# 1
Reproductive strategies

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Natural populations of animals exhibit a bewildering variety of dynamic behaviour. For some species local abundance remains roughly unchanging, year after year. For example, in *The Natural History of Selborne* (arguably the first book on ecology, published in 1789), Gilbert White observed that the number of swifts flying around the church tower was approximately constant, at eight pairs, every year; the same number of swifts are to be found in Selborne in the summer today. The abundance of other species waxes and wanes (often by factors in excess of 10000) in well-defined cycles: such are the 4-year cycles in the numbers of mice, voles and lemmings in most northerly regions, the 10- to 11-year cycles in abundance of snowshoe hares and lynx and other predators in Canada, and the cycles in many insect pest species in temperate forests, with periods ranging from 5 to 12 years. Yet other natural populations exhibit irregular fluctuations, with episodes of outbreak or rarity often keyed to the weather: examples are the African desert locust, or the wasps on Gilbert White's fruit trees ('in 1781 we had none; in 1783 there were myriads'). Fig. 1.1 shows the variety of dynamic patterns exhibited by four vertebrate populations in Wytham Wood in England.

Fig. 1.1. Fluctuations in the numbers of total owls, territory-holding owls, bank voles and wood mice in Wytham Wood, 1949–52. (From T. R. E. Southwood. Bioeconomic strategies of population parameters. In *Theoretical Ecology*, pp. 26–68. Ed. R. M. May. Blackwell Scientific Publications; Oxford (1976).)
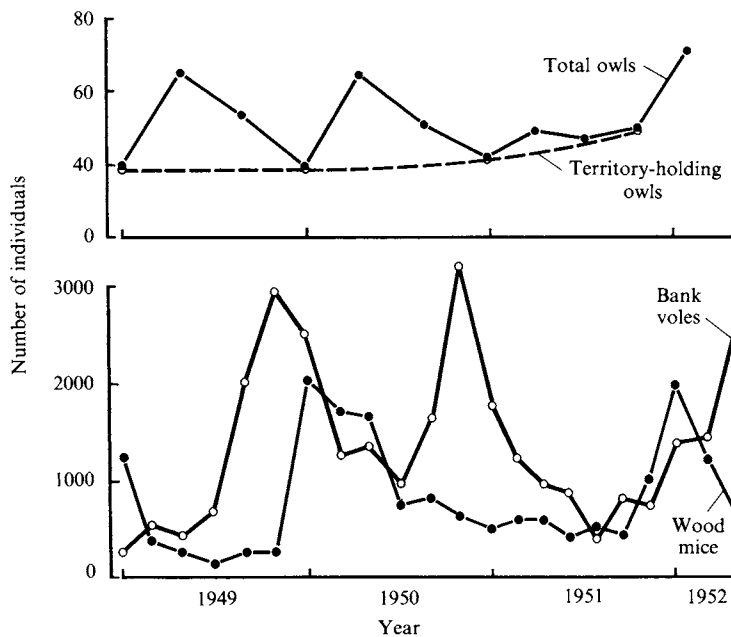
From Darwin's time to our own, much research has been directed towards codifying these patterns, and trying to understand them. In general, the overall dynamic behaviour of an animal population will depend on the character of the birth and death processes within it; these processes are forged – in an evolutionary 'furnace' – by the interactions between the population and its physical and biological environment. Thus, the reproductive biology of a mammalian species is ultimately entwined both with its evolutionary biology and with its population dynamics.

One crude generalization about the relation between a species' life-history strategy and its physical and biological setting invokes the deliberately oversimplified concept of r selection and K selection. The general ideas here were formulated by Darwin, Schmalhausen, Simpson, Stebbins and others, but it was MacArthur and Wilson who coined the phrase 'r and K selection', derived from the conventional parameters in the logistic equation, $dN/dt = rN(1 - N/K)$. This equation describes the familiar sigmoid curve of ultimately bounded population growth: at low population densities there is essentially pure exponential growth, at the rate r; at high densities the population tends to stabilize around a value K which is set by some 'environmental carrying capacity' (generally determined by biological factors, such as food supplies and/or interactions with competitors, mutualists, predators or parasites).

