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Joint phenotypes, evolutionary conflict and the fundamental theorem of natural selection

David C. Queller
Washington University in St Louis, queller@WUSTL.EDU

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David C. Queller

Department of Biology

Washington University in St. Louis

St. Louis, MO 63130 USA

Email: Queller@wustl.edu

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Abstract

Multiple organisms can sometimes affect a common phenotype. For example the portion of a leaf eaten by an insect is a joint phenotype of the plant and the insect and the amount of food obtained by an offspring can be joint trait with its mother. Here I describe the evolution of joint phenotypes in quantitative genetic terms. A joint phenotype for multiple species evolves as the sum of additive genetic variances in each species, weighted by the selection on each species. Selective conflict between the interactants occurs when selection takes opposite signs on the joint phenotype. The mean fitness of a population changes not just through its own genetic variance but though the genetic variance for its fitness that resides in other species, an updating of Fisher's fundamental theorem of natural selection. Some similar results, using inclusive fitness, apply to within-species interactions. The models provide a framework for understanding evolutionary conflicts at all levels.

Keywords:

Fundamental theorem of natural selection, evolutionary conflict, joint phenotypes, arms race, mutualism, inclusive fitness

Introduction

W. D. Hamilton's inclusive fitness theory [1, 2] has been important for many reasons [3-5]. It gave a way to calculate how selection would operate on social behaviors. It explained puzzling behaviors such as altruism and spite. In outline, it was simple to understand and easy to apply because it was relatively independent of most genetic details. Perhaps most importantly, inclusive fitness provided a quantity that is maximized by natural selection and by extension identifies an agent – either the individual or the gene – that is adapted to behave as if it were maximizing it.

In this, Hamilton was following Darwin's lead. Selection produces adaptations that perform as if they have been designed for survival and reproduction. One consequence of having the proper design criterion for social behavior was a clarification of how conflict operates within a species. Just as a cheetah and gazelle can be selected differently for whether the former catches and eats the latter, so too can individuals within a species be in conflict. Even a mother and offspring may be selected differently, for example with respect to the amount of food the mother provides, when their inclusive fitnesses differ [6]. Though conflict is an important part of behavioral ecology, and of evolutionary biology in general, it has not been formalized to the same degree as selection in the absence of conflict. In this paper, I attempt such a formalization, roughly in the quantitative genetic tradition, by treating selection on a joint phenotype that is created by multiple parties.

Hamilton was also following Ronald Fisher's lead. Fisher's fundamental theorem of natural selection states that fitness increases at a rate equal to the additive genetic variance for fitness [7]. As such, it provided a formal foundation for the optimality notion that selection maximizes fitness.   Hamilton's theory can be viewed as an adjustment to this notion, not considered by Fisher, that is required when individuals affect neighbors who share their genes in non-random ways [3, 4, 8].

Fisher believed that his fundamental theorem to be a very important contribution to biology, in some ways parallel to the second law of thermodynamics in physics [7]. But its reception was odd, in some ways parallel to the reception of inclusive fitness theory. Each was viewed by proponents as a spectacular synthesis, yet each was viewed by others as at best an approximation that fails in many cases.   The difference was that, for Fisher's fundamental theorem, proponents were very scarce for over 40 years. The problem was that fitness does not always increase to a maximum. Dominance, epistasis, and frequency-dependent selection often prevent fitness from reaching its highest possible value and can even cause average fitness to decline. Change of environment can do the same thing, particularly change in the biotic environment. Fisher knew this and was not bothered by it, but he never explained his position clearly enough. The fundamental theorem was regarded as "entirely obscure" [9] "recondite" [10], or "very difficult" [11]; it was suggested that it "mostly fails" [12] and that attempts to save it "are quite pointless" [13].

