



Allocation tradeoffs and life histories: a conceptual and graphical framework

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Tradeoffs – negative reciprocal causal relationships in net benefits between trait magnitudes – have not always been studied in depth appropriate to their central role in life-history analysis. Here we focus on allocation tradeoffs, in which acquisition of a limiting resource requires allocation of resource to alternative traits. We identify the components of this allocation process and emphasize the importance of quantifying them. We then propose categorizing allocation tradeoffs into linear, concave and convex relationships based on the way that resource allocation yields trait magnitudes under the tradeoff. Linear relationships are over-represented in the literature because of typically small data sets over restricted ranges of trait magnitudes, an emphasis on simple correlation analysis, and a failure to remove variation associated with acquisition of the limiting resource in characterizing the tradeoff. (We provide methods for controlling these acquisition effects.) Non-linear relationships have been documented and are expected under plausible conditions that we summarize. We note ways that shifting environments and biological features yield plasticity of tradeoff graphs. Finally, we illustrate these points using case studies and close with priorities for future work.

Tradeoffs shape life histories and ecological/evolutionary dynamics in nature (Stearns 1992, Tuda and Bonsall 1999, Roff 2002, Stearns and Hoekstra 2005, Roff and Fairbairn 2007) but pose empirical challenges (Mole 1994, Ebert and Bull 2003) and are seldom understood in depth. The basic concept is so intuitive that a negative correlation between traits linked to suppositions about them is sometimes considered sufficient documentation. Partial, qualitative, descriptive analysis, phenomenological rather than truly functional, has persisted in conjunction with a lack of conceptual clarity. Failure to grasp the causal linkages between constraints and the pattern of resource allocation has muddled the application of this central concept. Resource-related tradeoffs have been loosely categorized by the types of limiting resources that can constrain trait magnitudes, yet there have been few attempts to generalize across resources and draw other fundamental distinctions among tradeoff relationships.

Here we begin to address these issues with definitions and a conceptual diagram, presenting the logic of allocation tradeoffs stemming from the acquisition of limited resources in the context of natural selection. Based on the functional tradeoff relationship between traits, we propose a graphical classification scheme that highlights relatively unexplored territory. We link this scheme to empirical analysis, providing some new methods. Rather than re-hash the often-reviewed tradeoff literature, we note systematic omissions,

address instructive case studies, and then emphasize priorities for future work.

Definitions and logic

A tradeoff is a relationship between the magnitudes of two (or more) quantitative traits such that changes in the net benefits derived from one imply opposite changes in net benefits derived from the other(s). The core economic concept is based on amounts of a currency invested in alternatives under budget constraint (Fama and French 2002). In life-history analysis, the concept of the constraining ‘acquisition’ of a limiting resource and its resulting ‘allocation’ between traits representing conflicting demands is generally known as the Y model (van Noordwijk and de Jong 1986), the standard framework for allocation tradeoffs. We do not address acquisition tradeoffs – between resource acquisition and some alternative activity (Werner and Anholt 1993, Biro et al. 2006) – as a separate category, considering them to be another allocation tradeoff upstream of the focal allocation tradeoff (Angilletta et al. 2003, Berner and Blanckenhorn 2007, Boggs 2009, King et al. 2010, 2011). But we do consider the relationship between the amount of limiting resource acquired and the resolution of the allocation tradeoff (King et al. 2011). We avoid the oxymoronic “one-trait tradeoff” terminology (Agrawal et al.

2010) by identifying the trait in this case as the allocation pattern resulting from an allocation tradeoff.

