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 10,000) 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.

![Graph showing fluctuations in owl populations in Wytham Wood](image-url)
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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 phrases '\( r \) and \( K \) selection', derived from the conventional parameters in the logistic equation, \( \frac{dN}{dt} = rN(1 - N/K) \). 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 '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 \( N = K \)). 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 parental 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 episodic 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 million 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,
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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 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

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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 malleable. 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 tautly 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
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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

$$T = aW^b.$$  \hfill (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 (clove-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

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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 $W \sim L^{3}$ rather than the geometric $W \sim L^{4}$. Hence, Equation 1.1 corresponds roughly to $T \sim L^{b}$ 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

$$r \approx \ln \frac{R_0}{L_0}.$$  \hfill (1.2)

Here $R_0$ is the average number of female offspring produced over the lifetime of an individual female, and $L_0$ 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:

$$r \sim 1/T.$$  \hfill (1.3)
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Combining this with the scaling law, Equation 1.1, discussed above, we have the very rough relation

\[ r = \frac{1}{N^b}. \]

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 unincellular (and with b, overall, in the vicinity of \( b \approx 0.3 \)). 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

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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, \( x \), which measures the increase in average clutch size per 1° increase in latitude; the results for birds give \( x \) 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 \( x \) 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 adaptive 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;
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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>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Number of species in study</th>
<th>Increase in mean litter size per 1º increase in latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rabbits</td>
<td>21</td>
<td>0.25</td>
</tr>
<tr>
<td>Tree squirrels</td>
<td>16</td>
<td>0.05</td>
</tr>
<tr>
<td>Meadow voles</td>
<td>18</td>
<td>0.13</td>
</tr>
<tr>
<td>Chipmunks</td>
<td>7</td>
<td>0.05</td>
</tr>
<tr>
<td>Deer mice</td>
<td>14</td>
<td>0.15</td>
</tr>
<tr>
<td>Shrews</td>
<td>12</td>
<td>0.12</td>
</tr>
</tbody>
</table>

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 muskrats 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))

Fig. 1.8. Relationship between litter size and body weight for arctic (O), temperate (C) and tropical (V) animals. (From D. Rubenstein. Evolutionary Ecology of Mammalian Life-Histories and Social Organization (in press).)

Fig. 1.9. Relationship between litter size and body weight for mammals living in trees (O), burrows (C) or on the ground (only regression line shown). (From same source as Fig. 1.8.)

...arboREAL mammALS. These statistically significant patterns may plausibly be attributed to the relatively greater and more unpredictable hazards (mainly from predation) to which burrow-dwellers are exposed, compared to tree-dwellers.

Ideally, we could attempt a three-dimensional figure, combining Figs. 1.8 and 1.9, and in which species were codified into nine classes according to geography and nesting habits. Yet other aspects of behavioural ecology could also be considered. We hope, however, that the main points are clear from Figs. 1.8 and 1.9.

Self-reinforcing feedback loops in r and K selection

Looking back on the way environmental unpredictability, life-history strategies, scaling laws and population dynamics weave together, it is clear that the notion of r and K selection has the nature of a 'Gestalt' (overall shape) rather than a simple causal chain. Thus, taking one view, a relatively small organism will have a short generation time, resulting in an intrinsically high rate of population growth, which in turn makes for a propensity to track fluctuations of the environment in episodes of outbreak and crash. On the other hand, small size and the associated short generation time condemns an organism to seeing the environment as relatively unpredictable (whereas a longer-lived organism may average-over fluctuations, or adapt to seasonal changes), which favours the evolution of a capacity for rapid population growth. In short, there are self-reinforcing tendencies, supplying positive feedback as one runs around the various causal loops. Fig. 1.10a illustrates these ideas about r selection in more detail; Fig. 1.10b illustrates the corresponding, but opposite, tendencies manifested under K selection.

