

7.2 The components of life histories

growth and size – is bigger better?

Of the important components of any organism's life history, the size an individual attains is perhaps the most apparent. Large size may increase an organism's competitive ability, or increase its success as a predator, or decrease its vulnerability to predation, and hence increase its survival. Stored energy and/or resources will also be of benefit to organisms that pass through periods of reduced or irregular nutrient supply (probably true of most species at some time). Finally, larger individuals within a species usually produce more offspring. On the other hand, size can increase some risks: a larger tree is more likely to be felled in a gale, many predators exhibit a preference for larger prey, and larger individuals typically require more resources and may therefore be more prone to a shortage of them. Perhaps most important: becoming large itself takes time, during which an individual may be prone to a variety of mortality risks. An intermediate, not a maximum, size may therefore be optimal. In practice, however, most studies have found a larger rather than an intermediate size to be favoured

(Figure 7.1). This provides an explanation for 'Cope's rule' (Hone & Benton, 2004) – the tendency for the species in a lineage to increase in size over evolutionary time – but does not really explain why more contemporary species are not at or close to their maximum size (Kingsolver & Pfennig, 2008.)

Development is the progressive differentiation of parts, enabling an organism to do different things at different stages in its life history. Hence, rapid development can increase fitness because it leads to the rapid initiation of reproduction. As we have seen, reproduction itself may occur in one terminal burst (semelparity) or as a series of repeated events (iteroparity). Amongst iteroparous organisms, variation is possible in the number of separate clutches of offspring, and all organisms can vary in the number of offspring in a clutch.

development, differentiation and reproductive allocation

The individual offspring can themselves vary in size. Large newly emerged or newly germinated offspring are often better competitors, better at obtaining nutrients and better at surviving in extreme environments. Hence, they

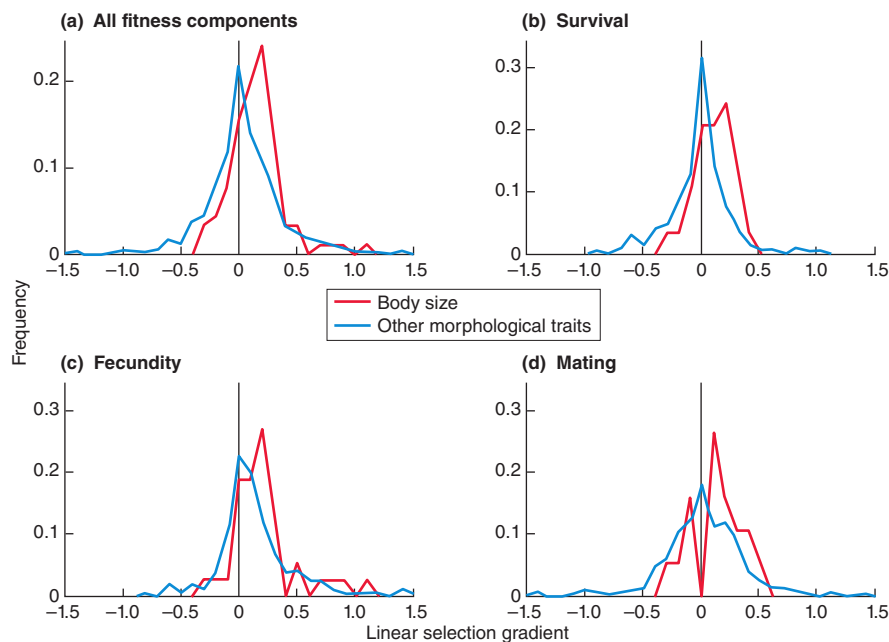


Figure 7.1 Studies of selection show a tendency for larger body size to be favoured but intermediate values of other morphological traits. Results of a survey from the published literature of studies measuring the strength of selection on body size (red line; a positive value means selection for increased body size) and other morphological traits (blue line) when this was determined by reference to (a) all fitness components combined, (b) survival, (c) fecundity and (d) mating success. In all cases, there was an overall tendency for larger size to be favoured (giving rise to higher fitness), whereas for traits other than body size the distribution was symmetrical around zero (no change). The selection gradient is the change in relative fitness that results from 1 standard deviation of change in a trait, such that a value of 0.5 means that a change of one standard deviation increases fitness by 50%. *Source:* After Kingsolver & Pfennig (2008).

often have a better chance themselves of surviving to reproduce.

