Traits traded off

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Contents

General Introduction

Two threads link the chapters of this thesis. Firstly, how do two traits evolve when they are coupled by a trade-off such that a fitness enhancing change in one trait entails a correlated response detrimental to fitness in another trait? Secondly, how is the evolutionary dynamics of such correlated traits affected by frequency-dependence, that is, by circumstances where the performance of a focal phenotype depends on the phenotype distribution of all conspecifics?

General Introduction

Trade-Offs

Evolutionary constraints must exist. Without constraints, organisms would evolve to live forever and to produce an infinite amount of offspring at an infinite rate. This is not what we observe in nature, and common sense suggests that such organisms cannot exist in a finite world. Trade-offs are a particular type of constraint, which appears as a strong coupling between different components of the phenotype such that these cannot evolve independently. Trade-offs are ultimately caused by functional constraints imposed by limited energy and time, or by other laws of physics (Arnold, 1992). A widespread idea among scholars of life-history theory is that such constraints are manifested at the level of the gene as antagonistic pleiotropy (Stearns, 1992; Bulmer, 1994; Charlesworth, 1994; Roff, 2002). This means that a single gene controls two or more seemingly unrelated traits in an antagonistic way. On a more proximate level hormones are a major regulatory intermediary for life-history traits (Ketterson and Nolan, 1992; Finch and Rose, 1995; Sinervo and Svensson, 1998). West-Eberhard (2003) stresses the importance of development as an underlying cause for trade-offs, for instance, in the form of internal resource competition for different developmental processes. Throughout this thesis it is assumed that phenotypic variation in two scalar traits subject to a trade-off occurs along a one-dimensional manifold, the trade-off curve (fig. 1). The rationale behind this choice is that selection will push the phenotype distribution close to the constraint relative to the mutational step size and from then onward keep it there. Different trade-off curves correspond to different outer boundaries of the set of possible phenotypes. Arnold (1992) refers to this scenario as the Charnov-Charlesworth model for equilibrium genetic covariance for a single pair of traits (cf. Charnov, 1989; Charlesworth, 1990).

The assumption that trade-offs exist lies at the very heart of life-history theory (Stearns, 1992; Roff, 2002) and functional morphology (Alexander, 1996). Mathematical models predict that the realized compromise between traits subject to a trade-off will often depend on the exact form of the correlated response to selection, or, in other words, on the curvature of the trade-off (Levins, 1962; Stearns, 1992; Roff, 2002). When intermediate phenotypes suffer from high costs in terms of the fitness benefits of the involved traits (strong trade-off) extreme phenotypes sacrificing one function for the other are expected. If, however, intermediate phenotypes perform relatively well on the different tasks when compared to extreme phenotypes (weak trade-off), then phenotypes showing a compromise between the different extremes are favored. Empirical knowledge of such curvature properties seems to be extremely scarce and this constitutes a major gap between empiricism and theory. For trade-offs that are manifested at the level of morphology, data suggest that trade-offs are more often strong than weak (Benkman, 1993; Schluter, 1993, 1995; Robinson, 2000; O'Hara Hines et al., 2004). Data on other kinds of trade-offs are dearly lacking.