We end this section with a discursive speculation. Ultimately, the set of life-history strategies for a group of species that live together will be shaped and constrained by patterns of community organization. These patterns are, at present, not well understood. Whatever the mechanisms, one outcome appears to be that there are more species of small creatures than of large ones; this is true both within broad assemblages cutting across...
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(a) r SELECTION

- SMALL SIZE
- Many offspring
- High net reproductive rate
- Less physiological homeostasis
- Less damping of environmental fluctuations
- Population tracks recent environmental changes
- Fluctuating birth and death rates

(b) K SELECTION

- LARGE SIZE
- Long development
- Deferred and internal breeding
- Few local opportunities for young
- Steady and crowded populations

Timing of reproduction

Iatroparity versus semelparity

One extreme and oversimplified aspect of the r- and K-selection dichotomy centres around whether an organism's reproduction is concentrated into a single, 'big bang' event (semelparity), or distributed over a repeated sequence of breeding events (iatroparity). It can be argued that extreme forms of r selection favour rapid attainment of sexual maturity, with all available resources channelled into one climactic production of offspring (followed usually by the death of the parent). Examples abound in many insect species, and in the celebrated self-sacrificial reproductive effort of Pacific sockeye salmon. Conversely, the K-selected paradigm is often represented as an animal maturing relatively slowly, and distributing reproductive effort over many breeding seasons once sexual maturity is reached.

Essentially all mammals are iteroparous, which suits their image as being to the K-selected extreme among all animals. There are, however, exceptions: nine small Australian marsupials in the genera Antechinus and Phascogale are known to be semelparous. Like most exceptions, they help to define the general rule. The young of A. stuartii are born in September–October (early summer), weaned in December–January, and by July (mid...
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winter) are mature. At this time males become aggressive, space themselves out and establish territories. Around August-September, females come into oestrus and are receptive for a period lasting about 2 weeks. During this period males mate repeatedly, their bodily condition deteriorates seriously, diseases set in and they all die. Babies are born 25-31 days after conception and are nursed until December-January, at which time 50-100 per cent of the adult females die.

As yet, no one has given an ineluctable reason why these species should be semelparous; they do, however, fit the criterion of being extremely r-selected, living in a forest environment where rainfall and insect abundances fluctuate seasonally and where fires are not uncommon. According to theories of life-history evolution, an individual should adopt a big-bang strategy of reproduction only if it can, by its suicidal transfer of energy, produce P/Y more young than a normal litter, where P and Y are the probabilities of the parent and young, respectively, surviving to the next year. The prolonged 5-month dependence of the Anotheus young on the mother leaves her nutritionally depleted, perhaps to the extent that she cannot sufficiently replenish her reserves before the onset of winter when insect abundance is low. If this were the case, P would be small, thus making it more likely that complete transfer of maternal reserves to the young would be favoured, as it would enable production of the largest possible litter and increase the survival prospects of the young. Apparently this is what occurs, as all the mother’s teats are occupied and, at weaning, the weight of the litter is three times that of the mother.

The notion that strong seasonality is a force favouring semelparity is supported by the observation that sibling species of A. stuartii living in habitats where rainfall is seasonal or monsoonal are also semelparous, whereas those living in tropical forests are not.

Litter frequency

The iteroparous mammals exhibit a great variety of breeding patterns. To some extent, these are influenced by the physical environment. Thus, in seasonal temperate regions, and especially in boreal and arctic regions, there is a tendency for offspring to be produced in the spring; such seasonal reproduction may produce one, or more than one, litter each year. In the less seasonal tropics, breeding can generally take place at any time. These considerations suggest that there may be, on average, systematic differences between the frequency at which litters are produced in tropical versus temperate environments. The nature of any such gradient is not clear a priori: one line of argument suggests that the relatively "K-selective" nature of the tropics will make for relatively lower litter frequencies; another line suggests that the less seasonal climate of the tropics permits year-round breeding, promoting increased litter frequencies.

Fig. 1.12 presents the facts, showing litter frequencies as a function of body weight for 174 mammalian species, grouped into two general classes (tropical and temperate). There is much scatter in these data points, particularly among small mammals. The regression lines for tropical and for temperate mammals both show the effects of systematic scaling, with large animals having greater spacing between litters. In addition, there is a small but statistically significant tendency for temperate mammals to have higher litter frequencies (shorter spacing between litters) than tropical mammals.

Many environmental complexities are glossed over in broad characterizations like 'tropical versus temperate'. In particular, many 'tropical' environments (for example, drought-prone regions) may be non-seasonal yet severely unpredictable. In such regions, evolutionary pressures will be geared to minimize the wastage of reproductive effort when drought unexpectedly strikes; the marsupial reproductive mode is arguably such a mechanism.