A K-selected organism sees its environment as relatively stable and predictable (and consequently the population is usually around its equilibrium values $N \simeq K$). This steady environment tends, however, to be biologically crowded with competitors (of the same and other species), predators and parasites. The evolutionary pressures on an organism in these circumstances are, crudely, to be a good parent and competitor, to increase the effective value of K, and to have fewer offspring but to invest more time and energy in raising them.

Conversely, an r-selected organism sees its environment as unstable and unpredictable (and is usually at low population values, growing exponentially, and undergoing episodes of boom and bust). The evolutionary pressures here are for opportunism, for large r to exploit the transient good times, and to have many offspring, few of which can expect to mature. For the r-selected organism, life is a lottery, and it makes sense simply to buy many tickets!

As emphasized above, the dichotomy of r selection versus K selection is a gross oversimplification, which deliberately polarizes what is, in fact, a complex continuum. Subject to this caveat, the ideas illuminate some of the broad trends among animal and plant species: between the r-selected insects and the K-selected mammals; between most fish (with their millions of eggs, and where next year's recruitment is roughly independent of this year's stock size) and marine mammals (where recruitment is explicitly dependent on stock size); between early successional weeds, and the trees and perennials of later successional stages. Also, as we shall see below,

they help explain interesting trends and patterns within a single taxonomic class, namely mammals.

The remainder of this chapter is organized as follows. In the next section, we explore general aspects of mammalian life-history strategies. The section begins with remarks about optimal strategies; goes on to document and discuss various correlations between birth rate, generation time and physical size in mammalian species. It then looks at the way average litter size varies systematically along certain environmental gradients and concludes by emphasizing various self-reinforcing tendencies among the factors involved in r and K selection. The third section deals with aspects of the timing of reproductive events: iteroparity versus semelparity (extended versus concentrated reproductive life), litter spacing, and marsupial versus eutherian mammals. The fourth section examines patterns in the care of young: weight of newborn infants relative to parental weight, altricial versus precocial young (slow versus fast maturing), and nursing periods.

Finally, we acknowledge that Darwinian selection acts to maximize an individual's genetic input into the next generation. This means we must pay attention not just to fecundity and survival, but also to sexual selection, and to social organization and behaviour (bearing in mind that your relatives carry your genes, proportionally to how closely related they are to you). Accordingly, the fifth section discusses mating systems and social groupings.

Size and life-history strategies

Optimal life-history strategies

The notion that an organism's life-history strategy – its patterns of mortality, fecundity and parental care – depends on its physical environment and on its interactions with other organisms dates back at least to Darwin and Wallace. Recent years, however, have seen the growth of a more quantitative approach to the subject, pioneered by Edward Deevy's demonstration in 1947 that data from natural populations of non-human animals could be used to construct actuarial tables of age-specific survivorship and fecundity, similar to those constructed by insurance companies for human populations.

The most interesting of these recent studies have emphasized that the number of offspring, and their chances of survival to maturity, depend on the amount of parental investment (for example, on the number and size of eggs, and on the amount of care, if any, given to offspring), and that this in turn influences the parent's survival probability. Thus, in any attempt to calculate optimum life-history strategies for particular environmental circumstances, it must be acknowledged that age-specific mortality and fecundity schedules are not independent, but are interwoven in a complicated way; the trade-off between reproduction and 'personal growth' made by an adult in any one year will affect its probability of

surviving that year, and thereby influence the possible trade-offs in all
future years.