Combining all of this detail, life histories are often described in terms of a composite measure of reproductive activity known as ‘reproductive allocation’ (also often called ‘reproductive effort’). This is best defined as the proportion of the available resource input that is allocated to reproduction over a defined period of time, but it is often not clear which resource’s allocation is the most appropriate to measure – that is, which resource is most limiting and therefore best reflects the effort invested by the organism concerned. Figure 7.2 shows an example comparing the allocation of dry matter on the one hand, and nitrogen on the other, to the various parts of garden tulips, *Tulipa gesneriana*, over their growing season in North Carolina, USA. Broad patterns are the same, but the details differ. In practice, even the better studies usually monitor only the allocation of energy, or just dry weight, to various structures at a number of stages in the organism’s life cycle.

7.2.1 Reproductive value

Natural selection favours those individuals that make the greatest proportionate contribution to the future of the population to which they belong. The life history components that we have described affect this contribution, ultimately through their effects on fecundity and survival. It is necessary, though, to combine these effects into a single currency so different life histories may be judged and

compared on a common scale. A number of measures of fitness have been used. All the better ones have made use of both fecundity and survival schedules. The intrinsic rate of natural increase, r , the basic reproductive rate, R_0 (see Chapter 4) and lifetime reproductive success have all had their advocates. Here, we will concentrate on ‘reproductive value’, because it is readily decomposed into current and future contributions to fitness (Fisher, 1930; Williams, 1966; Kozłowski, 1993). However, for an exploration of the basic patterns in life histories, the similarities between these various measures are far more important than the minor differences between them.

Reproductive value is described in some detail next. For most purposes though, these details can be ignored as long as we remember that: (i) reproductive value at a given age or stage is the sum of the contemporary reproductive output and the residual (i.e. future) reproductive value (RRV); (ii) RRV combines expected future survival and expected future fecundity; (iii) survival and fecundity are combined in a way that takes account of the contribution of an individual to future generations, relative to the contributions of other individuals; and (iv) the life history favoured by natural selection from amongst those available in the population will be the one for which the sum of contemporary output and RRV is highest.

The reproductive value of an individual of age x (RV_x) is the currency by which the worth of a life history in the hands of natural selection may be judged. It is defined in