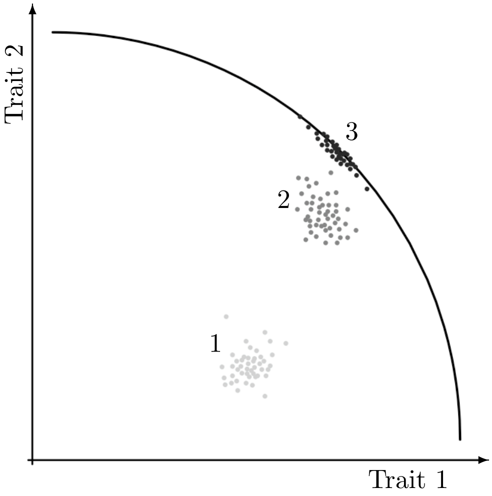

Figure 1: Trade-off curve for two traits coupled by a trade-off. It is assumed that fitness is an increasing function of both traits and that all trait combinations lying below the trade-off curve are biologically feasible while no genetic variation exists for trait combinations above the trade-off curve. Consider a population with a mean trait value far below the possible maximum value for both traits (1). Selection acts to increase both trait values simultaneously such that the phenotype distribution moves closer to the constraint (2). Close to the trade-off curve phenotypic variation in the direction orthogonal to the trade-off decreases when compared to variation in the direction of the constraint. Once the majority of the of the population has reached the constraint (3) the mean phenotype stays close to it relative to the mutational step size and phenotypic variation is restricted to be parallel to the constraint.

Frequency-Dependent Selection

Frequency dependence occurs because of direct or indirect interactions within a population. For example, frequency dependence can arise when individuals fight in pairwise contests for resources. In this case the fighting ability of all encountered opponents determines the costs and benefits resulting from contests. Alternatively, frequency dependence can be mediated through components of the environment. Whether a certain resource is widely abundant or not will often depend on the ability of conspecifics to find and pursue items of that particular resource. While it might be easy to agree on the meaning of frequency dependence on this verbal level, it is less trivial to define frequency dependence in a formal mathematical manner. The notion of frequency dependence arose in the context of population genetics and there it is defined as the dependence of selection coefficients on allele frequencies (e.g. Li, 1955; Wright, 1969). The theory of population genetics deals with changes in allele frequencies over short time periods. In this context it might be permissible to ignore the effect of population density as it is done in most classical models of population genetics. However, the population genetics' definition of frequency dependence is of little discriminating power when evolution is studied over long time scales as a sequence of mutation and substitution events. In this context density dependence cannot be ignored. An allele might have a fitness advantage when rare but loses its advantage after it has gone to fixation, and the population is at its population dynamical equilibrium. If one would apply the classical definition of population genetics to invasion fitness expressions, selection is always frequency dependent and the term becomes meaningless (Heino et al., 1998). A possibility for a meaningful definition of frequency dependence in the context of long term evolution should allow discriminating between cases where the direction of evolutionary change depends on the frequency of the different phenotypes within a density-regulated population. A definition will be given here that closely follows Heino et al. (1998). As mentioned above, frequency dependence arises from interactions between individuals. From the viewpoint of a focal individual all conspecifics can be considered as part of its environment. To accommodate cases where interactions are mediated by some component of the common environment such as resources, predators or parasites, it is useful to introduce the concept of "feedback environment". The feedback environment describes those components of the environment that are determined by the resident population and simultaneously feed back to affect the fitness of individuals in the population. Each of its components, called interaction variables, channels effects of population density and composition in a specific way to demographic parameters. On an ecological time scale, the defining property of the feedback environment is that individuals become independent of each other when the feedback is given as a function of time. On this time scale the trait values of the interacting individuals are assumed to be fixed and it is sufficient to collect the densities of the different types in the feedback vector. On an evolutionary time scale the trait values of the interacting types can change and in order to achieve independence between individuals on this time scale, the feedback environment has not only to account for the densities of the conspecifics but also for any direct effect through their traits. The dimension of the feedback environment, i.e., the number of interaction variables collected in the feedback environment, has important consequences. It constitutes an upper limit for the number of phenotypes that can possibly coexist (Meszéna et al., 2006). Consequently, whenever two types compete with each other in a one-dimensional feedback environment, one type will win over the other. For instance, if the interaction variable represents a resource, the type that can maintain a positive relative growth rate on a lower resource level will drive the other to extinction. In other words, when two types compete in a frequency independent setting one will show a positive and the other a negative relative growth rate, independent of the frequency of the two types. This holds true until one type has gone to fixation, so that its growth rate is zero, provided it has settled on its population dynamical attractor. On the other hand, if interactions are regulated via more than one interaction variable, the sign of the relative growth rate of each of the two competing types can change from positive to negative or vice versa as a consequence of altered frequencies. Hence, it seems natural

