	1.22	9.66
<i>Kobus kob</i>	0.65	2.6	1.22	9.11
<i>Loxodonta africana</i>	0.08	16.67	9.8	11.24
<i>Macaca sinica</i>	0.34	16.67	3.68	11.02
<i>Marmota flaviventris</i>	1.7	2.53	2.93	11.79
<i>Mephitis mephitis</i>	2.53	1.37	0.86	7.98
<i>Ochotona princeps</i>	2.73	1.77	0.77	10.1
<i>Odocoileus hemionus</i>	0.74	3.33	1.67	10.85
<i>Oryctolagus caniculus</i>	12.1	0.42	0.29	10.43
<i>Ovis dalli</i>	0.38	2.37	5.56	8.68
<i>Pan troglodytes</i>	0.1	13.89	6.6	9.13
<i>Peromyscus leucopus</i>		0.19	0.11	9.83
<i>Peromyscus maniculatus</i>	1.5	0.26	0.13	9.2
<i>Phacochoerus aethiopicus</i>	1	2.98	1.83	9.33
<i>Rangifer taradanus</i>	0.49	6.41	3.01	9.69
<i>Sciurus carolinensis</i>	2.38	1.7	0.67	11.26
<i>Spermophilus armatus</i>	2.22	1.52	0.94	12.94
<i>Sus scrofa</i>	2.16	1.81	1.62	9.23
<i>Sylvilagus floridanus</i>	8.84	0.65	0.29	8.83
<i>Syncerus caffer</i>	0.2	5.21	4.09	9.52
<i>Tachyoryctes splendens</i>	1.59	1.85	0.32	12.22
<i>Talpa europaea</i>	1.68	1.37	0.92	10.2
<i>Tamias striatus</i>	3.2	0.76	0.52	11.06
<i>Tamiasciurus hudsonicus</i>	1.57	1.46	0.96	9.02
<i>Taxidea taxus</i>	0.66	1.57	1.48	7.58
<i>Urocyon cinereoargenteus</i>	2.1	2.87	0.96	7.25
<i>Ursus americanus</i>	0.49	5.56	4.31	8.75
<i>Vulpes vulpes</i>	1.99	1.81	0.84	6.92
<i>Zapus hudsonius</i>	2.21		0.93	10.94
<i>Zapus princeps</i>	1.56	1.6	1.24	8.32

Note: *b* = daughters per year, *E* = average life expectancy (years), alpha = age of sexual maturity (years) and *C* = energy per hectare.

has received surprisingly little theoretical attention and has eluded a satisfying explanation (Brown, 1995; Ameberg *et al.*, 1998; Enquist *et al.*, 1998; Ritchie and Olff, 1999). Figures 2 and 3 display a balancing mechanism that produces approximately equal C values. Nothing in the mechanism we have proposed predicts the positions for the curves, although the E/a and $b \cdot E$ numbers may be predicted from evolutionary life-history theory (Charnov, 1991, 1993). However, the position of the S curve has not been predicted from anything more basic, at least not to date.

The population dynamics invoked here are very simple. Spatial and temporal variation are ignored. We are keenly aware that the population dynamics also ignore other stochastic factors such as extinction. Perhaps extinction probabilities are related to C values; for such a mechanism to produce approximately equal C across species would seem to require that the chance-of-extinction reach a minimum at (similar) C values that are independent of body size. We simply do not know if an *extinction symmetry* like this is realistic.

Finally, our mammal theory provides *reasons* why C may vary among species (Fig. 3), and so avoids a common pitfall in interpretation of this type of data (i.e. C is a constant); Fig. 1 shows substantial variation in C and merely says that the variation is uncorrelated with body size. Figure 3 would predict *this* if the *balancing curves* varied somewhat between species, but were uncorrelated with body size.