Consider Fig. 1. An example of each tradeoff component, based on studies of a parasitoid wasp exploiting its host (Saeki et al. 2009, Crowley and Saeki 2009, Saeki and Crowley 2012, 2013), is shown to the right of each component. The constraint is the amount or supply rate of the limiting resource (e.g. host mass in Fig. 1), establishing the tradeoff currency. Common examples of these currencies include energy (King et al. 2010), nutrients (Arnott et al. 2006), biomass (Saeki et al. 2009), space or volume (Clauss et al. 2003), time (Marler et al. 1995), and metabolites (Sinervo 1999). Often the constraint differs from the limiting variable (e.g. brood mass in Fig. 1) that is directly subdivided to produce the allocations, and in this case the relationship between the two must be determined. The quantitative relationship between allocations is often linear or assumed to be linear, as when a pie (the limiting variable) is sliced into portions, but this relationship may instead be multiplicative (e.g. in Fig. 1) or some other functional type. The allocation pattern is the

resulting quantitative combination of allocations. Trait magnitudes may be directly established by allocation (e.g. in Fig. 1) or may depend on additional relationships that must be specified (e.g. if energy allocation triggers a cascade of processes that result in enhanced immune function). Ways that the environment imposes selection on trait magnitudes connect the allocation pattern to its fitness implications.

A graphical classification scheme

Different types of linkage between allocations in a tradeoff and the mathematical forms of this relationship provide a useful means of classifying tradeoffs independently of constraint currency. We illustrate three different main types and then describe a general procedure for distinguishing among them.

'Linear' tradeoffs arise when allocations to traits are additive based on a fixed sum available through the limiting variable – and when each trait magnitude increases in proportion to the amount allocated to it (Fig. 2A). This

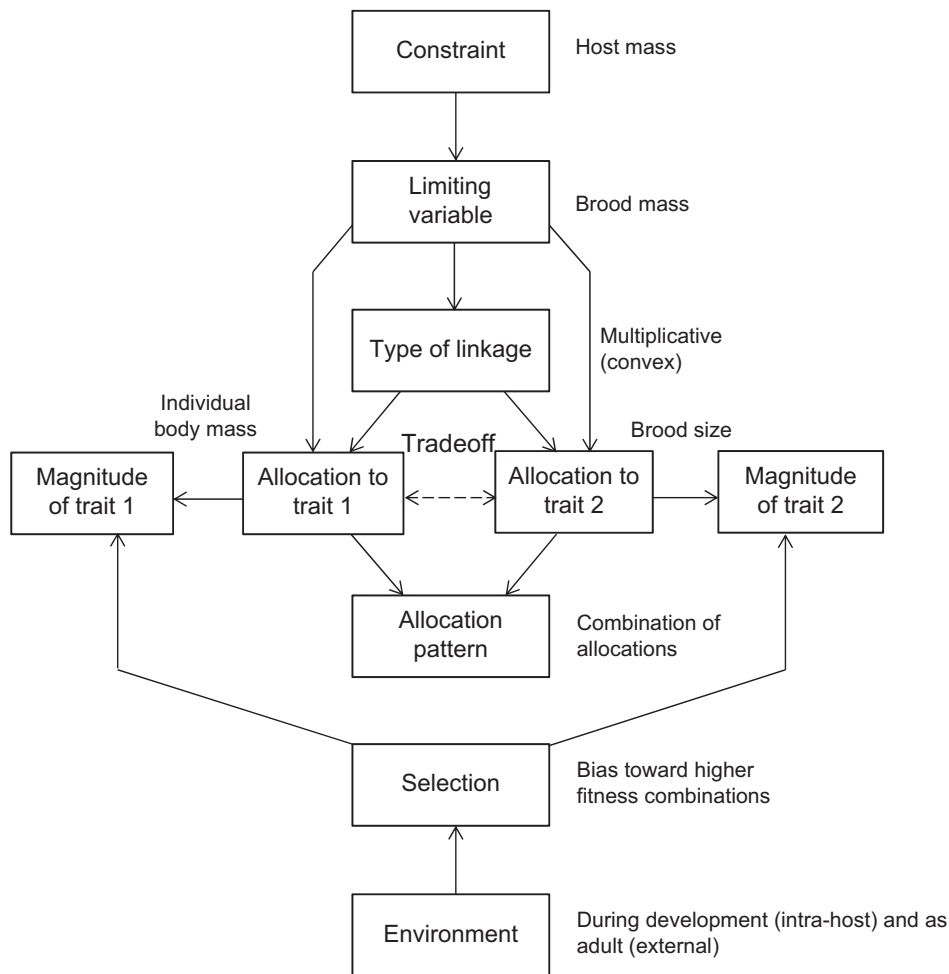


Figure 1. Components of a tradeoff. Once the *constraint* is identified and characterized, the *limiting variable* that is subdivided in support of traits 1 and 2 is quantified empirically. The most informative *type of linkage* between traits is recognized, from which the *allocation to traits* and *magnitudes of the traits* are established empirically. The combination of allocations is the *allocation pattern*. Finding the ways that the *environment* influences *selection* and selection adjusts the allocation pattern to increase fitness is a major empirical challenge. Beside or above the boxes are examples of each factor, based on the size–number tradeoff in parasitoid wasps; in this case, trait allocations and magnitudes are the same.