Fisher's reasoning was eventually clarified by George Price [14]. In his view, Fisher was not talking about the total change in fitness but rather just the part of it that is due to natural selection in the previous generation. Fitness might also change due to changes in the environment but this was not his focus; he could ignore it and still capture the essence of Darwin's insights about selection and adaptation.   Fisher considered that the environment would often deteriorate, often due to competitors and enemies, so that total fitness would not always increase. Change in the environment could also include dominance and epistasis changing the *genetic* environment of the next generation, a view that may have seemed odd at the time, but which feels comfortable today given the genic view of selection elaborated by Dawkins [15, 16]. Thus, Fisher 's result applies to the change in fitness due to selection, keeping the average effects or breeding values constant.

This revised and highly favorable view of the fundamental theorem seems to be the consensus opinion today [8, 14, 17-22]. I agree with this view but this paper will attempt a significant revision of the fundamental theorem, by trying to also capture part of the change in environment that has been ignored. This has been done to some degree for changes in the genetic environment but these effects are often small. Effects of changes in the physical environment would probably be hard to capture in a general way. Changes in the biotic environment are different, often being large, and typically (though not always) being deleterious. Moreover, certain changes in the biotic environment, specifically changes due to natural selection on other parties, are heritable, and can be easily captured. Indeed Fisher's result was not really about the full change due to natural selection; it was about the change in a party's fitness due to natural selection *on that party*. That is very important, but I will explicitly incorporate the effects of selection on other parties in order to get closer to the total change in a party's fitness due to natural selection and to explicitly model why it often decreases.

I begin by introducing the Price equation that will be the basis of the models. Before coming to within-species interactions and inclusive fitness, I treat the case of between-species interactions, which is simpler in some respects. Hamilton was of course also interested in these, as exemplified by his host-parasite work. In each case, I will consider how selection operates on joint phenotypes that are affected by multiple parties. This will lead to a formalization and definition of selective conflict between the parties. Versions of the fundamental theorem can then be derived simply by considering fitness of one party as a joint phenotype that is also affected by other parties. The chief goal is not to analyze particular cases but to capture some general principles.

The Price Equation

George Price is best known for his "Price equation" [21, 23], partly anticipated by Robertson [24]. It is a mathematical identity describing how selection operates that makes it easy to analyze selection through manipulation of high level statistical parameters like means, variances, and covariances. It states that average trait value $\bar{z}$ will increase in evolution as

$$\Delta\bar{z} = Cov(w_i, z_i) + E(w_i \Delta z_i), \qquad (1)$$

where z_i is an individual's trait value and w_i is its relative fitness [21, 23]. Hamilton was the first to appreciate the importance of Price's result and helped him to get it published it in *Nature*.

Oddly, Price did not use his own equation in his exegesis of Fisher's fundamental theorem even though, as Steve Frank has shown, one can derive Fisher from Price in two simple steps [21]. The two have very similar structures. The first term of the Price equation captures the effect of selection, just as Fisher's fundamental theorem did. The second term, the expected change in phenotype from a parent to its offspring Δz weighted by parental fitness, can include effect from dominance and epistasis that alter average effects in the next generation, and this is likely what allowed Price to see what Fisher had left out. I will follow the common practice of assuming the second term of Price's equation is negligible (or of secondary interest), but with one very large exception: I will explicitly model changes due to selection on other parties.

Joint Phenotypes

Organisms often have extended phenotypes [16]. Traits outside of the organism's conventional body, such as a beaver's dam, are affected by the organism's genes. When such traits affect the organism's fitness, they can evolve under natural selection. Some extended phenotypes do not belong entirely to one organism and can be influenced by the genes of multiple parties [16]. The indirect-genetic-effect (IGE) approach in quantitative genetics uses this insight fruitfully [8, 25-29] and my approach is fully in that spirit, but with a small shift in emphasis. Where IGE tends to speak of "interacting phenotypes" that produce some combined result, I will focus on the combined result itself as the joint phenotype. Instead of viewing one party as the owner of the phenotype that happens to be affected by another, I treat the two parties symmetrically as joint owners (though they usually contribute unequally). Examples of joint traits include the portion of a leaf eaten by an insect, the health of an infected host, whether a peacock and a peahen mate, the blood flow to an embryo from its mother, and the degree of meiotic drive during spermatogenesis. When individual *i* of one species interacts with individual *j* of another to produce a joint trait z, we can write it as the sum of the two individuals breeding values for the joint trait plus an environmental deviation:

$$z = g_i + g_j + e_{ij}\ , \qquad (2)$$

The transmissible part of the joint trait is the sum of the two breeding values, each of which can be estimated through quantitative genetic methods [30, 31].

For concreteness, let the two parties be gazelles (indexed by i) and cheetahs (indexed by j). They have many phenotypic traits like sensory acuity, speed, and agility that influence the interaction, but I will consider their summed effect on a joint phenotype: whether, when they encounter each other, the gazelle becomes dinner for the cheetah, which can be scored as zero or one for a single interaction.

Interactants of different species

We can modify the Price equation to accommodate a joint phenotype affected by two species. Two terms are needed because gazelle genes are passed only through gazelle fitness and cheetah genes only through cheetah fitness. Assuming no environmental change:

$$\Delta\bar{z} = \Delta\bar{g}_i + \Delta\bar{g}_j = Cov(w_i, g_i) + Cov\left(w_j, g_j\right). \qquad (3)$$

The w's used here are relative fitnesses. If they are interpreted instead as absolute fitnesses, then the two terms on the right hand side need to be divided by $\bar{w}_i$ and $\bar{w}_j$

respectively, and these denominators would be carried through in the derivations that follow.

Although equation (3) is based on interaction of two parties, it appears to leave no room for actual non-additive interaction between g_i and g_j, i.e. a between-individual epistasis. But as with normal epistasis, the non-additive component part of this interaction – the part not captured by breeding values – is relegated to the second term of Price's equation (1) and the uncaptured "change of environment" term of the fundamental theorem.

Equation (3) will be modified using methods that involve choosing appropriate components or predictors of fitness [32-34]. A set of familiar statistical identities will be used: if x, y, and z are variables and k is a constant, Cov(x,x)=Var(x); Cov(x,ky)=kCov(x,y); Cov(x,y+z)=Cov(x,y)+Cov(x,z); β_{yx}=Cov(x,y)/Var(x) where β_{yx} is a simple regression coefficient of y on x [35].

First, we can model the effects of an interaction, here assumed to be linear, on fitness of gazelles and cheetahs as,

$$w_i = a_i + n_i \bar{z}_{i.} b_{w_i z} \qquad (4)$$

$$w_j = a_j + n_j \bar{z}_{.j} b_{w_j z} \quad . \qquad (5)$$

The a's are the fitnesses in the absence of the interaction. n_i and n_j are the numbers of interactions experienced by the i^{th} gazelle and the j^{th} cheetah (i.e the number of encounters, which may be zero for some individuals). If the joint phenotype involves one individual of each species, the sums of n_i and n_j would be equal in the two species. $\bar{z}_{i.}$ and $\bar{z}_{.j}$ are the mean joint phenotype experienced by gazelle *i* and cheetah *j*, across all their interactions. $b_{w_i z}$ and $b_{w_j z}$ represent the expected fitness change to the gazelle and cheetah respectively, in a single interaction, per unit change in the joint phenotype *z*. The *b*'s are considered to be constants and they can be estimated by regression.

As noted earlier, this is essentially an indirect genetic effects approach [8, 25-29], extended to multiple species, but with some minor differences from conventional usage. Instead of treating each party's individual traits, such as speed and agility, as the phenotypes, I use the joint phenotype caused by their interaction. As such, I do not view one party as the owner of the trait but instead treat both parties' effects on the trait symmetrically. Each simply makes its contribution to the trait, with the breeding value representing the heritable component, with neither necessarily considered less direct than the other. It seems likely that similar results could be obtained with the standard indirect genetics effects model, and this would may lead to more insight on the individual traits that lead to the joint phenotype, but my goal is to highlight conflict over joint phenotypes.