Birds (Maurer and Brown, 1988) appear to follow a different 'energy-equivalence rule': add together the population densities of the j species at body size i to get a total population density N_{iT} :

$$N_{iT} = \sum_j N_{ji}$$

Then, $N_{iT} \cdot W_i^{0.75} \approx C$, energy equivalence among *body size groupings*. For the arguments of Figs 2 and 3 to predict this equivalence, we must replace N_i with N_{iT} . It is plausible that birds (perhaps owing to the mobility of flight and the fact that the young are already of adult size at independence) interact to make immature survival in any single species a function of the impact density ($N_{iT}W^{0.75}$) of *all birds of similar size*, not just the single species, leaving us to wonder if mammals of the same body size sometimes also combine in this manner.

Our theory suggests a very general meaning for the quantity $N \cdot W^{0.75}$: the adult population resource utilization impacts juvenile recruitment in similar ways for all mammal species (Figs 2 and 3). This 'density-dependent invariance', if true, demonstrates how macroecological patterns can yield insights into more fundamental processes of nature.

ACKNOWLEDGEMENTS

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APPENDIX 1: INTRINSIC RATE OF INCREASE (r) VERSUS $N \cdot W^{0.75}$

The theory developed in Fig. 2b uses R_0 and the 'density-dependent invariance' is shown as $S \cdot a \cdot b$ versus $N \cdot W^{0.75}$. It may be very difficult to observe $a \cdot b \cdot S$ versus N . What we can observe is N through time; suppose we observe the percentage of change in N each year and can plot this versus N . Now the percentage of change in $N = dN/Ndt =$ intrinsic rate of increase (r).

For a life history with constant fecundity (b) and a constant adult instantaneous mortality rate of M (so $E = M^{-1}$), the intrinsic rate of increase (r) is given by (Charnov, 1993, p. 118):

$$e^{a \cdot r} \left(\frac{a}{E} + a \cdot r \right) - a \cdot b \cdot S = 0 \quad (\text{A1})$$

Note that species with the same $a \cdot b \cdot S$ and a/E will have the same $a \cdot r$ values. Thus, the (assumed) existence of the relation in Fig. 2b means that a plot of $a \cdot r$ versus $N \cdot W^{0.75}$ will be the same for all mammal species, as illustrated in Fig. A1.

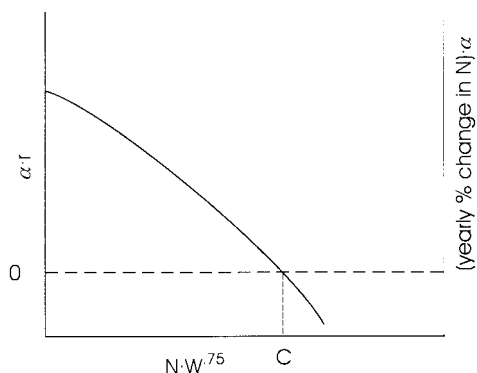


Fig. A1. The invariance rules of Figs 2a,b imply that the intrinsic rate of increase (r) multiplied by the age of first reproduction (a) will be the same for all mammal species when plotted against $N \cdot W^{0.75}$.

APPENDIX 2: S VERSUS $N \cdot W^{0.75}$?

Suppose that populations fluctuate around an equilibrium value with S declining with density as in Fig. 2a. Consider the intrinsic rate of increase ($a \cdot r$), measured in units of a , as given by equation (A1) of Appendix 1. $a \cdot b$ and a/E have been estimated for mammals to take on values 1.75 and 0.7, respectively (Charnov, 1993). If we put these numbers into equation (A1), we can plot $a \cdot r$ versus S ; Fig. A2 shows that, for $0.25 \leq S \leq 0.80$, the relation is *close to* linear with a slope of 1: $S \approx 0.42 + a \cdot r$. The population is not growing when $a \cdot r = 0$, or $S = 0.42$. This suggests that estimates of $a \cdot r$ estimate S directly. Table A1 summarizes an analysis of $a \cdot r$ versus $N \cdot W^{0.75}$ for seven rodent species each followed over approximately 20 years; the data are displayed in Fig. A3. All show a statistically significant decline in $a \cdot r$ with increasing $N \cdot W^{0.75}$ (see also Maurer, 1999). The regressions are not very strong, but they are consistently *negative*. Although we do not know that $a \cdot b$ and a/E are invariants for *these*