Richard Southwood discusses the problem in a way that is particularly
simple and clear, yet which retains all the biological essentials. He invokes
an imaginary animal, the parthenogenetic block-fish which has a
productivity of two blocks each summer and one block each winter. The
two summer blocks can be added to the fish itself, or used in reproduction,
in any proportion (any fish that does not add to itself dies); the one winter
block is necessarily added to the fish itself. What is the optimal life-history
strategy for the block-fish? Obviously there is no unique answer, but rather
it depends on the environmental setting. Fig. 1.2 illustrates the genealogy
of two mutant strains of the block-fish: mutation 1 puts all its summer
productivity into reproduction; mutation 2 puts only half its summer
productivity into reproduction. If half the juvenile one-block fish are killed
by predators each year, mutation 2 does better. Conversely, if the carrying
capacity of the fish's environment is limited to a total of eight blocks,
mutation 1 is represented at the end of 3 years by many more individuals,
and is better placed to 'bounce back' from adverse environmental
fluctuations. Other assumptions could clearly be explored; for example,
block-fish over a certain size could exploit additional resources, or

Fig. 1.2. Results of two different resource allocation strategies in a hypothetical animal, the block-fish: (*a*) mutation 1, in which summer productivity is entirely devoted to reproduction (2 blocks); (*b*) mutation 2, in which half the summer productivity is devoted to reproduction (1 block) and half is devoted to growth (1 block) and, hence, to adult survival. (From T. R. E. Southwood. Bioeconomic strategies of population parameters. In *Theoretical Ecology*, pp. 26–48. Ed. R. M. May. Blackwell Scientific Publications; Oxford (1976).)
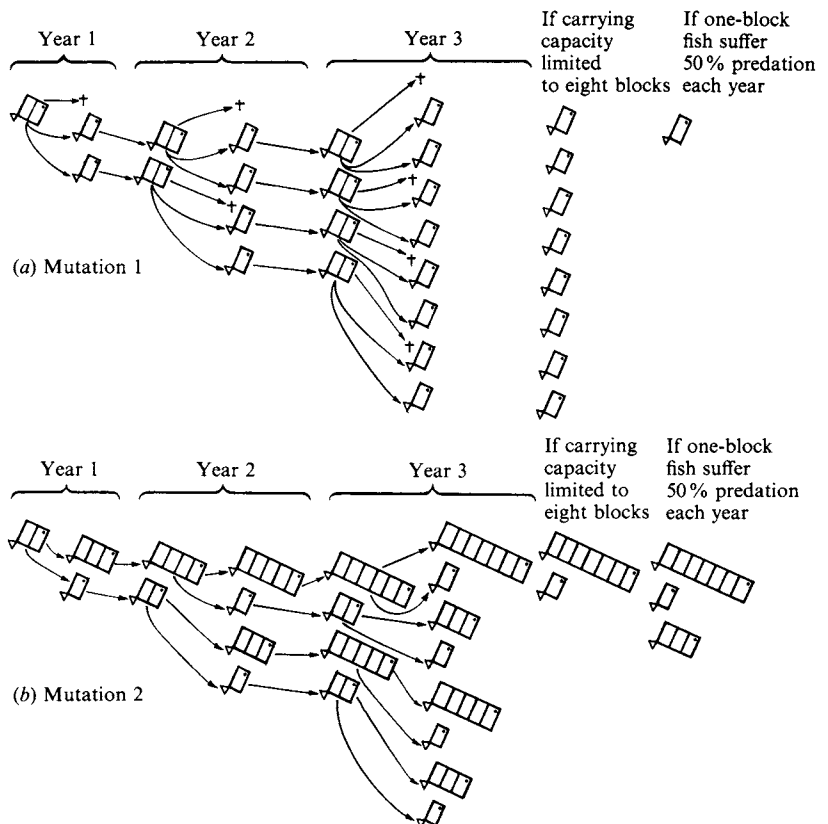
mortality could be higher or lower for larger block-fish, or the environmental carrying capacity could be subject to random variations.

