

# Big houses, big cars, superfleas and the costs of reproduction

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**The assumption of costs of reproduction were a logical necessity for much of the early development of life history theory. An unfortunate property of 'logical necessities' is that it is easy to also assume that they must be true. What if this does not turn out to be the case? The existence and universality of costs of reproduction were initially challenged with empirical data of questionable value, but later with increasingly strong theoretical and empirical results. Here, we discuss Ken Spitze's 'superfleas', which represent what we consider to be the strongest empirical challenge to the universality of costs, then offer a possible explanation for their existence.**

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In 1991, Ken Spitze published a paper about a life history (Box 1) selection experiment in the waterflea *Daphnia pulex*<sup>1</sup>. He compared the life histories of control populations with ones that had been exposed to predation by *Chaoborus* larvae. These larvae are voracious predators that feed on small microcrustacea. He found that, relative to the controls, the populations that experienced predation evolved such that they were younger and larger at maturity, and had higher fecundity. This combination of traits suggested that predation had caused the evolution of a 'better' flea because it increased reproductive output with no apparent cost: on the contrary, the selected population gained because it both developed and grew more quickly.

In a second paper, Spitze *et al.*<sup>2</sup> evaluated the genetic variance-covariance matrices of life history traits for *Daphnia* from two of the four populations that provided the clones for the selection experiment described previously. In both cases, they found consistent, positive genetic correlations among growth rate at different ages, fecundity at different ages, and growth rate and fecundity. They also found negative correlations between age at maturity, size at maturity and fecundity<sup>3</sup>, thus indicating that clones that developed more quickly also grew faster and had higher fecundity throughout life. For those researchers who had accepted theories of life history evolution based upon the assumptions of balanced costs and benefits associated with different life history traits, these results were profoundly disturbing. They suggest that there is genetic variation within each population that defined an axis ranging from the 'uberflea', which

was superior in all regards, to the 'unterflea', which was inferior in all regards. It seems reasonable that natural selection will favor the 'uber' clones and eliminate the 'unter' clones, thus variation should not be seen. However, it is seen and, according to several accounts, is of significant magnitude<sup>4</sup>.

## Background on costs of reproduction

Assumed costs of reproduction (Box 1) are an essential part of almost every theoretical treatment of life history evolution published since Williams<sup>5</sup> presented his refinement of Lack's principle (Box 1)<sup>6</sup>. Williams partitioned the resources that organisms allocated to reproduction into what they invest now, which he called reproductive effort (Box 1), and what they save for the future, which he called residual reproductive value. The optimal life history was the one that maximized the sum of these two entities. Williams did not envision this partitioning as being strictly a subdivision of some finite resource. It would also include things such as the risk factors associated with alternative behaviors (e.g. the decision of a parent bird either to forage once more for food for the nestlings or to call it a day). Nevertheless, it became convenient to think of the life history as being similar to a pie divided into slices, each slice being devoted to a different function, such as growth, maintenance, storage or reproduction. Because the pie is of fixed size, increasing the size of a given slice necessarily decreases the size of another slice.

Another reason that costs became an essential feature of most models is that they seemed to make intuitive sense. In the absence of costs, it is assumed that

natural selection will favor the evolution of the 'darwinian demon'; an organism that matures instantly and produces an infinite number of offspring. We assume that this does not occur because of limited resources, and the costs and benefits associated with different activities. Examples of costs that were often built into theoretical models include increased mortality in response to an increase in reproductive effort, decreased future reproduction in response to an increase in current reproduction, or decreased fecundity in response to earlier reproductive maturity.

Given the apparent central importance of costs in molding the way life histories evolve, it soon became imperative among empiricists to try to characterize costs. In 1985, Reznick<sup>7</sup> reviewed the progress in this area and concluded that researchers were approaching the issue from at least four different perspectives, which were labeled as environmental correlations (Box 1), environmental manipulations (Box 1), genetic correlations (Box 1) and selection experiments. The nature of the information derived from each of these approaches was not the same and it was argued that not all of them were applicable to considerations of the evolution of life history patterns. The premise was that to be evolutionarily relevant, estimates of cost must have a genetic basis. Although the details of each approach are not important to this discussion, the conclusions are. It was concluded that the evaluations of costs that were most relevant to theories of life history evolution were those that quantified the genetic bases for costs and the patterns of genetic variation in natural populations, because these were the ones that would predict most effectively how life histories would evolve. The evaluation of genetic correlations among life history traits and correlated responses to selection were thus favored as the best ways to characterize the costs that shape life history evolution. Spitze's<sup>1,2</sup> papers support this expectation very well, because there is such a strong correspondence between the structure of the genetic variance-covariance matrix and the way the life histories evolved in the selection experiment.