reproductive value
described in words

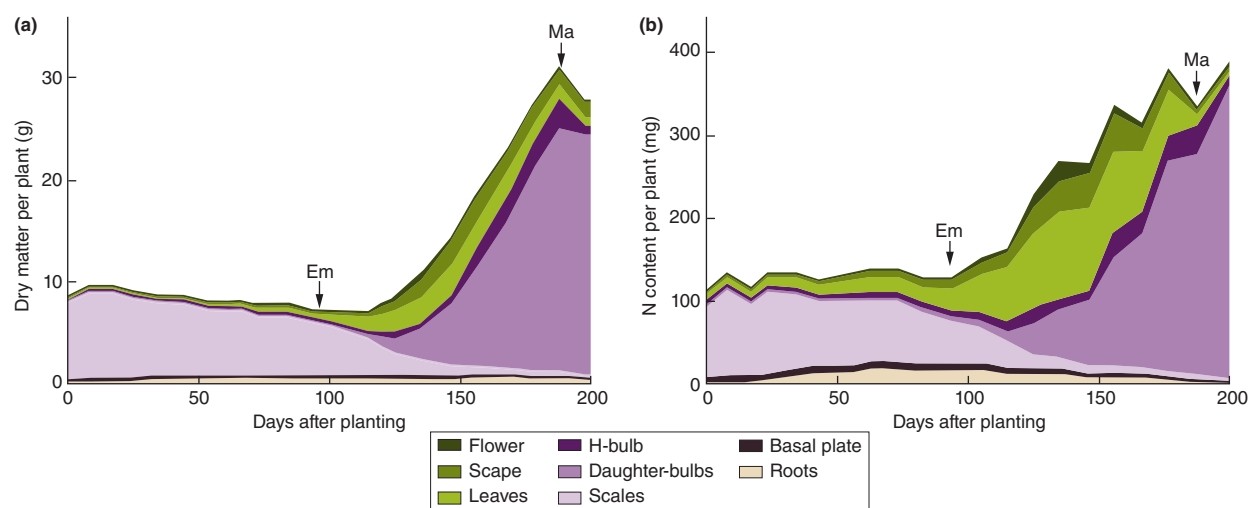


Figure 7.2 Allocations of dry matter and nitrogen to the parts of a plant vary over its lifetime. The allocation of (a) dry matter and (b) nitrogen to the various organs (see key in figure) of the garden tulip, *Tulipa gesneriana*, over the course of the growing season. Em, shoot emergence; Ma, bulb maturity. The scape is the flower-supporting stem; the H-bulb is the outermost, ‘tunic’ bulb amongst the daughter bulbs. Source: After Niedziela *et al.* (2015).

terms of the life-table statistics discussed in Chapter 4. Specifically:

$$RV_x = \sum_{y=x}^{y=y_{\max}} \left(\frac{l_y}{l_x} \cdot m_y \cdot R^{x-y} \right) \quad (7.1)$$

where m_x is the birth rate of the individual in age-class x ; l_x is the probability that the individual will survive to age x ; R is the net reproductive rate of the whole population per unit time (the time unit here being the age interval); and Σ means 'the sum of'.

To understand this equation, it is easiest to split RV_x into its two components:

$$RV_x = m_x + \sum_{y=x+1}^{y=y_{\max}} \left(\frac{l_y}{l_x} \cdot m_y \cdot R^{x-y} \right). \quad (7.2)$$

Here, m_x , the individual's birth rate at its current age, can be thought of as its *contemporary reproductive output*. What remains is then the *residual reproductive value* (Williams, 1966): the sum of the 'expectations of reproduction' at all subsequent ages, modified in each case by R^{x-y} for reasons described later. The 'expectation of reproduction' for age class y is $(l_y/l_x \cdot m_y)$, i.e. it is the birth rate of the individual should it reach that age (m_y), discounted by the probability of it doing so given that it has already reached stage x (l_y/l_x).

Reproductive value takes on its simplest form where the overall population size remains approximately constant. In such cases, $R = 1$ and can be ignored. The reproductive value of an individual is then simply its total lifetime expectation of reproductive output (from its current age class and from all subsequent age classes).

However, when the population consistently increases or decreases, this must be taken into account. If the population increases, then $R > 1$ and $R^{x-y} < 1$ (because $x < y$). Hence, the terms in the equation are reduced by R^{x-y} the larger the value of y (the further into the future we go), signifying that future (i.e. 'residual') reproduction adds relatively little to RV_x , because the proportionate contribution to a growing population made by a given reproductive output in the future is relatively small – whereas the offspring from present or early reproduction themselves have an early opportunity to contribute to the growing population. Conversely, if the population decreases, then $R < 1$ and $R^{x-y} > 1$, and the terms in the equation are successively increased, reflecting the greater proportionate contribution of future reproduction.

In any life history, the reproductive values at different ages are intimately connected, in the sense that when natural selection acts to maximise reproductive value at one age, it constrains the values of the life table parameters – and

thus reproductive value itself – for subsequent ages. Hence, strictly speaking, natural selection acts ultimately to maximise reproductive value *at birth*, RV_0 (Kozłowski, 1993).