Physical size and its implications

An organism's life-history strategy and other adaptations to its environment are not, however, infinitely maleable. Rather they are confined within broad bounds by the exigencies of developmental processes and mechanical constraints associated with the design of workable living machines. It simply is not possible to evolve a creature having the size of an elephant, yet attaining sexual maturity at the age of 3 months!

Some of these 'design constraints' are well understood, others less so. Thus, the mechanical scaling laws or 'allometries' (connecting quantities such as body weight, length, brain size, weight of offspring at birth) are well documented empirically and fairly well understood theoretically. On the other hand, the correlations between dynamic variables (life expectancy, age at sexual maturity, and the like) and physical variables (body weight, length), although demonstrated in many empirical surveys, lack a definitive explanation; they are likely to be associated with developmental processes, and with the fact that smaller creatures tend to have higher weight-specific metabolic rates, living more frenetic lives and thus 'wearing out' faster.

Fig. 1.3 shows John Bonner's computation of the roughly linear relationship between generation time and body length, which extends over

Fig. 1.3. Relationship between generation time and body length. (From J. T. Bonner. *Size and Cycle: an Essay on the Structure of Biology.* Princeton University Press (1965).)
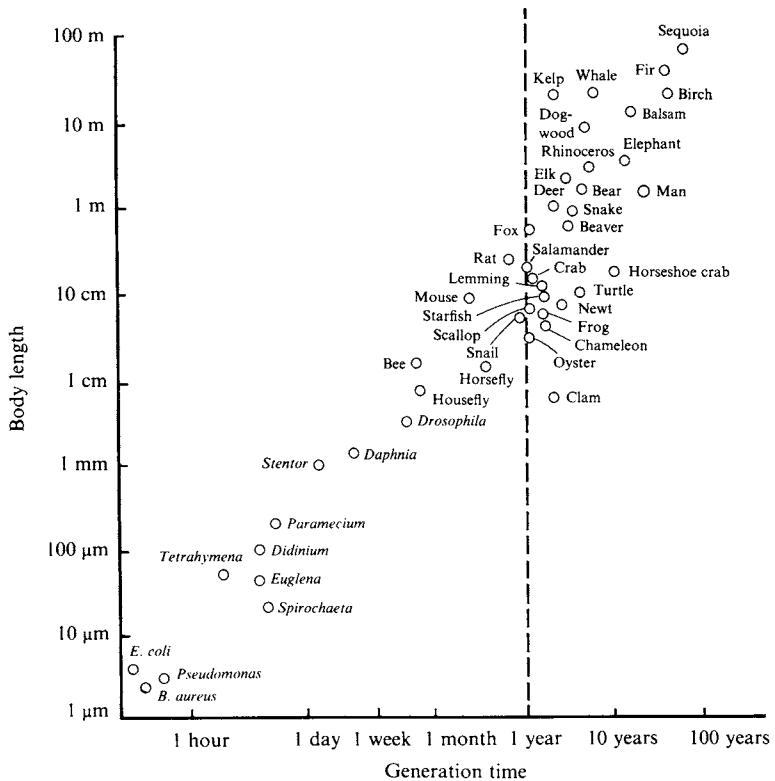
a wide range for an extraordinarily diverse array of organisms. This general relation continues to hold when the focus is narrowed to include only mammalian species. In particular, Western has studied data for African mammals, and has shown that dynamic quantities, such as age at first reproduction, T, are empirically related to body weight, W, by scaling laws of the form

$$T = aW^b. \tag{1.1}$$

Here a and b are constants, estimated as the intercept and the slope, respectively, of the regression line when the data points are displayed on a log–log plot. African mammals can be grouped into three broad taxonomic categories: artiodactyls (cloven-hoofed), primates and carnivores. Fig. 1.4 is typical, showing the relation between age at first reproduction and body weight for African artiodactyls; in Equation 1.1 here the exponent $b = 0.27$, and similar results exist for primates and carnivores (with $b = 0.32$ in both). The analysis made by one of us (D.I.R.) pulls together information for a larger, global assembly of some 180 mammalian species, grouped into ungulates (all hoofed animals), primates, small mammals and carnivores, a sample size considerably larger than Western's. Again, log–log plots of age at first reproduction against body weight yield statistically significant relations of the form of Equation 1.1 (with slopes of $b = 0.37$ for ungulates, $b = 0.41$ for primates, $b = 0.25$ for small mammals, and $b = 0.20$ for carnivores).