This correspondence increases our distress over the results because they seem to run so counter to expectations. Spitze was not the first to report such counterintuitive results, but many of the earlier studies were arguably weak in design or execution and thus were not necessarily reliable<sup>7,8</sup>. No such flaws were present in Spitze's work. Recently, Roff has reviewed additional examples in the form of positive correlations between development time and adult size<sup>9</sup>.

## Box 1. Glossary

**Costs of reproduction and/or tradeoffs:** we assume that evolution maximizes individual fitness by maximizing the number of successful offspring produced during the individual's lifetime. Thus, reproduction is a positive contribution to fitness, but it is presumably attained at some cost, which is a measurable reduction in some other component of fitness caused by the allocation of resources to reproduction. Examples of such costs are a reduced probability of survival or a reduced capacity to reproduce in the future. 'Tradeoff' is a more general term that applies to the costs and benefits associated with any single activity.

**Environmental correlations:** these are correlations among traits that are attributable to environmental, rather than genetic, factors. For example, an increase in food supply, which is a feature of the environment, could cause an increase in the number of offspring produced, growth rate and survival.

**Environmental manipulations:** costs of reproduction have often been evaluated by experimentally manipulating some feature of the environment. One of the most common methods involves the addition of eggs to a bird's clutch, then comparing their success in fledging young with birds with unaugmented clutches. Another method is to prevent one group of individuals from reproducing, then comparing them with a control group that reproduces normally. The differences among treatment groups are described as 'environmental' because they are not attributable to genetic differences. It is often assumed that the response to such environmental manipulation mimics how organisms will respond to selection.

**Genetic correlations:** correlations between traits are evaluated with the same formal breeding designs that are used to evaluate the heritability of a single trait. They measure the extent to which two different traits, such as fecundity and longevity, are determined by the same genes.

**Lack's principle:** this was one of the earliest proposals for a general principle of life history evolution. Lack either increased or decreased a bird's clutch size, then compared the average number of young raised to fledging with that of unmanipulated clutches. Either an increase or decrease often resulted in fewer fledglings than the average unmanipulated clutch size. He defined the clutch size that maximized the number of fledglings as the 'optimal clutch size' and interpreted it as the largest number of young for which the parents are able to provide sufficient food.

**Life history:** the life history consists of all of the traits that contribute directly to offspring production and survival. Important variables include the age at first reproduction, frequency of reproduction, number of eggs and/or offspring produced per reproductive event, and parental investment in each offspring.

**Reproductive effort and/or residual reproductive value:** Williams<sup>7</sup> subdivided Fisher's<sup>29</sup> 'reproductive value' into two components. The first component, reproductive effort, describes the resources that are allocated to the current reproductive event. An increase in reproductive effort might take the form of producing more eggs, producing larger eggs, or providing more care to the current litter of young. Residual reproductive value represents what is saved for future reproductive events. It is assumed that these two quantities are inversely related, thus increasing what is invested in reproduction now necessarily reduces what is available for reproduction later.

As an aside, we note that there are now new ways of evaluating costs that circumvent some or all of the objections raised in the earlier review<sup>7</sup>. One is phenotypic engineering, as practised so well by Sinervo in his studies of lizard life histories (e.g. Ref. 10). A second is the combination of selection experiments with either genetic or environmental manipulations, as employed by Sgro and Partridge in their study of *Drosophila*<sup>11</sup>.

### Theoretical perspectives

The first workers to try to resolve the apparent absence of costs of reproduction in some empirical life history studies were Van Noordwijk and de Jong<sup>12</sup> (Box 2). They hypothesized that unexpected results can arise if there is genetic variation for both the acquisition and allocation of resources. In terms of our pie analogy, they postulated that there could be genetic variation for pie size and genetic variation for how the pie is sliced. Whether we see positive or negative correlations between the amounts of resources allocated to reproduction compared with other areas, such as somatic tissue development, depends on the relative amount of genetic variation

in acquisition and allocation. If acquisition is less variable than allocation, then negative correlations among life history traits are expected. Conversely, if acquisition is more variable than allocation, positive correlations will arise. The model was further elaborated by de Jong and Van Noordwijk<sup>13</sup>.