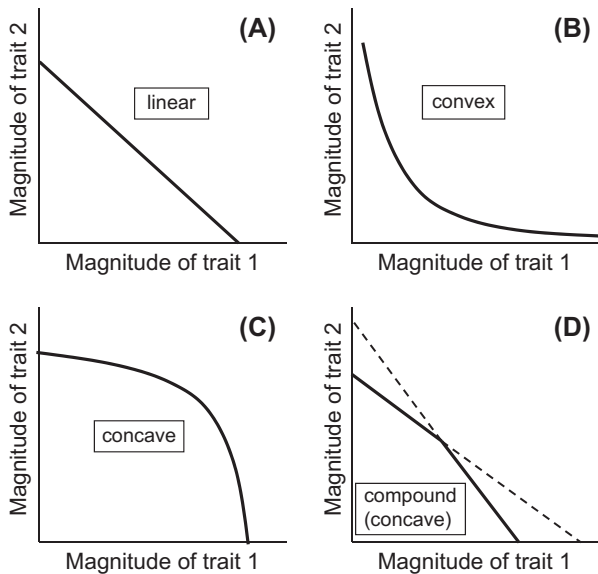


Figure 2. Shapes of tradeoff curves that provide a useful means of classifying tradeoffs. (A) Linear, based on additive linkage. (B) Convex, which includes the multiplicative linkage type as a special case. (C) Concave—the smooth-curve version. (D) Intersecting compound curves that form a concave shape from the segments closest to the origin.

is allocation by slicing the pie and can be easy to recognize, but the relationship between allocation and trait magnitude is determined far less often. Linear tradeoffs are believed to be common (e.g. growth rate vs reproductive rate: Fischer and Fiedler 2002, Stearns and Hoekstra 2005, Jørgensen and Fiksen 2006, Bolmgren and Cowan 2008; survival vs current reproduction: Tatar and Carey 1995, Sevenster et al. 1998, Karlsson et al. 2008; reproductive rate vs locomotor performance: King et al. 2010). But many putatively linear patterns are simply a first approximation obtained from small data sets, from negative correlations incorporating enough random variation to obscure the actual underlying trend, or from data based on varying constraint (acquisition) magnitudes. Effects of variation in constraint magnitudes can be evaluated and if necessary removed from the graphical relationship by transformation (Appendix 1) or removed as a co-variate in statistical analysis.

‘Convex’ tradeoffs arise when increasing allocation to either trait increases the trait magnitude in an accelerating fashion (Fig. 2B), which may indicate accelerating net benefits (Jessup and Bohannan 2008). In the best-known subset of these, the limiting variable is the multiplicative product of the two trait allocations (e.g. offspring body mass vs brood size: Smith and Fretwell 1974, Sinervo and Licht 1991, Sadras 2007, Paul-Victor and Turnbull 2009, Saeki et al. 2009, Saeki and Crowley 2012; reproductive investment vs somatic maintenance: Rosenheim 1996). Whereas linear tradeoff relationships require two parameters for specification, multiplicative relationships require only one, because the inverse relationship already determines the shape characteristics of the curve. Despite the insights to be gained from recognizing the multiplicative relationship, such tradeoffs may frequently remain incognito.

Multiplicative relationships are to be expected for tradeoffs between intensity and duration (e.g. locomotion speed vs time spent moving, with total distance moved as a constraint; growth rate vs time to reach a certain size), between quality and quantity (e.g. offspring mass or parental care investment per offspring vs offspring number), or between rates and efficiencies (e.g. rate of food processing in an animal’s gut vs the fraction of the food assimilated, constrained by total amount assimilated). For the multiplicative case, acquisition-dependence and its potential removal by transformation are also addressed in Appendix 1.