Substituting (4) and (5) into (3) and assuming the baseline fitnesses (a) are uncorrelated with breeding values g_i and g_j yields:

$$\Delta\bar{z} = Cov\left(g_i, n_i \bar{z}_{i.} b_{w_i z}\right) + Cov\left(g_j, n_j \bar{z}_{.j} b_{w_j z}\right). \qquad (6)$$

We can extract the constant *b*'s from the covariances and also the means of the *n*'s, provided that these are independent of the breeding values (g) in their terms. This means that the genes determining the *outcome* of an interaction are independent of the *number* of interactions experienced, as when the number of interactions is determined by environmental factors.

$$\Delta\bar{z} = \bar{n}_i b_{w_i z} Cov(g_i, \bar{z}_{i.}) + \bar{n}_j b_{w_j z} Cov(g_j, \bar{z}_{.j}) \qquad (7)$$

The mean phenotypes experienced by gazelle *i* and cheetah *j* can be written as

$$\bar{z}_{i.} = g_i + \bar{g}_j{}' + e \qquad (8)$$

$$\bar{z}_{.j} = g_j + \bar{g}_i{}' + e \qquad (9)$$

where $\bar{g}_j{}'$ is the mean breeding value for the joint phenotype of a gazelle's cheetah interactants and $\bar{g}_i{}'$ is the mean breeding value of the cheetah's gazelle partners, each being weighted by the number of interactions with that partner. Note that in the equations (7-9) above the means of *n*'s are over all individuals of a species, while the means of *z*'s and *g*'s are taken over the partners of one individual. Substituting (8) and (9) into (7), assuming no gene-environment correlation, yields:

$$\Delta\bar{z} = \bar{n}_i b_{w_i z}\left[Var(g_i) + Cov\left(g_i, \bar{g}_j{}'\right)\right] + \bar{n}_j b_{w_j z}\left[Var\left(g_j\right) + Cov\left(g_j, \bar{g}_i{}'\right)\right] \qquad (10)$$

The variance terms are for direct effect of an individual's genes on its own fitness and the covariance terms are indirect selection. The indirect terms will be relevant when there are genetic correlations between interactants, for example due to partner choice or due to selection favoring particular combinations of interactants in the same way that epistasis can favor correlation among genes (linkage disequilibrium) [36, 37]. But these terms will often be at or near zero, in which case (10) becomes simply

$$\Delta\bar{z} = \bar{n}_i b_{w_i z} Var(g_i) + \bar{n}_j b_{w_j z} Var\left(g_j\right). \qquad (11)$$

The joint trait evolves according to the additive genetic variance in the two parties, each multiplied by the mean selective effect on that party. Considering selection on a joint phenotype provides a clear definition of conflict: current selective conflict exists when the two effects of the joint phenotype on fitness, $b_{w_i z}$ and $b_{w_j z}$, are of different sign. Then the two parties push the joint phenotype in opposite directions, as when gazelle genes are selected to decrease the gazelle-as-cheetah-meal trait, while cheetah genes are selected to increase it.

For pairwise interactions $\bar{n}_i N_i = \bar{n}_j N_j$, where N_i and N_j are the population sizes of gazelles and cheetahs. Substituting $\bar{n}_j = \bar{n}_i N_i / N_j$ into (11) makes the role of population size explicit. For example, if there are more gazelles than cheetahs, then the second term is elevated relative to the first, reflecting that the average cheetah must experience more interactions than the average gazelle.