Marsupials versus eutherian mammals

Reproduction in marsupials is quite different from that of eutherians and represents a successful alternative. Marsupials are born at a very early developmental stage and make their own way to the mother's pouch while still naked, blind and very small. There they fasten to a teat and begin to suckle. In macropod (big-footed) marsupials, like the kangaroos and wallabies, a new ovum is fertilized at a postpartum estrus. Its development is, however, arrested by the effects of the older embryo's suckling (see Fig. 2.8 in Book 2, Second Edition). In species that live in predictably seasonal environments, such as the tammar wallaby, this lactational diapause is supplemented by a photoperiodically controlled seasonal diapause. Only with the return of favourable conditions at mid summer does development of the blastocyst resume.

In more marginal desert habitats, where conditions are less predictable, a more flexible system has evolved. For both the red kangaroo and the euro, reduced rates of sucking by the joey as it starts to vacate the pouch
allows the blastocyst in diapause to resume development. After about a month it is born, and attaches to a teat. The mother ovulates again within a day of birth, and this new fertilized egg enters a state of suspended development in the uterus. Thus, a marsupial mother inhabiting an unpredictably changing environment may be nourishing three youngsters simultaneously, all in different stages of development: an older infant who is semi-independent but who returns to the pouch for occasional sips of milk rich in fats and proteins; a middle-aged infant permanently attached to the teat who receives a milk more deficient in these ingredients; and a real tot who is nothing more than a blastocyst, lying dormant in the uterus. This contrasts sharply with eutherian mothers who suckle only a one-age cohort of young at a time, although they may do so while a second cohort is developing in the uterus.

Such a flexible developmental system has advantages in unpredictable environments. In an area such as the Australian desert, where drought is common yet where its onset and termination are unpredictable, attempts at reproduction, if poorly timed, could be fatal to both the mother and her offspring. Rather than tying the onset of mating to environmental cues, the red kangaroo and euro mate at any time and then take advantage of their ability to arrest the initiation of development of the fertilized embryo until the pouch offspring have reduced their suckling rate. This can come about either because the offspring has matured and stands a chance of making it on its own, or because it has perished because environmental conditions have adversely affected the mother. In either case, when suckling stops, the arrested embryo in the uterus begins to develop. If harsh conditions persist, the resulting newborn may itself perish, allowing the mother to ovulate and become pregnant once more. This process could repeat itself as long as conditions remain poor, but is soon as the rains return there is always a blastocyst ready to go. Moreover, if conditions deteriorate rapidly, some (the older cohort) or all (both cohorts) of young could be jettisoned quickly and easily, with less risk to the marsupial than to a eutherian mother who would have to abort a fetus. And even after such a loss, the marsupial mother, with her waiting embryo, would be able to capitalize on any return of favourable conditions more quickly than her eutherian counterpart. By having short generations that can be prolonged at will by an older infant, the large K-selected marsupials inhabiting uncertain environments can become efficient opportunistic breeders.

Care of young

Birth weight relative to parental weight

One rough index of the amount of parental investment up to the time of parturition is the weight of offspring at birth relative to maternal weight (often called the "proportionate birth weight"). Fig. 1.13 shows this proportionate birth weight as a function of maternal weight for some 69 species of hoofed mammals. Ungulates are especially interesting because they inhabit a wide range of environments and comprise species in many different stages of domestication.

Fig. 1.13 shows that the maximum relative reproductive effort among ungulates apparently occurs in pronghorn antelope and the goat, at around 15 per cent, decreasing to a minimum of around 4-5 per cent for the very large ungulates and subungulates. The trend to diminishing proportionate birth weight with increasing maternal weight is fairly steady for the larger animals, but there is much variability among the small species (adult weights less than or around 100 kg). Although there is too much scatter for any crisp generalization, Fig. 1.13 shows that several north temperate and arctic ungulates (for example, caribou, muskox, bighorn sheep) tend to produce relatively smaller offspring than most African ungulates, with other North American species typically being intermediate.
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The explanation for the relatively small single fetus of caribou, muskox and bighorn sheep may lie in inadequate food supplies during winter, and the need to optimize maternal survival relative to reproductive effort; these factors may override thermodynamic considerations, which would argue for the largest possible neonate, to minimize heat loss in a cold environment.

Revealingly, there are yet further complications among the smaller species represented in Fig. 1.13. The Mexican red brocket deer, a shy tropical animal which has one of the lowest proportionate birth weights of the smaller ruminants, has a postpartum oestrous. So do muntjac deer and several African boids. These species live in relatively stable environments, and the combination of relatively low birth weight and postpartum oestrus enables them to distribute reproduction throughout the year, in a way that may well increase total reproductive output.