‘Concave’ tradeoff relationships (Fig. 2C) have commonly been assumed or derived in theoretical studies (Schaffer 1974, Bell 1980, Charnov and Skinner 1984, Charnov 1986, Hernandez and León 1995, Yoshida 2006). Concave relationships could result from diminishing returns or accelerating costs associated with a high level of allocation to either of the two traits (e.g. parental reproductive effort vs survival and growth: Schaffer 1974). In other words, more allocation to one trait yields a disproportionately small increase in that trait’s magnitude but a disproportionately large reduction in the other trait’s magnitude. Another mechanism involves compound constraints based on stoichiometry: when the tradeoff relationships constrained by different potentially limiting nutrients intersect, it is the line-segments closest to the origin that apply, yielding a concave shape with one or more kinks in it (Fig. 2D). Despite these plausible expectations, there were apparently no empirical demonstrations of concave relationships in the literature (Rueffler et al. 2004, Michod et al. 2006) until a recent study of bacteria and bacteriophage (Jessup and Bohannan 2008), considered in the case studies below.

A general procedure for distinguishing among the three general tradeoff curve shapes begins with a fit to data for the respective allocations z_1 and z_2 to traits 1 and 2 according to $z_2 = a + bz_1$ using model 2 regression (Warton et al. 2006). If the entire confidence interval surrounding the mean for parameter a lies above 0 and for parameter b lies below 0, the relationship is consistent with (though not definitive for) a tradeoff. Next, using nonlinear model 2 regression (Ebert and Russell 1994, Kegl et al. 2000) or maximum likelihood methods, the quadratic relationship $z_2 = a + bz_1 + cz_1^2$ is fit to the data. For the regression, assuming $a > 0$ and $b < 0$ as before, then the confidence interval of the $c > 0$ indicates a convex relationship, and $c < 0$ implies a concave relationship. For maximum likelihood, the model with the lower AIC value (Akaike 1974), the best combination of precision and low dimensionality, is selected. If the linear model is thus chosen, the tradeoff can be considered linear. Otherwise, the tradeoff is nonlinear and either convex or concave, depending as above on the sign of c .

Special cases may allow additional tests to better characterize the relationship. For example, in the case of a possible multiplicative tradeoff, the allocation variables can be log-transformed, and the resulting linear relationship checked to see if the confidence interval of the slope includes -1 using model 2 regression. Similarly, a linear-bent relationship can be tested for the best fit to two linear relationships, comparing against a single linear relationship or a concave continuous curve via AIC evaluation.

Plasticity of tradeoff relationships

Shapes and magnitudes of tradeoff relationships may vary among environmental conditions (Sibly and Calow 1989, Jessup and Bohannan 2008), life stages (Schaffer 1974), sexes (Saeki et al. 2009) and species (Charnov and Skinner 1984). These factors (jointly referred to as environment) may alter 1) the magnitude of the constraint(s) on the tradeoff relationship (Bohannan et al. 1999, Saeki and Crowley 2013), 2) the curve shape or slope instead of or in addition to any effects on the constraint(s) (Bohannan et al. 2002), and/or 3) the allocation pattern generated along the tradeoff curve (Stearns 1992, Saeki and Crowley 2013, Saeki et al. 2009 show sex differences in allocation pattern along the same tradeoff curve) (Fig. 3, 4).

Plastic responses to different environments are essential for species developing in variable conditions (Fischer et al. 2011). These plastic responses may be genetically-based (reviewed by Via et al. 1995, Moczek et al. 2011), and plasticity of the two traits settling at an allocation pattern is subject to natural selection (Nylin and Gotthard 1998). For example, higher temperature can cause ectothermic organisms to develop faster but with smaller adult body sizes (e.g. damselflies in De Block and Stoks 2003, and parasitoid wasps in Saeki and Crowley 2012). High food availability can shorten development time, resulting in smaller adult body size (Johansson et al. 2001), while low food availability lengthens development time and decreases body size and longevity (Agnew et al. 2002). The timing of food availability during development also influences these patterns (Saeki and Crowley 2013).