Now assume that the trait of interest z is the fitness of gazelles, w_i. Equations (10) and (11) become:

$$\Delta\bar{w}_i = \left[Var(g_i) + Cov\left(g_i, \bar{g}_j{}'\right)\right] + \bar{n}_j b_{w_j w_i}\left[Var\left(g_j\right) + Cov\left(g_j, \bar{g}_i{}'\right)\right] \qquad (12)$$

$$\Delta\bar{w}_i = Var(g_i) + \bar{n}_j b_{w_j w_i} Var\left(g_j\right) \quad . \qquad (13)$$

The breeding values g_i, and g_j are now interpreted as breeding values of gazelle and cheetah genes *for gazelle fitness*. The b in the first term of each equation disappears because $b_{w_i w_i}$ must equal 1 (as the phenotype – now fitness – of a gazelle changes, it changes gazelle fitness by 1). $\bar{n}_i$ also disappears because each gazelle experiences only one instance of the phenotype gazelle fitness and $\bar{n}_j$ is now interpreted as the number of cheetahs affecting the gazelle's fitness.

Note that if the fitness model (equations 4-5) is more appropriate for *absolute* rather than *relative* fitness, as will often be the case, then the two terms of the right hand sides of equations (10-13) should to be divided by $\bar{w}_i$ and $\bar{w}_j$.

Equations (12) and (13) represent extensions of the fundamental theorem for gazelle fitness when affected by cheetahs, with (13) being the simpler form that applies in the usual case when partners' breeding values are uncorrelated. If cheetahs have no heritable effect on gazelle fitness, then the second term of (13) is zero, yielding Fisher's original fundamental theorem. If there are cheetah genes that affect gazelle fitness (Var(g_j)≠0) and this in turn affects cheetah fitness ($b_{w_j w_i} \neq 0$), there will be selection in cheetahs for genes that change mean fitness in gazelles. More simply, if cheetahs evolve to be better at catching gazelles, it will reduce gazelle fitness. This is hardly a novel concept, but it has not one that has been formally incorporated into the fundamental theorem. Mean gazelle fitness can decline if cheetah genes (for gazelle fitness) have a larger variance or have a larger selection gradient. Exactly parallel expressions for change in cheetah fitness can be written with g_i, and g_j now being the breeding values for cheetah fitness, by switching the subscripts *i* and *j*.

More generally, it is easy to show that if the fitness of gazelles is affected by multiple species indexed by S=2…S_{max}, (13) becomes

$$\Delta\bar{w}_i = Var(g_i) + \sum_{S=2}^{S_{max}} \bar{n}_j b_{w_j w_i} Var(g_j) \quad , \qquad (14)$$

where the j's now index separately for each partner species (and again, if w is absolute fitness each term would be divided by the species' mean fitness). Covariance terms such as those in (12) can be added if necessary. The summation, when negative, describes much of Fisher's "deterioration of the environment" [7]. It is also a way of representing van Valen's Red Queen effect [38], that because of other species it is necessary to keep evolving just to stay in the same place. However, for some species the $b_{w_j w_i}$ effects may be positive (e.g. mutualism) and will enhance the fitness of their partner species.

Conspecific interactions

In this section, I address the question of joint phenotypes and conflict between individuals of the same species playing different roles. Interactions within a species give a similar result to those between species, but can be complicated by several factors. First, when partners are related, there are inclusive fitness effects, and the fundamental theorem should take an inclusive fitness form [8]. In addition, where conflicts involve individuals in two roles, such as male and female, owner and intruder, or mother and offspring, each individual carries genes for both roles, even if it does not express both. In some cases each individual might play either role at different times. To fix ideas and to draw a close parallel to the first model, consider small tadpoles (potential victims) that may be cannibalized by large tadpoles (potential cannibals) of the same species. Unlike the gazelle-cheetah case, there is only one fitness, so the equation parallel to (3) is

$$\Delta\bar{z} = \Delta\bar{g}_i + \Delta\bar{g}_j = Cov(w, g_i) + Cov(w, g_j), \tag{15}$$

where g_i, and g_j are now the breeding values for joint trait z for genes expressed in victims and cannibals (note that Bijma's derivation [8] uses different meanings of g's; as direct and indirect effects, with roles not explicitly treated).