The 'allometric' scaling laws that connect various physical quantities – for example, body weight W and length L – in terrestrial vertebrates can be satisfactorily explained by structural mechanics. The essential message

Fig. 1.4. Relationship between age at first reproduction and body weight in African artiodactyls. (From D. Western. Size, life history and ecology in mammals. *African J. Ecol.* **17**, 185–205 (1979).)
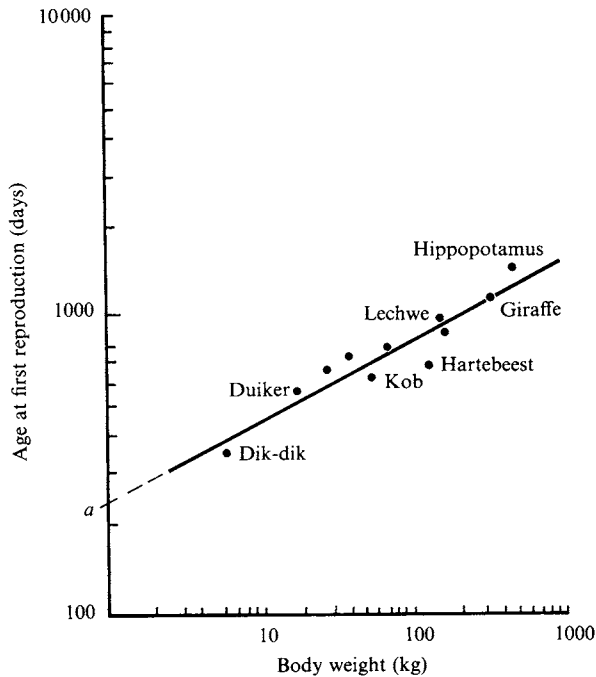
is that, for organisms large enough for gravity to be a significant factor (and this is true for all vertebrates), physical dimensions do not scale geometrically; instead, larger animals need to be relatively more squat and thick-boned to withstand the greater gravitational stresses to which they are subject. Thus, in general, body weight W tends to be related to length L as $W \sim L^4$ rather than the geometric $W \sim L^3$. Hence, Equation 1.1 corresponds roughly to $T \sim L^{4b}$ for mammals; with values of b lying in the range from 0.41 to 0.20, this gives an exponent ranging from 1.6 to 0.8 for the relation between age at first reproduction and length in mammals. This is crudely consistent with the slope $b = 1$ for the vast range of organisms in Fig. 1.3.

These scaling laws have direct implications for the population dynamics of the various species. To an excellent approximation, the intrinsic growth rate of a population, r, can be related to quantities characterizing its life-history strategy by

$$r \simeq \frac{\ln R_0}{T_c}. \qquad (1.2)$$

Here R_0 is the average number of female offspring produced over the lifetime of an individual female, and T_c is the 'cohort generation time' (which is a precisely defined quantity, related to fecundity and survival schedules, but roughly corresponding to one's intuitive notion of 'generation time'). The symbol 'ln' denotes the natural logarithm. The intrinsic growth rate, r, is the effective compound interest rate at which the population is capable of growing; the population can double in $0.69/r$ years (if r is expressed as a growth rate per annum). We note that r depends only logarithmically – which is to say insensitively – on R_0. Moreover, the cohort generation time is roughly proportional to the age at first reproduction, T. Thus, to a very crude approximation, the intrinsic growth rate of a mammalian population depends simply on the age at first reproduction:

$$r \sim 1/T. \qquad (1.3)$$

Fig. 1.5. Relationship between a mammalian population's intrinsic growth rate and age of first reproduction. (From T. Fenchel. Intrinsic rate of natural increase: the relationship with body size. *Oecologia*, **14**, 317–26 (1974).)