When the acquired resources are allocated to different traits, the allocation that maximizes fitness may vary among environments (van Noordwijk and de Jong 1986,

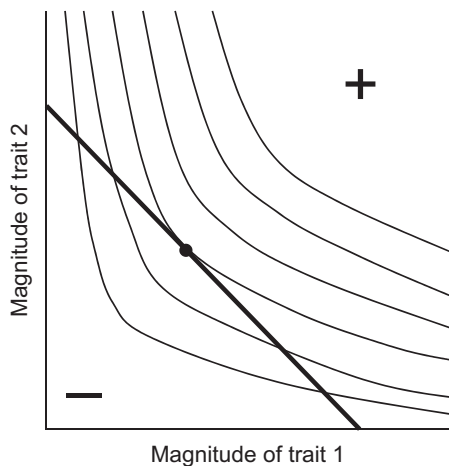


Figure 3. The optimal allocation pattern (black dot) is the point along the tradeoff curve (heavy line) at which one of the fitness contours (curved lines) is tangent. Each contour line represents all combinations of trait magnitudes corresponding to a particular value of fitness, such that contours more toward the upper right indicated increasingly higher fitness. Thus the optimal allocation pattern is the combination of trait magnitudes along the tradeoff curve corresponding to the highest achievable fitness. This is based on the classic analysis of Levins (1962) and can accommodate frequency-dependent fitness under both evolutionary and convergence stability (de Mazancourt and Dieckmann 2004).

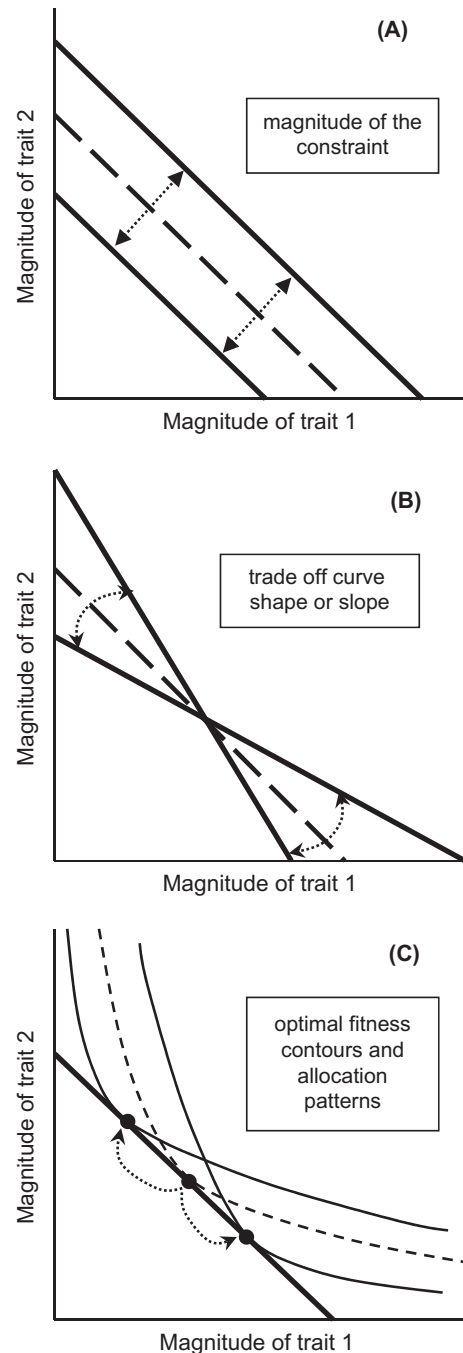


Figure 4. Environmental effects on tradeoff curves and allocation patterns. Dashed lines indicate reference conditions for comparison with the solid lines for altered conditions A. (A) relaxed constraint yields a higher limiting variable, moving the tradeoff line up and to the right, whereas a more stringent constraint has the opposite effect. (B) Altered environmental conditions may instead or in addition change the shape or slope of the tradeoff curve. (C) A modified environment may shift the fitness contours, moving the optimal allocation pattern along the tradeoff curve.