The way in which reproductive value changes with age in two contrasting populations is illustrated in Figure 7.3. It tends to be low for young individuals, since these, individually, have only a low probability of surviving to reproductive maturity. It then rises and eventually peaks as the age of first reproduction is approached, as it becomes increasingly likely that surviving individuals will reproduce, and then declines again to low values for old individuals, since their reproductive output is likely to have declined and their expectation of future reproduction is even lower. The detailed rise and fall, of course, varies with the detailed age- or stage-specific birth or mortality schedules of the species concerned. Note also that there is no contradiction between this pattern (reproductive value low for young individuals) and the fact that natural selection acts

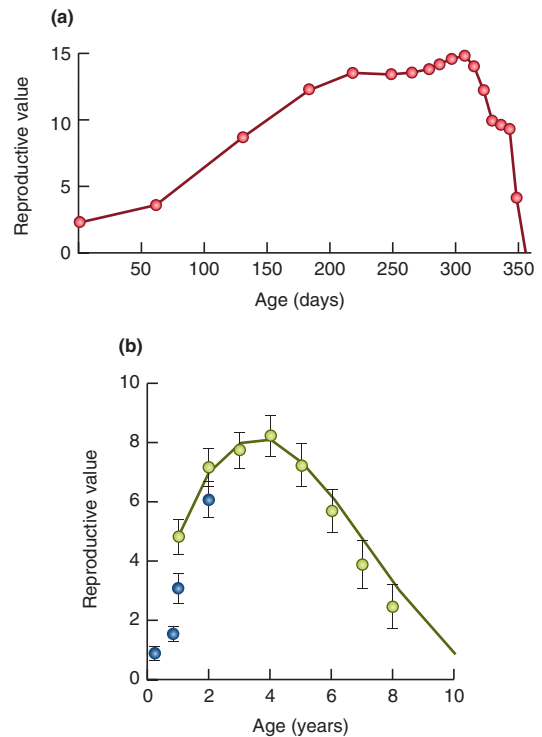


Figure 7.3 Reproductive value generally rises and then falls with age. (a) The annual plant *Phlox drummondii*. (b) The sparrowhawk, *Accipiter nisus*, in southern Scotland. Green symbols (± 1 SE) refer to breeders only; blue symbols include non-breeders. Note that in both cases the vertical scale is arbitrary, in the sense that the rate of increase (R) for the whole population was not known, and a value therefore had to be assumed. Source: (a) After Leverich & Levin (1979). (b) After Newton & Rothery (1997).

ultimately to maximise reproductive value at birth. Natural selection can discriminate only between those options available at that stage.

7.3 Trade-offs

In addressing one of our key questions – are there patterns linking life history traits? – we should note immediately that any organism's life history must be a compromise allocation of the resources available to it. Resources devoted to one trait cannot then be invested in other traits. We might therefore expect to see negative relationships between two life

history characteristics in which increases in one are associated with decreases in the other as a result of such compromises, and there are certainly examples of this. For instance, trees benefit both from reproducing and from growing (which, amongst other things, enhances future reproduction). But the more seeds trees produce, the less they grow, and the more they grow the less they reproduce (Figure 7.4a). Similarly, squirrels benefit from both surviving and reproducing, but the more they reproduce, the less well they survive (Figure 7.4b). And mountain goats benefit from reproducing both now and in the future, but the more they reproduce now the less likely they are to reproduce the following year (Figure 7.4c).