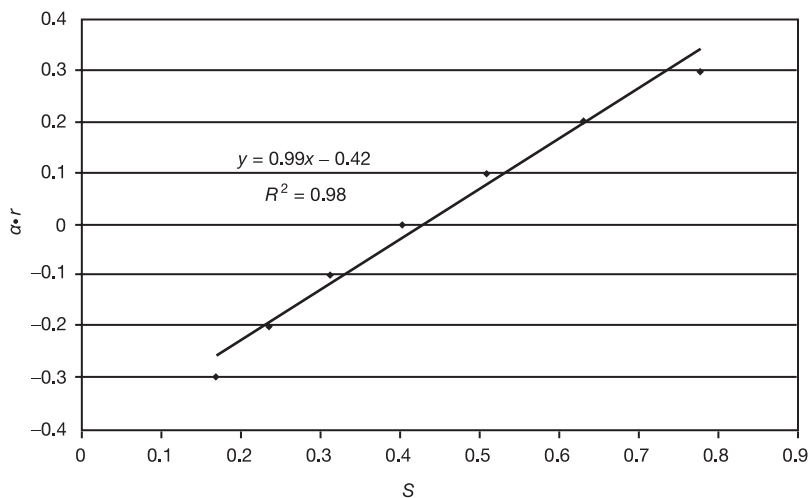


Fig. A2. The intrinsic rate of increase ($a \cdot r$) versus survival of immatures into adulthood (S), from equation (A1). The slightly non-linear relation is well fitted by the line for intermediate S values. $a/E = 0.7$, $a \cdot b = 1.75$.