Interaction changes an individual's fitness by the sum of what happens when it is a victim and a cannibal. Letting primes designate genes of partners, the model is:

$$w = a + n_i \bar{z}_{i.} b_{w_i z} + n_j \bar{z}_{.j} b_{w_j z} \quad . \qquad (16)$$

n_i and n_j are the number of times an individual interacts in the roles of potential victim and potential cannibal, respectively, $\bar{z}_{i.}$ and $\bar{z}_{.j}$ the mean joint phenotypes it experiences in the two roles, and $b_{w_i z}$ and $b_{w_j z}$ are the effects of phenotype z on fitness of individuals playing potential victim and potential cannibal. Substituting into (15) and carrying out steps directly parallel to the multi-species derivation yields the following results parallel to (10) and (11) respectively:

$$\begin{aligned} \Delta\bar{z} = {} & \bar{n}_i b_{w_i z}\left[Var(g_i) + Cov\left(g_i, \bar{g}_j{}'\right) + Cov\left(g_j, g_i\right) + Cov(g_j, \bar{g}_j{}')\right] \\ & + \bar{n}_j b_{w_j z}\left[Var\left(g_j\right) + Cov\left(g_j, \bar{g}_i{}'\right) + Cov\left(g_i, g_j\right) + Cov(g_i, \bar{g}_i')\right] \end{aligned} \qquad (17)$$

$$\Delta\bar{z} = \bar{n}_i b_{w_i z}[Var(g_i) + Cov\left(g_j, \bar{g}_j'\right)] + \bar{n}_j b_{w_j z}[Var\left(g_j\right) + Cov(g_i, \bar{g}_i')] \, . \qquad (18)$$

As before, in moving to (18) we simplify by omitting terms due to correlation between genes for being a victim and cannibal, g_i and g_j. In contrast to the two-species case, such correlations are here easily caused by pleiotropic genes affecting both roles [39] but we neglect this to highlight the role of social selection. Grouping term 1 with 4, and 2 with 3, and then factoring out the variances yields an inclusive fitness form:

$$\Delta\bar{z} = Var(g_i)[\bar{n}_i b_{w_i z} + \bar{n}_j b_{w_j z} \beta_{\bar{g}_i' g_i}] + Var(g_j)[\bar{n}_j b_{w_j z} + \bar{n}_i b_{w_i z} \beta_{\bar{g}_j' g_j}] \qquad (19)$$

The first bracket term is the inclusive fitness effect of genes expressed in the victim role (g_i), with the effect on self, $\bar{n}_i b_{w_i z}$, added to the effect on cannibals, $\bar{n}_j b_{w_j z}$, multiplied by the regression relatedness of victims to the cannibal interactants, $\beta_{\bar{g}_i' g_i}$. The second bracketed term is a similarly constructed inclusive fitness effect for the cannibal role. Selection on the joint phenotype operates on the two inclusive fitnesses, weighted by their additive genetic variances. Because the variances are always positive, selective conflict occurs when the victim and cannibal inclusive fitness effects are of different sign.

Letting the phenotype z be the fitness of a gazelle w_i, we get a version of Fisher's fundamental theorem, but for change in victim fitness only:

$$\Delta\bar{w}_i = Var(g_i)[1 + \bar{n}_j b_{w_j w_i} \beta_{\bar{g}_i' g_i}] + Var(g_j)[\bar{n}_j b_{w_i w_i} + \beta_{\bar{g}_j' g_j}] \qquad (20)$$

where again $b_{w_i w_i}$ and $\bar{n}_i$ both equal 1 (the latter because each individual has only one fitness. As in the multispecies case, declines in fitness can outweigh gains, a well known result in social evolution [40]. This is for two reasons. First, victims could be selected to lose personal fitness (1st term) if it gave sufficient gains to victim genes in related cannibals (second term). This is Hamilton's altruism [1, 2]. Second, in the absence of relatedness, victim fitness can still decline because of selection on cannibals (3rd and 4th terms), that is, because of conflict. Just as in the multi-species case, individuals acting in other roles can reduce (or sometimes increase) the fitness obtained in the focal role.