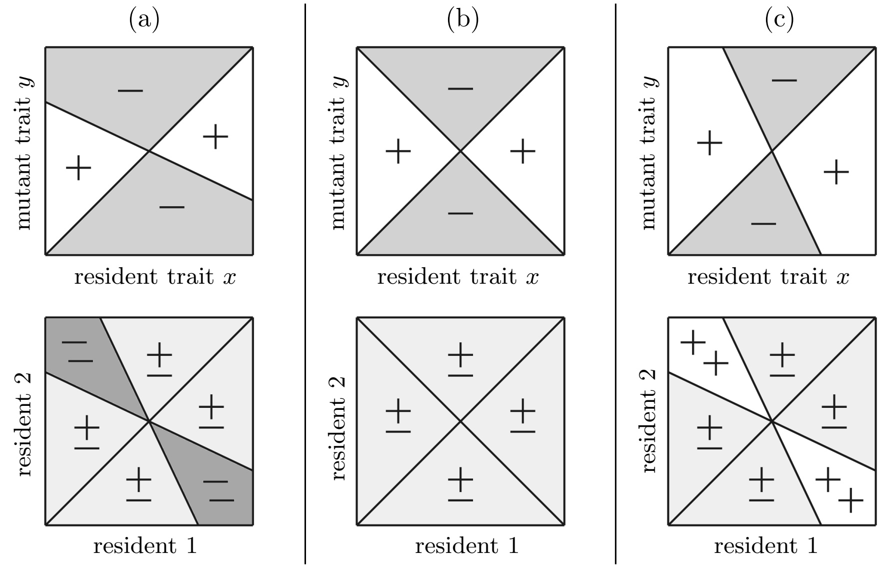

Figure 2: **Top row:** Three pairwise invadability plots (PIPs). These are contour plots of invasion fitness of a mutant with trait value y given a resident population with trait value x. Areas marked with a plus sign correspond to combinations of mutant and resident traits such that mutants have a positive probability to invade whereas areas marked with a minus sign correspond to trait combinations such that the mutant is unable to invade. All three PIPs depict a situation where the singular point (the trait value given by the intersection of the two zero-contour lines) is both an attractor of the evolutionary dynamics (convergence stable) and uninvadable by any mutant type. **Bottom row:** Plots depicting the ability of two types to invade each other. These plots are derived from the corresponding PIPs by plotting the PIP and its mirror image around the diagonal on top of each other. Each axis corresponds to the trait value of one type and the sign structure indicates whether each type in a given pair can invade the other one when rare itself (++ region) or whether each type in such a pair has a negative invasion fitness (−− region) or whether one type is superior over the other and going to replace it after invasion (+− region). The three PIPs differ in the slope of the non-diagonal zero-contour line giving rise to different sign patterns.

to refer to selection in feedback environments with more than one dimension as frequency dependent while selection in one-dimensional feedback environments should be considered as frequency independent. This is the meaning in which these terms are used in this thesis. Heino et al. (1998) refer to frequency dependence according to this definition as "weak frequency dependence" as opposed to "trivial frequency dependence" in one-dimensional feedback environments. In case of negative frequency dependence a focal type can have a positive growth rate when rare and a negative growth rate when common and in case of positive frequency dependence it can have a negative growth rate when rare and a positive growth rate when common.