In short, Fig. 1.13 again shows that there tend to be systematic scaling patterns, which are common to natural and domesticated species. Within these broad tendencies, particularly for the smaller species, there resides a fascinating richness of detail that overwhelms any easy generalization.

Altricial versus precocial young

The relative size of offspring at birth is, of course, only part of the story of parental care. Some young are born relatively independent; such 'precocial' young are relatively able to thermoregulate, and to forage and fend for themselves. In contrast, 'altricial' young require significantly more parental care in the first stages of their life. Since most of the energy demands of altricial young must be met by the parents, such offspring cost their parents more in terms of total expenditure of energy than do precocial young. Thus, only under special conditions will it be 'cost effective' for a species to have a relatively short pregnancy resulting in the production of altricial young.

One such condition arises when the postpartum rearing environment

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offers more security than the womb. All else being equal, selection will favour depositing the young in such safe places as early as possible. As Fig. 1.14 shows, mammals placing their young in nests have shorter gestation periods than those carrying their infants about, or those whose young are independent from birth. A second condition favouring the production of altricial young arises when juvenile adjustments to the vagaries of feeding and competing with adults, or socializing, require so much skill and physiological maturity that only an extraordinarily and unobtainably long period of gestation would be required. Since catching large prey is not an easy task for youngsters or pregnant females – in contrast to grazing on grass or browsing on herbs (which are more abundant and continuously distributed) – we would expect carnivores to bear relatively smaller young than ungulates. Fig. 1.15 shows that this is indeed the case.

Whether or not a female should bear relatively large young should also depend on whether or not she can offset the investment of a disproportionate

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Fig. 1.14: Relationship between gestation period and body weight for mammals placing their young in a nest, carrying them about, or having young that fend for themselves, i.e. are independent. (From same source as Fig. 1.8.)

Fig. 1.15: Relationship between birth weight and maternal weight for ungulates and carnivores. (From same source as Fig. 1.8.)

Fig. 1.16: Relationship between infant birth weight and maternal weight for monogamous and polygynous primates. (From same source as Fig. 1.8.)
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share of her reserves in current reproduction by sharing the demands of lactation and postpartum care with others not experiencing such large physiological stresses. Since males of monogamous species assist in carrying the young or provisioning the young or its mother, we would expect monogamous mammals to produce larger young than polygynous ones. This is often the case, and is clearly portrayed by the primates in Fig. 1.16.

Mating systems and social groupings

Strategies for bearing and caring for young are certainly essential features of reproduction, but they represent only half the story. Activities associated with mating are equally important; again, the patterns adopted by particular species are influenced by features of the environment.

The asymmetries inherent in sexual systems are such that one sex usually ends up investing more of its resources than the other sex in the rearing of young. In mammals this disproportionate parental investment is usually performed by females. Since females cannot rear offspring as quickly as males can father them, selection will favor female investment strategies that maximize the number of young raised to maturity. As a consequence, female behavior will be dominated by activities associated with acquiring food or avoiding predators. For males, however, selection will favor strategies that maximize the number of females mated; searching or competitive activities such as guarding females or defending a territory are likely to predominate in their behavioral repertoire. Apparently, the invention of lactation did little for the home life of mammals; most mammals exhibit polygynous breeding systems.

Polygyny can take a variety of forms because the success of males in gaining mating access to more than one female ultimately depends on how the environment affects patterns of female social groupings. If critical food resources are distributed unevenly in patches and are of low quality, then, on average, patches will not reliably be able to support female groups with permanent membership. Without groups to defend, males can become polygynous only if they can exclude other males from an area comprising one or more of the patches that the females require. Grevy's zebras and langurs both seem to practice this form of "resource defense polygyny".

When resources are distributed in patches of higher quality, large aggregations of females can regularly be supported. Most likely these will meld into coalitions with fixed membership, as intergroup competition will be intense. Once such groups are formed, superior males will be able to defend them against other males and thus gain exclusive mating access ("female defense polygyny"). Gelada and hamadryas baboons, Burchell's zebra, impala and scores of other mammals exhibit such harem breeding systems.