However, as pointed out to me by Piter Bijma, this does not really capture the essence of Fisher's fundamental theorem, because when relatives are affected, it is not the change in fitness that is important, but the change in inclusive fitness [8]. So, if we let the joint phenotype *z* be the *inclusive* fitness of victims – call it w_i^* – equation (19) becomes:

$$\Delta\bar{w}_i^* = Var(g_i)\left[b_{w_i w_i^*} + \bar{n}_j b_{w_j w_i^*}\beta_{\bar{g}_i' g_i}\right] + Var(g_j)\left[\bar{n}_j b_{w_j w_i^*} + b_{w_i w_i^*}\beta_{\bar{g}_j' g_j}\right]$$

$$= Var(g_i) + Var(g_j) b_{w_j^* w_i^*} \qquad (21)$$

As in (13) the multiplier of Var(g_i) reduces to 1, though the logic is more complicated. Note that $\bar{n}_j\beta_{\bar{g}_i' g_i}$ is a constant, while the two *b* terms describe how w_i and w_j change with a unit change in *i*'s inclusive fitness, w_i*. Thus, the whole expression is the change in $w_i + \bar{n}_j\beta_{\bar{g}_i' g_i} w_j$, which is *i*'s inclusive fitness, for a unit change in *i*'s inclusive fitness, and this is clearly 1. Similarly, the second bracket asks how a unit change in *i*'s inclusive fitness affects the summed inclusive fitness of its partners, which I write as as $b_{w_j^* w_i^*}$. Equations (20-21) can be converted to equations for change in cannibal fitness and inclusive fitness by switching the *i* and *j* subscripts throughout.

Once again, if the fitness model (here equation 16) describes absolute rather than relative fitness, then the right hand side of equations (17-21) should be divided by $\bar{w}$.

Equation (21) shows that if there are no cannibal genes that affect victim inclusive fitness (Var(g_j)≠0) then the rate of change of victim inclusive fitness is equal to its additive genetic variance. However, if there are cannibal genes that affect victim inclusive fitness (Var(g_j)≠0) and this in turn affects cannibal inclusive fitness ($b_{w_j^* w_i^*} \neq 0$), there will be selection in cannibals for genes that change mean fitness in victims. If cannibals evolve to be better at catching victims, it will reduce victim fitness. Thus, this inclusive fitness formulation (21) captures a reason for decline in fitness – conflict – not explicitly treated in prior formulations [8]. This conflict of course remains (indeed is enhanced) in the absence of relatedness.

Discussion

The results derived here model how selection works on joint phenotypes, highlighting the role of conflict between two parties. Considering joint phenotypes in useful because they are the objects of conflict. Selective conflict exists when the two parties are selected to push the joint phenotype opposite directions – when the selection terms in (11), or the inclusive fitness terms in (18) differ in sign for the two parties. The outcome of such selection depends on the relative magnitudes of these selection terms, but also on the genetic variances. If Fisher's fundamental theorem of natural selection is regarded as a design principle, the versions here incorporate conflicting design criteria.

Social evolution theorists have found it useful to distinguish potential conflict and actual conflict [41, 42]. Potential conflict exists over the range of possible selection regimes that would lead to different signs of selection on the two parties. For the two-species equation (11) potential conflict exists for any values of the joint phenotype z that would affect the fitness of gazelles and cheetahs in opposite directions ($b_{w_i z} > 0 > b_{w_j z}$ or $b_{w_j z} < 0 < b_{w_i z}$). Within a species with two roles affecting the same joint phenotype (equation 18) it is opposite signs effect of the joint phenotype on inclusive fitness ($\bar{n}_i b_{w_i z} + \bar{n}_j b_{w_j z} \beta_{\bar{g}_i' g_i}$ and $\bar{n}_j b_{w_j z} + \bar{n}_i b_{w_i z}$) that determine potential conflict.