Roff 2002, Worley et al. 2003, Malausa et al. 2005) in accord with shifting fitness contours (Stearns 1992). For example, in the progeny size–number tradeoff when the mother controls the allocation, she optimizes individual offspring mass and total number within a finite total mass

of resources available in the given environment. She thereby maximizes the number of her grand-offspring, presumably corresponding to the tangent point on the highest-fitness contour (Fig. 2; Smith and Fretwell 1974, Saeki et al. 2009). Documenting allocation patterns and tradeoff curves across environments would provide empirically testable predictions and help clarify complex responses of the two traits in dynamic environments.

Three case studies

The tradeoff between flight capability and reproduction in the sand cricket *Gryllus firmus*

The sand cricket system and the tradeoff in adults between flight capability and reproduction have been extensively studied (Harrison 1980, Dingle 1996, Zera and Denno 1997). Recent work by King and colleagues (2011) used this tradeoff to test the Y model of van Noordwijk and de Jong (1986). Based on the means and variances of proportional allocation and the magnitude of acquisition, the Y model predicts the covariance between the two traits in a linear allocation tradeoff. Acquisition was estimated as energy obtained and devoted to the two traits. By quantitatively relating energy allocated to reproduction and flight capability to the corresponding ovary and flight muscle masses, the tissue masses could then be used as allocation proxies. Experimental manipulation of the environment (food levels) allowed direct tests that corroborated the Y model. This is an unusually complete implementation of the approach described in Fig. 1, though the impact of selection was not directly assessed.

The Y model provides an explanation for weak or undetectable tradeoff relationships when the magnitude of acquisition varies substantially (Spitze et al. 1991, Reznick et al. 2000, Vorburger 2005). An assumption of the model – that variation in acquisition and in proportional allocation are independent – was also tested by King et al. (2011) and found to be violated (see also Christians 2000). The crickets allocated more energy to reproduction than to flight capability at higher levels of acquisition. There are many other examples of allocation varying with acquisition for other tradeoffs as well (Gebhardt and Stearns 1988, Ellers and van Alphen 1997, Ruf et al. 2006). Our Appendix 1 is complementary to the Y model in providing a means of removing variation in acquisition to uncover the tradeoff relationship, including when allocation is linked to the magnitude of acquisition (i.e. when the allocation bias $\beta_1 \neq 0$) – and for both linear and multiplicative linkage types.

The tradeoff between body mass and brood size in the parasitoid wasp *Copidosoma bakeri*

The size–number tradeoff is well studied across plants and animals (Roff 2002), but rarely are more than two or three of the tradeoff components of Fig. 1 measured, and the linkage is not always recognized as multiplicative. As a polyembryonic parasitoid, *C. bakeri* produces large clonal broods, permitting precise, sex-specific assessment of the tradeoff. In Saeki et al. (2009) and Saeki and Crowley (2013), most components and relationships of Fig. 1 were measured for both sexes and in different environments

(Saeki and Crowley 2012, 2013). The role of selection was addressed in a preliminary model (Crowley and Saeki 2009) and is the focus of work in progress (PHC, Paul Ode and Éric Wajnberg). The tradeoff relationships are convex and statistically consistent with the multiplicative relationship between trait magnitudes.

Two methods from these studies are of general importance in tradeoff analyses. One is statistical transformation to remove variation in constraint (and limiting variable) magnitude from the data so that the tradeoff relationship can be displayed graphically. A special case of the methods presented in Appendix 1 was used by assuming no trait bias ($\beta_1 = 0$) (Saeki et al. 2009). The other method is model 2 regression (Warton 2006), in which the regression variables are assumed to be equally and reciprocally causal. This mutual dependence rules out model 1 regression, in which an independent variable's magnitude is assumed to determine the dependent variable's magnitude. The distinction between regression models is important, because any random variation in the tradeoff relationship implies that the best-fit tradeoff function will be inaccurately estimated by model 1 (Saeki et al. 2009), as in many published studies.

By manipulating food availability at different developmental stages of host and wasp, Saeki and Crowley (2013) documented shifts in tradeoff relationships: the magnitude of the host-mass constraint (as in Fig. 4A) and the position of the allocation pattern along the tradeoff curve in response to differences in brood sex (Fig. 4C). In contrast, a study of responses to temperature in this system detected no consistent shift in tradeoff relationships (Saeki and Crowley 2012).