The biological importance of this model is that some individuals will command more resources than others, hence our subtitle 'big houses, big cars', which alludes to the human analogy of differences among families in resource acquisition. Some individuals will have more resources to allocate to all aspects of their life history. Although the split between acquisition and allocation provides a possible explanation for the unexpected positive correlations, it raises a crucial question: why don't the superfleas take over the world? Houle<sup>14</sup> investigated this problem by examining the potential role of mutation-selection balance, which is the maintenance of genetic variation through the constant input of new mutations, tempered by the constant removal of those mutations that are deleterious. He showed that mutation-selection balance could create positive

genetic correlations, if the number of genes associated with acquisition was substantially higher than the number determining allocation. Charlesworth<sup>15</sup> examined this problem more generally using a quantitative genetic model. He showed that, although large negative genetic correlations are expected among some life history traits, the interrelationships among traits can generate unexpected positive correlations. When we evaluate the quantitative genetics of life history traits, we are only considering a subset of everything that contributes to fitness; components of fitness that are not included in the evaluation might well be genetically correlated with life history traits. Negative correlations among some of these unmeasured traits could cause positive correlations among others. What is observed is a function of what is measured. Some of this complexity was captured by de Jong<sup>16</sup> in her model of multi-step allocation trees. She concluded that traits within a system of allocation tradeoffs will form into clusters of traits, with positive correlations among traits within a cluster and negative correlations between clusters.

### Costs of acquisition

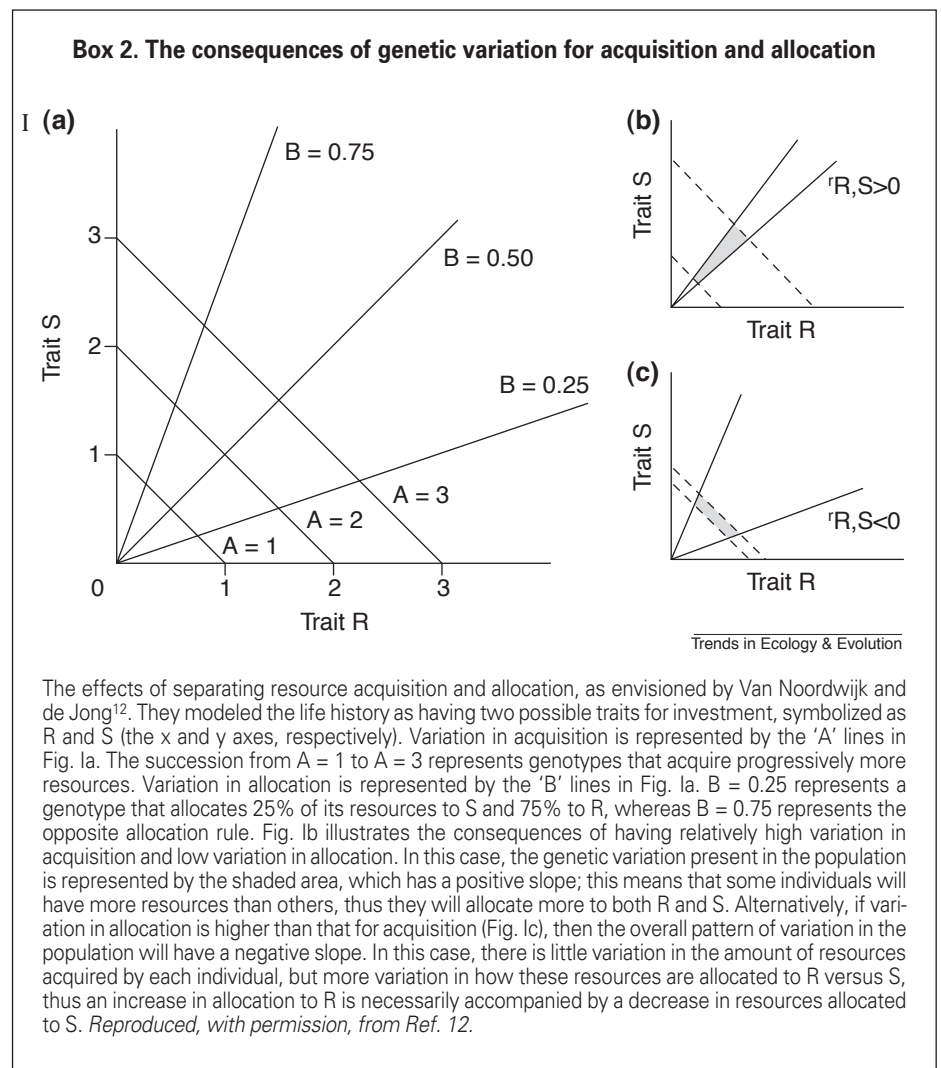
Spitze *et al.*<sup>2</sup> were well aware of the surprising nature of their results, with respect to costs of reproduction, and offered some possible solutions to the dilemma. One proposition was that this variation might be sustained through fluctuating selection or through genotype  $\times$  environment interactions. First, they noted that the pattern of size-selective predation that *Daphnia* experience varies predictably across the season. *Chaoborus*, an invertebrate, is the dominant predator early in the season. It preys selectively on smaller size classes of *Daphnia*. Vertebrates (amphibians and fish) are the dominant predators late in the season. They prey selectively on large *Daphnia*. There is also predictable seasonal variation in resource availability because food for *Daphnia* tends to be abundant early in the season but declines as the season progresses. Spitze's experiments were carried out with high food availability and high rates of *Chaoborus* predation to mimic the early season environment. Given the seasonal environmental change, there might be genotype by environment interactions for fitness, with the 'high acquisition', large bodied phenotype having higher fitness early in the season and the 'low acquisition', small bodied phenotype having higher fitness late in the season. There might also be spatial variation in resource concentration in some bodies of water, because phytoplankton abundance