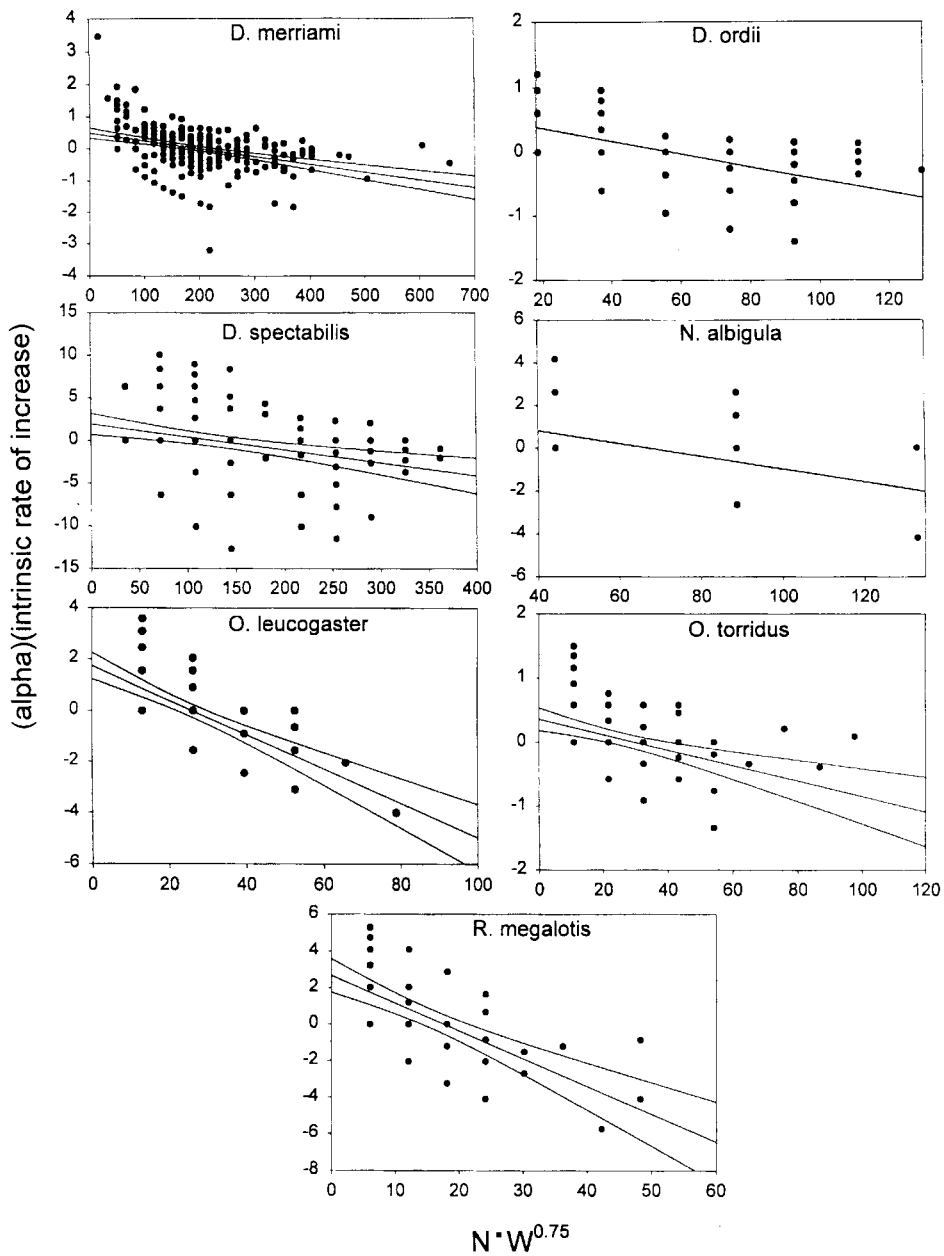


Fig. A3. Population dynamics for seven rodents (see text and Table A1).

species through time, it seems likely that S changes mostly in a density-dependent fashion (see discussion in Charnov, 1993); then, the equations of Table A1 give S versus $N \cdot W^{0.75}$ by the substitution of $S - 0.42$ for $a \cdot r$ (y in Table A1). All of the rodents are small-bodied (<200 g); it remains to be seen if plots like Fig. A3 for large-bodied mammals yield $a \cdot r$ (S) versus $N \cdot W^{0.75}$ relations that make the large-bodied species look similar to these small-bodied species.

Table A1. Results from linear regression of (alpha)(intrinsic rate of increase) onto $N \cdot W^{0.75}$ for seven species of rodents

Species	Mass (g)	Sample size	Equation	Equilibril C	P
<i>Dipodomys merriami</i>	43	261	$y = -0.002x + 0.50$	250	0.0001
<i>Dipodomys ordii</i>	49	162	$y = -0.01x + 0.57$	57	0.0001
<i>Dipodomys spectabilis</i>	120	127	$y = -0.01x + 1.89$	189	0.0001
<i>Neotoma albigula</i>	157	87	$y = -0.03x + 2.02$	67.3	0.0001
<i>Onychomys leucogaster</i>	31	82	$y = -0.06x + 1.61$	28.8	0.0001
<i>Onychomys torridus</i>	24	94	$y = -0.01x + 0.36$	36	0.0001
<i>Reithrodontomys megalotis</i>	11	54	$y = -0.14x + 2.44$	17.4	0.0001

Note: Population data for each species were obtained from the monthly census data from J.H. Brown's long-term site near Portal, Arizona in the Chihuahuan Desert. Intrinsic rate of increase was calculated using the equation:

$$R_i(t) = \frac{\ln N_i(t + \Delta t) - \ln N_i(t)}{\Delta t}$$

where $R_i(t)$ is the per capita rate of change of species i (Maurer, 1999). Although the data set included 261 monthly censuses, $R_i(t)$ can only be calculated when population size is not equal to 0, resulting in different sample sizes for each species. Age at sexual maturity (alpha) was corrected by age at weaning (obtained from Feldman, 1935; Svihla, 1936; Horner and Taylor, 1968; Hoffmeister, 1986; Nowak, 1999).