Whether frequency dependence according to the above definition is present in a specific model can often be deduced from pairwise invadability plots (PIPs) (Metz et al., 1996*a*; Geritz et al., 1998). Figure 2 depicts three selection scenarios that all result in convergence to an intermediate trait value that, once adopted by the majority of the population, is uninvadable by any other type. The three scenarios differ in the slope of the non-diagonal zero-contour line, which is rotated clock-wise from figure 2a to figure 2c. This results in different patterns of mutual invadability. The plots in the bottom row of figure 2 show the ability for two types to invade each other. The area marked with $(--)$ in the bottom plot of figure 2a corresponds to pairs of phenotypes where each type has a positive growth rate when common and a negative growth rate when rare. This is the signature of positive frequency dependence. In figure 2b the PIP is skew symmetric, meaning that the sign pattern below and above the diagonal are reversed and mirrored around the diagonal. In this constellation any type that has a positive growth rate when rare will increase in frequency until fixation. The sign of the growth rate cannot change from positive to negative or vice versa. The bottom plot in figure 2c shows an area marked by $(++)$, indicating that trait combinations in this area have each a positive growth rate when rare and a negative growth rate when common. Such types can coexist in a protected dimorphism and it indicates the presence of negative frequency dependence.

The three described scenarios could be specific cases of the very same model where one parameter is altered such that the non-diagonal zero-contour line turns clockwise in a continuous manner. In this case the intraspecific interactions in the underlying model are frequency dependent and figure 2b corresponds to the non-generic case that separates scenarios with positive frequency dependence from those with negative frequency dependence. Alternatively, figure 2b could illustrate the results of a different model that lacks frequency dependence, because the picture is in accordance with the absence of frequency dependence as described above. In fact, in the absence of frequency dependence PIPs are skew symmetric by necessity. The observation that under frequency independence a change in the sign of the relative growth rate is impossible translates into the absence of both $(++)$-regions and $(--)$-regions in the type of plot shown in the bottom row of figure 2. Hence, all combinations of two phenotypes lie in a $(+-)$-region, which requires skew symmetry. It is important to realize that selection is frequency dependent for all combinations of phenotypes in models corresponding to a PIP that is not skew symmetric. Scenarios that do allow for coexistence, show special cases of negative frequency dependence to which Heino et al. (1998) refer as “strong frequency dependence”.

Why is it interesting to focus on the evolution of traits that are traded off on the one hand and that are subject to frequency dependence on the other hand? In the absence of frequency dependence we expect that evolution comes up with a compromise of the competing fitness components that is optimal in the sense that no other realized compromise can be more successful. With frequency dependence this idea becomes fuzzy. What is optimal in one environment might be maladaptive in another environment and when conspecifics constitute part of the environment it is less straightforward to predict the course of evolution. With frequency dependence each component in a fitness trade-off can be affected by the phenotypes of the conspecifics which causes the fitness landscape to change in a continuous manner as evolution proceeds. This thesis investigates how frequency dependence can be detected in a given model and how it alters the evolutionary dynamics.

Outline of the Thesis

The first two chapters are similar in spirit in the sense that both present a classification of models that involve two evolving traits coupled by a trade-off. In **chapter 1** this classification is done in terms of two geometric properties that are held in common by all evolutionary models that involve two evolving traits subject to a trade-off, the trade-off curve and the contour lines of the fitness landscape. The presented approach can be seen as an extension of Levins' graphical fitness set approach (Levins, 1962, 1968) because it is based on the same ingredients. Levins' approach is limited by the assumption that the fitness landscape is fixed, a scenario that corresponds to the absence of frequency-dependence. In chapter 1 this assumption is relaxed and the focus is on fitness landscapes that change with the population state. It appears that all relevant information from the fitness landscape can be deduced from a single contour line, the "invasion boundary". It is given by all phenotypes in trait space that are initially selectively neutral with respect to a given resident community. The direction of evolutionary change at any resident type follows from the intersection pattern of the trade-off curve and the invasion boundary at the focal resident type. The developed method can also be applied to populations that consist of more than one resident type. An important insight from chapter 1 is that some qualitative aspects of the evolutionary dynamics can be predicted a priori without carrying out a detailed invasion analysis. It is also shown that the presented geometrical framework can be used to prove results that in some cases could only be conjectured based on numerical results or that constituted open problems in the literature.