Intrinsic growth rate of population (log r. 10^{-1})

Age at first reproduction, as measured by body weight (log W [g])
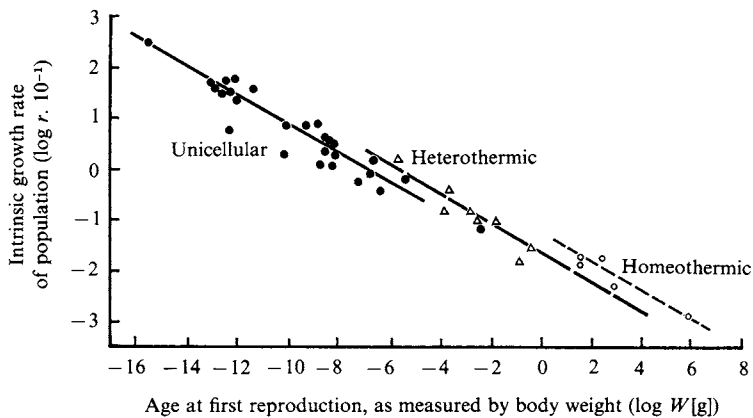
Combining this with the scaling law, Equation 1.1, discussed above, we have the very rough relation

$$r \sim 1/W^b. \tag{1.4}$$

As shown by Fig. 1.5, the simple relation given by Equation 1.4 holds for an astonishingly wide range of organisms, homeothermic, heterothermic and unicellular (and with b, overall, in the vicinity of $b \simeq 0.3$). Again focusing back on mammalian species in particular, Fig. 1.6 shows the scaling law between per capita birth rates (r is the difference between per capita birth and death rates) and body weight for African mammals (here $b = 0.33$). At the lower end of the body weight series there are two closely

Fig. 1.6. Relationship between per capita birth rates (percentage of young born each year to the whole population) and body weight of African mammals. (From D. Western. Size, life history and ecology in mammals. *African J. Ecol.* **17**, 185–205 (1979).)
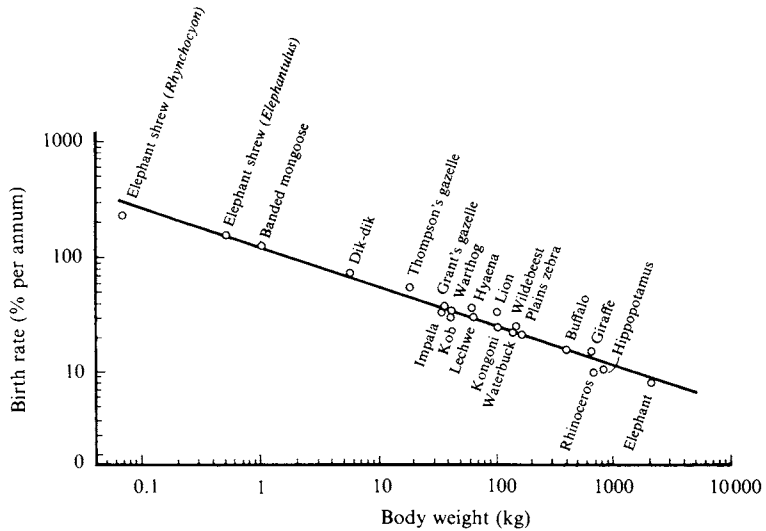

Fig. 1.7. A specimen of the rufous elephant shrew *Elephantulus*. (By courtesy of Professor John Hearn, Zoological Society of London.)

related members of a rare African rodent group, *Rhynchocyon* and *Elephantulus*. A specimen of the latter genus is illustrated in Fig. 1.7.