The tradeoff between virus resistance and competitive ability in the bacterium *Escherichia coli* B

All three of these types of responses and all three basic tradeoff curve shapes from Fig. 2 (A–C) were documented in work on *E. coli* B and the bacteriophage T2 (Jessup and Bohannan 2008). Under three different culture conditions in that study (glucose-limited batch, trehalose-limited batch, and glucose-limited continuous culture), responses by 86 genetically distinct isolates of the bacteria documented the tradeoff between competitive ability and resistance to phage T2. This appears to be the most comprehensive empirical demonstration of graphical patterns and environmental effects to date for a single tradeoff relationship.

This study contrasts with others we address by including the impact of natural selection on the phenomena of interest and because the tradeoff arises from antagonistic pleiotropy rather than from constraints on the allocation of limiting resources (also see Guillaume and Otto 2012). Bacterial surface proteins that facilitate uptake of sugars are also docking targets of bacteriophage, so that certain mutations may interfere with these functions differentially, resulting in different tradeoff relationships between competitive ability and phage resistance of the bacteria. The measures used for competitive ability (i.e. the ratio of relative Malthusian growth rates for a particular isolate relative to that of a phage-susceptible control) and for phage resistance (i.e. the ratio of mortality rate for the isolate relative to that of the phage-susceptible

control, subtracted from one) seem reasonable. But there are many possible alternatives, implying that the documented curve shapes have comparative meaning rather than a direct functional interpretation and thus convey less specific information than those in Fig. 2. This underscores the advantage of the approach in Fig. 1 for allocation tradeoffs: the ways that constraint magnitudes lead to trait magnitudes are fully specified.

Priorities for future work

With the central role of tradeoffs in life history analysis long established and many diverse examples documented or under study, an important goal is analyze tradeoffs more systematically and thoroughly: the bar for these studies needs to be raised. For allocation tradeoffs, the approach in Fig. 1 emphasizes expressing acquisition of limiting resource in units of currency, quantifying its partitioning by allocation to traits as an allocation pattern, and determining the trait magnitudes that correspond to these traits. There will always be a place for partial descriptions of tradeoffs and their graphical representation, but life-history analysis will advance more rapidly as the basis for allocation patterns in nature is analyzed in greater depth and ultimately understood at a functional level (Zera and Harshman 2001).

The graphical classification scheme proposed here requires a mechanistic understanding of trait linkage and the logical basis for allocation. Future studies following this approach should identify non-linear tradeoff relationships by minimizing or statistically removing variation in acquisition and using model 2 regression to avoid the biasing effects of model 1. Also, linking tradeoff studies to natural selection in the field and evolutionary dynamics of microbial systems in the laboratory will provide a much more complete picture of how tradeoffs give rise to successful life histories in nature.

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Appendix 1

Acquisition-dependent allocation

Here we derive transformations to remove any effects of differences in acquisition - determining the total amount to be allocated - on magnitudes of traits in additive and multiplicative allocation tradeoffs. We take account of possible biases in allocation between traits and indicate how to obtain confidence intervals for proportional allocations and bias.

Let A_1 be allocation to trait 1, let A_2 be allocation to trait 2, and let Q be the total acquisition that must be allocated to traits 1 and 2. Let \bar{A}_1 , \bar{A}_2 , and \bar{Q} be the corresponding means over observations in the data set. First consider an additive (linear) tradeoff, such that $A_1 + A_2 = Q$. At \bar{Q} , the proportion of total acquisition allocated to trait 1 is $\bar{A}_1/(\bar{A}_1 + \bar{A}_2)$, and the proportion allocated to trait 2 is $\bar{A}_2/(\bar{A}_1 + \bar{A}_2)$. Let β_1 ($-1 \leq \beta_1 \leq 1$) be a measure of bias favoring trait 1 when acquisition changes from \bar{Q} to $Q \neq \bar{Q}$. Allocation of additional acquisition $Q - \bar{Q}$ may favor one trait over the other (i.e. $\beta_1 \neq 0$). Taking bias into account by weighting the mean allocations, these proportional allocations become

$$\alpha = \frac{(1 + \beta_1)\bar{A}_1}{(1 + \beta_1)\bar{A}_1 + (1 - \beta_1)\bar{A}_2} \text{ and}$$

$$1 - \alpha = \frac{(1 + \beta_1)\bar{A}_2}{(1 + \beta_1)\bar{A}_1 + (1 - \beta_1)\bar{A}_2}, \text{ respectively.}$$