Sometimes males will not be able to exclude all other males from these female associations; this might happen when female groups are so large that pressure from excluded males is tremendous, or when females encourage males to immigrate as allies in their intergroup struggle. In the presence of other males, superior males will attempt to maintain their priority of access to females by aggressive domination of subordinates ("male dominance polygyny"). Yellow and olive baboons, macaques and many middle-sized ungulates exhibit these multi-male, multi-female groups. Here the reproductive success of dominant males will depend somewhat on the extent to which female reproductive cycles are synchronized and on the length of courtship.

When resources are evenly distributed, competition for any individual resource item is lessened. As a result, tight-knit female associations may not be selected, for when this occurs males will have to wander about searching out solitary females or temporary aggregations of females. A female in oestrus is likely to be found and courted for by many males (unless the pool of males is small and the dominance relationships among them are well established); here extreme polygyny may be possible to achieve and may give way to promiscuity. Large grazing mammals, such as African elephants and Cape buffalo, that tend to perceive grasslands as a more-or-less continuous award, exhibit this type of wandering polygyny. Sometimes, however, females inhabiting these even stands of densely packed resources form groups because they help to protect against predators. At other times, food resources are not the critical resource but rather sites for resting or breeding are limited or patchily distributed, which makes it necessary for females to aggregate. In such instances, males should attempt to form harems.

Not all evenly distributed resources need consist of densely arranged prey items, and when resource items are sparse females may have to range over large distances to obtain them. In this case, groups will not form, and males will have to search widely for solitary females. Perhaps this explains why some insectivores, carnivores and marine mammals are often widely dispersed and breed promiscuously.

Breeding and social systems are not strictly governed by the distribution of critical resources such as food or nest sites. Sometimes the potential for polygyny is present and not realized, as is often the case where the survival prospects of the young can be greatly augmented by the assistance of two parents, and where female receptivity is highly synchronized so that philandering by males is precluded. Under these conditions males that abandon polygyny and mate monogamously will be favoured. In most monogamous species males share some of the parental responsibilities by defending the young, bringing food to the female or the young, or carrying the young. The adoption of parental duties by males is clearly evidenced in the monogamous arboreal primates (such as the siamang, marmosets and tamarins), where the weight of the young is large relative to that of the mother, and where the young are carried for extended periods; the contrary is the case among polygynous primate species. And, as discussed
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earlier, the monogamous carnivores (such as canids), which bear large litter sizes consisting of many altricial young, assist in meeting the large energetic demands of a litter by augmenting both the mother's and the offspring's diet by regurgitating captured prey.

In summary, resource quality and dispersion will in general affect a female's reproductive success, and thus play a central role in determining adaptive patterns of association among females. These in turn determine the mating strategies of males. When the two are taken together, the basic mammalian breeding systems and social systems emerge.

Obviously deviations from these ideal patterns do occur. Some can be accounted for by examining other important ecological variables that have been omitted in the above analysis. Others, however, can be accounted for only by expanding the analysis to incorporate the proposition that not all individuals in a population should adopt the same strategy. Since the expected reproductive success associated with one individual's mating activities depends to a large extent on what other individuals in the population are doing, the rewards of any particular strategy will often be frequency-dependent. As a result it is highly likely that equally successful alternatives (polymorphisms) will occur. Thus, it is not surprising to find that in some populations of horses, gelada baboons and red deer some males establish harems and guard females, while others will be sneaky raiders attempting to steal copulations surreptitiously. Likewise, in some populations of elephant seals and of impala, some males establish territories while others become satellites, mating with the females before they arrive at the territory. Clearly, much more work is needed to identify the reasons for the striking diversity of mammalian mating patterns. The foregoing discussion, however, shows that environmental quality and predictability have an important influence on patterns of breeding and sociality among mammals.

We see that no single, crisp pattern emerges from our survey of the kaleidoscope of factors that work together to fashion the reproductive strategies of mammals.

One broad pattern that is, however, discernible is the existence of design constraints on the construction of living machines, which makes for systematic correlations between the physical size of a mammal and the magnitude of various quantities that characterize its reproductive behaviour (such as litter size and weight, or time to reproductive maturity). Within any one size class there are finer patterns, moulded by the ecology and environment for the individual species, and having to do with its reproductive biology, its mating system and its social organization. Ultimately, the physical size of the animal of a given mammalian species is itself the product of natural selection, subject to the restrictions imposed by the environment and by interactions with other species in the community.

Suggested further reading


The Natural History and Antiquities of Selbourne. G. White. B. White & Son; London (1879).