Since the publication of chapter 1 two independent studies have appeared that present related geometrical approaches (de Mazancourt and Dieckmann, 2004; Bowers et al., 2005). These differ in their focus but are essentially equivalent to each other. Both studies introduce a third type of curve that allows to determine the convergence stability of a singular point by comparing the curvature of this new type of curve with the curvature of the trade-off and the invasion boundary at the singular point. Hence, the approach of de Mazancourt and Dieckmann (2004) and Bowers et al. (2005) allows for a classification of singular points by analyzing the curvature patterns of three different curves at the singular point whereas the approach presented in chapter 1 also requires analyzing the intersection pattern of the trade-off curve and the invasion boundary in the neighborhood of the singular point. The strength of the approach by de Mazancourt and Dieckmann and Bowers et al. is that it allows to determine the range of trade-offs that correspond to a specific evolutionary outcome. The drawback of these alternative approaches is that in most cases the curvature properties of the third curve can only be determined numerically, although Bowers et al. (2005) were able to provide and example that allows for a fully analytical treatment. The focus of chapter 1 is on a priori predictions that can be derived without any numerical calculations, and that serve to hone a more intuitive understanding of the model at hand.

As mentioned above, the classification in chapter 1 is based on properties of the fitness landscape. These properties have to be derived from specific eco-evolutionary models. In **chapter 2** an attempt is made to classify all models within a specific model family, based on the tools developed in chapter 1. In chapter 2 attention is restricted to life cycles that can be described with two states in discrete time. Two traits, coupled by a trade-off, are allowed to evolve. Individual models within the considered class differ in the choice of traits that are allowed to evolve and in the assumed ecology. Any trait affecting life cycle transitions can be subject to density dependence and different traits can be affected by different groups of individuals of the resident community. The categories of the classification are the shape of of the invasion boundaries and whether or not an optimization criterion exists. The first category allows to determine whether or not a singular trait value is invadable by nearby mutants while the second category delineates cases that do not show frequency dependence from cases where frequency dependence does play a role. In the latter case the classification can be extended for models with certain symmetry properties by partitioning fitness into a density-dependent and a frequency-dependent component. A result of the classification is that key features can be identified that correspond to certain model behaviors. Evolution in different diagonal components of the population projection matrix favors the occurrence of disruptive selection and diversification. Evolution in different off-diagonal components favors the occurrence of stabilizing selection on intermediate phenotypes. Evolution of traits that occur in different summands of the fitness function are a prerequisite for evolutionary branching. Such traits correspond to “alternative routes” in the life cycle. Finally, evolution of traits that occur in a single product in the fitness function makes evolutionary branching impossible. Such traits correspond to “consecutive steps” in the life-cycle.

In chapters 3 and 4 the same specific model for the evolution of specialization of one consumer feeding on two resource is investigated. These chapters differ only in one assumption. In **chapter 3** it is assumed that consumers behave as opportunists, which means that any encountered prey item will be attacked. In chapter 4 consumers show a flexible behavior and each individual decides upon encounter with a resource item whether it attacks the resource or ignores it. This decision is made according to the rules of optimal foraging such that resource intake is maximized. These chapters share with the previous two chapters the assumption that only two traits evolve and that these are coupled by a trade-off. Five different pairs of traits are considered in turn. Each pair consists of two resource specific traits such as search efficiency or manipulation time. The trade-off assumption means that phenotypes with a high search efficiency for one resource have a low search efficiency for the other, or that phenotypes with a short manipulation time for one resource need a long time to manipulate items of the other resource. The main results of chapter 3 are that a resource generalist is an uninvadable and globally convergence stable trait when the trade-off curve is weak but that in case of strong trade-offs the evolutionary dynamics depend on the trait under consideration. While for some traits, such as search efficiency, the generalist is an evolutionary branching point, the generalist's trait is an evolutionary repellor for other traits such as manipulation time. The explanation for these different dynamics lies in the way the evolving traits affect the abundance of the resources. In the first case these interactions are such that selection is frequency-dependent. A resident consumer specialized on one resource depletes this resource more strongly while the other resource remains underused. This gives a rare type that is more specialized on the second resource an advantage. In the second case the interaction between consumer traits and resource abundances does not produce such an rare type advantage and selection is frequency independent.