can vary with depth in thermally stratified lakes<sup>17</sup>. This hypothesis suggests that there could be a cost or tradeoff associated with an enhancement of the ability to acquire resources. Superfleas really are super, but only when resource availability is high. When resource availability is low, they should have lower fitness than their nonsuperflea conspecifics. Such a cost would exist if the ability to acquire resources in some way demanded a higher level of resource availability. Recent results suggest that such a cost or tradeoff does exist. We will review some of these results and suggest a new way of thinking about costs of reproduction, which capitalizes on what Spitze *et al.*<sup>2</sup> suggest.

### Empirical perspectives

Hammond and Diamond's work on the maximum sustainable metabolic rate (MSMR) of mice offers one example of a cost of acquisition<sup>18</sup>. An experimental paradigm for increasing the MSMR is to expose subjects to circumstances that are energetically demanding. For example, they studied lactating mice that were kept in relatively cold conditions. Because lactation and thermogenesis are both energetically demanding, allocating sufficient resources to both at the same time should be especially demanding. Because the experiments were always conducted with *ad lib* feeding, the problem for the mice was to maximize their ability to acquire and process resources, rather than one of differential allocation. One consequence of such a treatment is that an increase in MSMR was matched by an increase in the basal metabolic rate, and an increase in the mass of organs associated with food processing and metabolism. Thus, the increase in MSMR seems to have been obtained at the cost of enlarging all aspects of the metabolic machinery associated with acquisition, with an accompanying increase in the resting metabolic rate. Although these are studies of phenotypic plasticity and thus are not directly applicable to an evolutionary argument, they nevertheless offer an empirical example for how acquisition can be costly.