Notice that without bias (i.e. $\beta_1 = 0$), α and $1 - \alpha$ are unchanged from their magnitudes at \bar{Q} . But bias favoring trait 1 increases the proportion α and decreases $1 - \alpha$, while bias favoring trait 2 has the opposite effects on magnitudes of the proportions. When $\beta_1 = 1$, all additional acquisition goes to trait 1, whereas $\beta_1 = -1$ means that all additional acquisition goes to trait 2.

Under the assumption that shifts in allocation to each trait remain proportional to the shift in acquisition even with biases present, we can find acquisition-dependent allocations for the additive case using the proportional allocations determined above:

$$A_1 - \bar{A}_1 = \alpha(Q - \bar{Q}) \text{ and } A_2 - \bar{A}_2 = (1 - \alpha)(Q - \bar{Q}).$$

A confidence interval on α can be obtained by model 1 regression between the independent acquisition variable $Q - \bar{Q}$ and the dependent allocation variable $A_1 - \bar{A}_1$, and the β_1 values can be calculated from the confidence limits via the above equation for α . If these limits include zero, then

bias is considered to be negligible (i.e. no bias has been demonstrated statistically); otherwise, the sign and magnitude of the bias are found from α .

These relationships also provide the basis for transforming data to remove the effects of differences in acquisition that mask the tradeoff pattern. Let A'_1 and A'_2 be the transformed allocations with acquisition effects removed. These variables simply replace A_1 and A_2 , respectively, and then solving yields

$$A'_1 = A_1 - \alpha(Q - \bar{Q}) \text{ and } A'_2 = A_2 - (1 - \alpha)(Q - \bar{Q}).$$

To evaluate the possibility of a non-linear relationship between the shift in allocation and the shift in acquisition, we can include a quadratic term, resulting in

$$A_1 - \bar{A}_1 = \alpha(Q - \bar{Q}) + \theta(Q - \bar{Q})^2$$

and

$$A_2 - \bar{A}_2 = (1 - \alpha)(Q - \bar{Q}) - \theta(Q - \bar{Q})^2,$$

where θ is the quadratic coefficient. If regression analysis determines a confidence interval around θ that fails to include zero, then the magnitude of bias depends on acquisition. Fully characterizing the acquisition-dependence of bias and thus allocation in that case would require a more complex analysis than can be presented here.

Now consider a multiplicative tradeoff, such that $A_1 A_2 = Q$. Acquisition-dependent allocations for the multiplicative case are

$$\frac{A_1}{\bar{A}_1} = \left(\frac{Q}{\bar{Q}}\right)^\gamma \text{ and } \frac{A_2}{\bar{A}_2} = \left(\frac{Q}{\bar{Q}}\right)^{1-\gamma}, \text{ where}$$

$$\gamma = \frac{1 + \beta_1}{2} \text{ and thus } 1 - \gamma = \frac{1 - \beta_1}{2}.$$

Here again γ (the equivalent of α for the multiplicative case) can be estimated by model 1 regression from $\log(A_1/\bar{A}_1) = \gamma \log(Q/\bar{Q})$; confidence limits of β_1 are found from the confidence limits of γ , and magnitudes of β_1 are interpreted as for the additive case. The transformed variables A'_1 and A'_2 are $A'_1 = A_1 \left(\frac{\bar{Q}}{Q}\right)^\gamma$ and $A'_2 = A_2 \left(\frac{\bar{Q}}{Q}\right)^{1-\gamma}$. Note that in the unbiased case with $\beta_1 = 0$, $\gamma = 1 - \gamma = 0.5$, as in Saeki et al. (2009).