Actual conflict depends on the effects of real genes that actually create selection. Potential conflict may not result in actual conflict if one party has no power to affect the joint phenotype. The equations derived here describe the process that leads to actual conflict, but they do not fully describe actual conflict. The process of selective conflict described here depends on segregating genetic variation, but much of the actual conflict observed in nature presumably results from variation previously fixed by selection. Most of the genes underlying gazelle and cheetah conflicts – for example genes underlying speed, agility and perception – are presumably fixed. Actual phenotypic conflict can be defined as occurring when two parties push a joint phenotype in opposite directions, as the result of either current or past selective conflict. Such phenotypic conflict can occur, for example, even when one party is currently depleted of genetic variation for the trait. Cheetahs may have little genetic variation left for increasing their speed, but they nevertheless use their accumulated speed genes accumulated, through past selective conflict, to capture escaping gazelles.

The equations are agnostic with respect to the size and direction of fitness effects so they can represent the evolution of cooperation as well as conflict. When the fitness effects of the joint phenotype in multi-species interactions have the same sign, or when the inclusive fitness effects in same-species interactions have the same sign, then both parties are being selected in the same direction. I have emphasized conflict because it has been relatively neglected in indirect-genetic-effect models and because conflict is likely the biggest driver of Fisher's deterioration of the environment. Moreover, the division into effects due to different species or due to different roles within species emphasizes that potential for conflict generally remains even over potentially cooperative or mutualistic traits. When the fitness effects have the same sign, selection operating on both parties will push the joint trait in a common direction until it reaches a point where it is no longer beneficial for one party, at which point selective conflict may commence. For example, a pea plant and its rhizobial symbiont may both benefit from the nitrogen provided by the latter, but the legume may try to extract more [43].

Ultimately, conflicts are about fitness, and if we use the fitness of either party as the joint phenotype, the equations become versions of Fisher's fundamental theorem of natural selection, extended to multiple parties. Fisher showed that fitness changes at the rate of the additive genetic variance for fitness [7] and the result has been generalized to inclusive fitness (Bijma 2010b), but the new versions derived here emphasize that it can also change as a function of genetic variances of all the parties that have an effect on that organism, and that fitness can decline because of conflict. Previous versions of the fundamental theorem emphasize how an individual *own* genes are selected to influence its (inclusive fitness); the versions derived here add in the effects of genes residing in others.

Additional generalizations of these results are desirable, for example combining both within and between-species effects, unequal generation times, age structure, correlated traits, gene-environment correlations, overlapping fitnesses, and non-linear effects on phenotypes and fitness. These results are also still partial in the sense of ignoring change due to other factors. They also assume that the effects of the predictors remain constant in the next generation. The models do not include the entire effect of the biotic environment, only that part that arises from change in gene frequency of other species. Fitness might also decline (or increase) owing to changes in the population sizes of the various parties [44]. But the main point of Fisher's fundamental theorem is to capture the effects of the adaptive engine of evolution [18], and here it is done much more completely by including the sometimes potentially conflicting adaptive engines of multiple parties.

The message can be illustrated through another model for fitness increase that, like Fisher's theorem, that has been both useful and controversial: Wright's adaptive landscape. Imagine that each of the parties has its own fitness landscape. Instead of a lonely mountaineer steadily climbing his peak we have multiple mountaineers, each climbing his own peak, but roped to the others. As one climbs, he often drags another down from his peak. While this metaphor should not be pushed too far, it does suggest that Dobzhansky [45] may have been wrong in proposing that life is concentrated near fitness peaks. Instead, there are forces keeping the valleys and lower slopes populated and, because their inhabitants are constantly pulling and being pulled, this is where much of evolution occurs.

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