Litter size and environmental gradients

Within these broad scaling laws are, however, fine-grained patterns associated with local environmental or ecological factors. In other words, the design constraints discussed in the previous section set the larger patterns, which may then be fine-tuned by the specific strategic considerations discussed in the first section.

One way of seeing this is to consider, for example, how the average litter size for a particular taxonomic group varies over a latitudinal gradient. By dealing in this way with an assembly of species that have roughly similar physical sizes and behaviour, one may hope to tease apart from those differences in life-history strategies that depend on environmental differences. A classic early study of this kind was made by David Lack, who compared the clutch sizes of bird species in tropical and temperate regions. The underlying thinking is that environments tend to be more predictable and biological interactions to be relatively more important in the tropics (and make for '*K* selection', with relatively small clutch sizes and more parental care), whereas temperate environments are relatively less predictable (making for '*r* selection', with relatively large clutch sizes). The facts support these predictions. In a more detailed study, Cody took some 200 species of birds, grouped in five families, and showed that there was a significant linear regression of clutch size against latitude for each family. Cody's regression lines can be expressed in terms of their slope, *s*, which measures the increase in average clutch size per 1° increase in latitude; the results for birds give *s* around 0.06, with a range from 0.03 to 0.09, corresponding to clutch size increasing from around two to five or six, as we go from the Equator to 50° north or south latitude.

For mammals in North America, a study by Rexford Lord showed similar relations for the slope *s* of the regression line, expressing the increase in average litter size with increase in latitude, within each group studied. Lord's results are summarized in Table 1.1. They show significant patterns of increases in litter size along the expected '*K*- to *r*-selected' environmental gradient for six of the twelve groups; three of the remaining groups show litter size increases that are, however, not significant at the 95 per cent confidence level.

Fig. 1.8 shows average litter size as a function of body weight (plotted, as always, on a log–log scale) for a compilation of mammalian species. In this figure each species is assigned to one of three geographical zones, namely tropical, temperate or arctic, and it provides a clear demonstration of adaptative fine-structure within broad constraints (set here by body size), as discussed above. All three regression lines show an allometric tendency for average litter size to decrease with increasing adult body weight. Within this overall pattern, the three lines are clearly distinguishable;

particularly for small mammals (as for birds) there is a strong propensity towards larger litter sizes along an arctic–temperate–tropical gradient.

Life-history strategies will, of course, not depend simply on the physical environment, as crudely reflected in the latitude, but will also involve all manner of behavioural and ecological considerations. To illustrate this, we redraw Fig. 1.8, regrouping the 172 mammalian species into three new categories, according to whether they house their litters in trees (arboreal), on the ground (terrestrial or fossorial), or in burrows (Fig. 1.9). Again, all three regression lines show the general tendency for average litter size to decrease with increasing body weight, but, superimposed on this overall pattern, there is a tendency for burrowing mammals to have larger litters than ground-nesting ones, which in turn tend to have larger litters than

Table 1.1. *Litter size as a function of latitude among North American mammals. The tabulated six groups show patterns of increase in litter size with latitude that are statistically significant at the 95 per cent confidence level. Ground squirrels, pocket gophers and rats show increases that are not statistically significant, while foxes, cats and mustelids show no apparent correlation between litter size and latitude.* (R. D. Lord. Litter size and latitude in North American mammals. *Amer. Mid. Nat.* **64**, 488–99 (1960))

Taxonomic group	Number of species in study	s = increase in mean litter size per 1° increase in latitude
Rabbits	21	0.25
Tree squirrels	16	0.05
Meadow voles	18	0.13
Chipmunks	7	0.05
Deer mice	14	0.16
Shrews	12	0.12

Fig. 1.8. Relationship between litter size and body weight for arctic (△), temperate (○) and tropical (●) animals. (From D. Rubenstein. *Evolutionary Ecology of Mammalian Life-histories and Social Organization* (in press).)