Secor and Diamond<sup>19</sup> offer a second example in the form of an interspecific comparison of snakes with different foraging strategies. They compared 'sit-and-wait' predators (pythons and vipers) with active foragers (colubrids). The sit-and-wait predators typically consume large meals with long intervals between feeding, whereas the active foragers eat small meals at shorter intervals. The intestinal tract of sit-and-wait predators regresses between meals, then rapidly recrudesces after feeding. The regression



of the intestinal tract is associated with a lower resting metabolic rate when the animal is not digesting a food item, but is also associated with a higher energetic cost of processing a food item because this cost includes the reactivation of the food-processing machinery. When the energetic demands of sit-and-wait predators and active foragers were compared, they found that the active-foraging strategy has a lower metabolic cost (resting metabolic rate plus specific dynamic action) than sit-and-wait predators when meals are frequent and small, but a higher metabolic cost when meals are infrequent and large. This interaction is caused by the balance between the metabolic benefit that sit-and-wait predators accrue between meals and the metabolic cost of reactivating the digestive machinery when they feed. Although such a broad interspecific comparison is again not ideal for characterizing evolutionary costs, it reinforces the idea that the machinery associated with acquiring resources can be costly to maintain.

Leroi *et al.*<sup>20</sup> provide a third example in which they discovered the evolution of resource acquisition ability in a selection

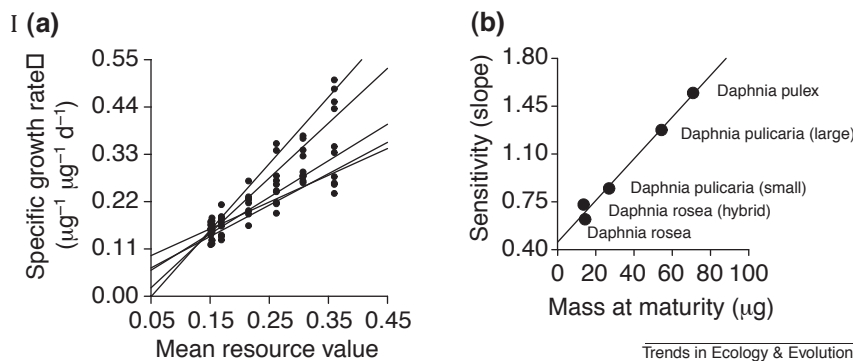
experiment on *Drosophila melanogaster*. They worked with the B- and O-lines (short-lived and long-lived, respectively) of fruit flies developed by Michael Rose<sup>21</sup>. B-line flies are kept on a strict 14-day generation, which means that the eggs for the next generation are collected from adults shortly after eclosion. O-line adults are kept on a maintenance diet for up to 70 days after eclosion, then the adults are given a yeast-enriched diet for two days before eggs are collected for the next generation. This long prereproductive hiatus selected O-line flies that had longer lifespans. This enhanced longevity was attained, at least initially, at the cost of reduced fecundity early in life. However, after ten years of selection, this fecundity cost apparently disappeared, thus the O-line flies had higher fecundity throughout their lifespans. Leroi *et al.*<sup>20</sup> demonstrate that this apparent disappearance of the tradeoff arose as a by-product of the O-line flies adapting to differences in the B- and O-line culture regimes. One key adaptation was their ability to acquire new resources more rapidly during the conditioning period and to allocate these resources to

### Box 3. Sensitivity of *Daphnia* to resource richness

*Daphnia* are cyclical parthenogens that can be maintained indefinitely as clonal lines. Five clones representing multiple species were simultaneously raised in six natural assemblages of food items from different lakes. Natural food includes planktonic bacteria, protozoa and algae. The specific rate of juvenile growth ( $g$ ) was estimated twice for each clone raised on each resource. Because daphniid juveniles gain dry mass exponentially until maturity,  $g$  is estimated as the slope of an ordinary least squares regression of the natural logarithm of dry mass ( $\mu\text{g}$ ) versus age in days (repeated sampling from replicated cohorts of equal-aged juveniles for each clone and resource; see Tessier *et al.*<sup>22</sup> for details). From life table studies it is known that  $g$  is a good predictor of stable age population growth ( $r$ ). Thus,  $g$  is a good estimate of the fitness of a clone for exploiting a given resource environment.

All clones exhibited the same rank preference, measured by  $g$ , for the different resources. However, there was a highly significant interaction between the clone and the resource environment (two-way ANOVA) indicating that the response of clones differed.

Joint regression analysis, which involves assigning each resource environment a quantitative value equal to the mean  $g$  of all clones raised on that resource, showed that this clone–resource interaction was largely explained by clonal differences in slopes of response to resource value (Fig. 1a). The slope for each clone was used as a measure of sensitivity to resource richness, and was found to be strongly associated with the mass of adults among the five clones (Fig. 1b). Figures reproduced, with permission, from Ref. 22.



reproduction. A consequence of this adaptation is that they only had higher fecundity than the B-flies when they were compared in 'O' conditions: the B-flies still had higher fecundity when they were compared in the 'B' conditions.