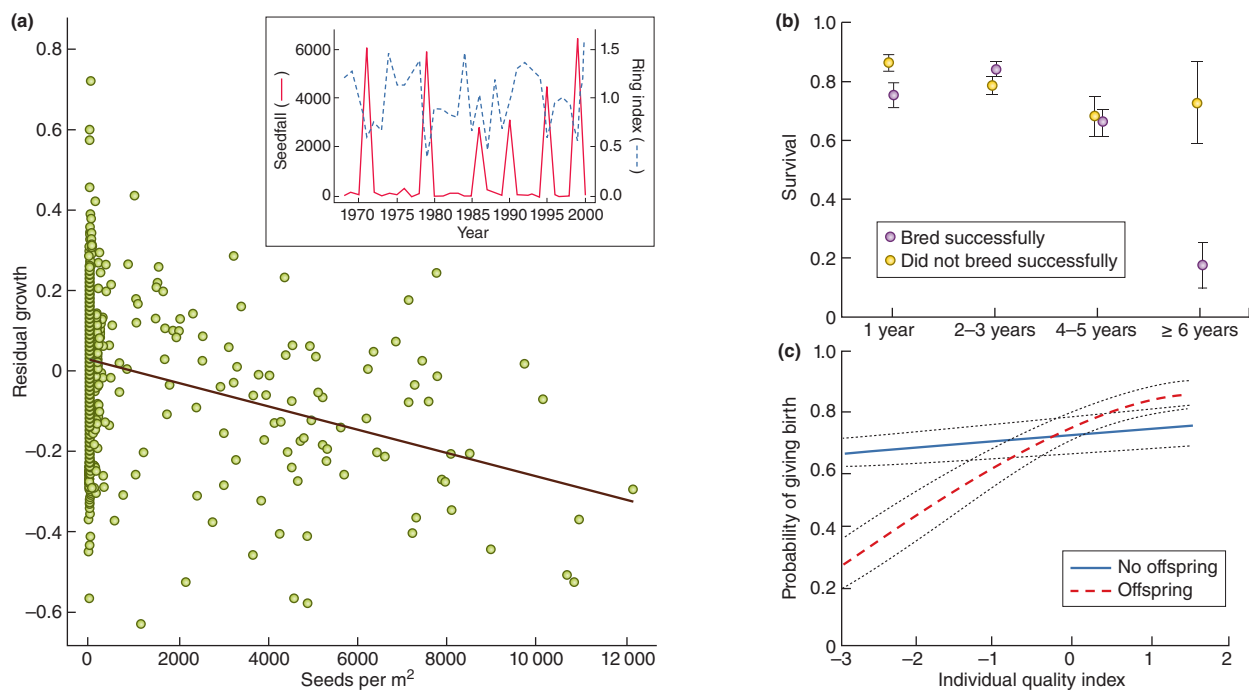


Figure 7.4 Life history trade-offs demonstrate the costs of reproduction. (a) The tree *Nothofagus truncata*, growing in the Orongorongo Valley, New Zealand exhibits 'mast seeding' (inset): years of massively increased seed production (i.e. reproduction) exhibited by whole groups of trees growing together. Much of this growth variation was attributable to prevailing weather conditions, but once this had been accounted for in a statistical model, the remaining 'residual growth', higher or lower than the weather would predict, was significantly negatively correlated with seed output ($P < 0.0001$): trees that reproduced most grew least; trees that grew most reproduced least. (b) Among North American red squirrels, *Tamiasciurus hudsonicus*, from the southern Yukon, Canada, survival was lower in females that bred successfully in the previous season (means \pm SEs) than in those that did not, but only among the youngest and oldest: those in their first year or more than five years old. (c) In mountain goats, *Oreamnos americanus*, from Alberta, Canada, the probability of giving birth one year was reduced among females that had given birth the previous year, but only for females in relatively poor condition, measured on a scale according to which females were either relatively light and subordinate (negative values) or heavy and dominant (positive values). The lines are not the original data but the output of best-fit statistical models, with associated standard errors. Source: (a) After Monks & Kelly (2006). (b) After Descamps *et al.* (2009). (c) After Hamel *et al.* (2009).