In **chapter 4** it is shown that the results from chapter 3 change in several ways when consumers have a flexible diet choice. Behavior guides the the direction of selection because only resources that are included in the consumer's diet influence its fitness. Flexible diet choice reduces the basin of attraction of the generalist's trait value because specialized consumers forage selectively on their preferred resource and they will evolve to become even more specialized. Whenever two types differ in their behavior they are able to coexist. Flexible diet choice behavior therefore allows for coexistence of types that could not coexist otherwise. Such polymorphisms arise not only at evolutionary branching points but whenever a mutant occurs that is sufficiently different from the resident such that the mutant shows a different diet choice behavior. In some cases this can happen even for small mutational steps. In chapter 3 the only evolutionary stable dimorphic community consists of two highly specialized types. With flexible diet choice a community of an opportunistic generalist and a selective specialist is an alternative dimorphic stable coalition.

Chapter 5 addresses a fundamental modeling issue. Evolutionary change occurs through changes at the level of the DNA sequence and ultimately affects the make-up of a population. The step from individual sequences to population level characteristics can be described by a cascade of mappings. Genotypes are mapped to gene products, for example enzymes and regulating proteins. During development these traits are mapped to morphological, physiological or behavioral traits which in the end affect population level characteristics such as the intrinsic growth rate r or the carrying capacity K. Chapter 5 focuses on the mapping from traits that can in principle be measured at the level of the individual to traits that are properties of populations. Trade-offs between different traits are manifested at the level of the individual. If such traits affect different population level characteristics, then the trade-off is mapped onto a trade-off at this higher level. The point made in chapter 5 is that curvature properties are conserved from one level to the next only if the mapping is of a particularly simple type. In chapter 5 a two habitat version of the logistic and the Ricker equation is derived from underlying processes at the individual level. From these derivations follows that certain trade-off curvatures for a trade-off in habitat specific carrying capacities can not be derived from a trade-off in an underlying individual level trait and that the evolutionary dynamics in habitat specific carrying capacities differ strongly when evolutionary change is modeled either directly in these traits or in underlying mechanistic traits contributing to the carrying capacities.

In chapter 1-4 the conditions leading to evolutionary branching were of special interest. At an evolutionary branching point disruptive selection acts to increase phenotypic variation. In asexual populations this is achieved by a splitting of one lineage into two and it is this scenario that earned such points their name. In freely interbreeding sexual populations, however, the distribution of phenotypes is constrained by the processes of segregation and recombination, which causes many individuals to have maladaptive intermediate phenotypes. A splitting into two discrete lineages can be restored when populations evolve to mate assortatively with respect to the trait under disruptive selection. This scenario can lead to sympatric speciation and it has recently received an enormous amount of attention by theoreticians and empiricists alike. However, next to assortative mating many other processes can lead to an increase in phenotypic variation under disruptive selection and **chapter 6** provides a review of the different adaptive responses to disruptive selection. These responses can be divided into three categories: processes that cause an increase in phenotypic variation through an increase in genetic variation, processes that cause in increase in phenotypic variation without involving an increase in genetic variation and processes at the community level that involve immigration of species from outside the considered population or evolutionary change in species that interact with the focal species. Chapter 6 concludes with an outlook on factors that might influence the likelihood for each response to occur. Variation that is most readily available at the onset of disruptive selection might have a head start and can respond first, possibly preempting other responses. Without immediately available variation, relative selection pressures and genetic and developmental constraints are likely to be important.