Our final example, and the one most appropriate to our argument, describes work carried out by Tessier *et al.* on inter- and intraspecific comparisons of *Daphnia*<sup>22</sup> (Box 3). Species of *Daphnia* and clones within species of *Daphnia* appear to face a tradeoff between adult body size and the ability to sustain specific growth rate (a measure of relative fitness; Box 3) at high versus low levels of resource availability. The comparisons included *D. pulex* (largest adult body size), large and small clones of *D. pulicaria* (second and third largest), *D. rosea* and *D. rosea*  $\times$  *mendotae* hybrids (smallest). Growth rate was evaluated for a range of food concentrations. Sensitivity of the growth rate to a decline in food availability was evaluated as the slope of the regression of specific growth rate on resource availability. These regressions all have positive slopes, meaning that specific growth rate increases with resource availability, but species and/or clones differ in the steepness of these slopes (Box 3). There was a strong positive correlation between the slope of this

regression and the body size of the adult species and/or clone. This correlation exists because the growth rate of large bodied species and/or clones declines more rapidly with food availability than small-bodied species and/or clones. There is a low theoretical value of resource availability, not evaluated in this study, where the low-sensitivity, small-bodied clones and/or species are predicted to have higher growth rates than the high-sensitivity, large bodied clones and/or species. This prediction has been confirmed elsewhere<sup>23</sup>.

Tessier *et al.* also evaluated the ability of these species and/or clones to sustain population growth in lake mesocosms by suspending polyethylene tubes in natural lakes, filling them with microcrustacea-free lake water and then adding a different study organism to each tube. Smaller bodied *Daphnia* species (and the smaller clone of *Daphnia pulicaria*), were able to reduce the available resources to a lower concentration than larger bodied species and/or clones. A plausible explanation for these results is that some *Daphnia* are better able to convert resources into reproduction, but only if resource availability is high. They do not seem to be able to sustain themselves when resources fall below some threshold value. In these leaner environments, the other *Daphnia* taxa

appear to have an advantage, perhaps because they are more efficient at using scarce resources or perhaps because their metabolisms require fewer resources for growth and reproduction. In either case, these results provide circumstantial evidence for higher costs of acquisition in some taxa, such that they are only superior when resource concentrations are high.

### Conclusions

The 'superflea' is real, but can only be super under particular environmental conditions. In our examples, the 'super' phenotype appears to be restricted to situations where resources are abundant. The interaction between resource availability and the relative fitness of *Daphnia* might be caused by the presence of a cost of resource acquisition. If such costs are present, they create the potential for sustained, positive genetic correlations among life history traits that are expected to be negative under the usual assumptions of life history theory. Thus, we postulate that there is genetic variation in resource acquisition ability, but that an enhanced ability to acquire resources is only attained with a cost. In *Daphnia*, that cost seems to be the requirement that resources are abundant. Such costs are different from the usual notion of costs of reproduction because the negative correlations are apparent across environments, or as genotype by environment interactions, rather than across life history traits within a single environment.

This 'high food and cost of acquisition' scenario is a special case of a genotype  $\times$  environment interaction. More generally, we expect that the suite of characteristics that maximize fitness can change as the environment changes. The relevant environmental variable could be resource level, temperature or, for plants, the chemical composition of the soil. Under such circumstances, positive correlations among fitness traits are to be expected.

Invoking genotype  $\times$  environment interactions provides a possible answer to the question of why 'superflea' genotypes fail to spread to fixation. They are advantageous only in certain places and/or at certain times. In conditions that vary through time and space, such interactions can maintain polymorphism<sup>24,25</sup>, particularly when the environmental variation is spatially distributed<sup>26</sup> or if there is a means of storing fitness gains through time (e.g. seed or egg banks<sup>27</sup>). Although there is currently little evidence to support the generality of our suggestion, other examples exist (e.g. Simmons and Roff's<sup>28</sup> work on crickets).

Together with the waterfleas, they provide models for different ways of thinking about the origins of puzzling genetic correlations.

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