



Stability with Inheritance in the Conditional Strategy

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The conditional strategy is a theoretical framework that explains the existence within populations of individuals that express alternative behavioral, physical or life history tactics (phenotypes). An example is fighters and sneakers in many animal mating systems. In the conditional strategy the alternative tactics are chosen by individuals based on their state, for example large or small bodied. Since state is often heritable, due for example to additive genetic variance, the alternative tactics may also have inheritance. As the tactics do not have equal fitnesses, it is generally believed that any such inheritance would prevent the evolutionary stability of the conditional strategy. However, in previous work we introduced an Inheritance Theorem and were able to prove that a conditional strategy with tactic inheritances can have a unique equilibrium proportion of the tactics. We now prove a second property of our Inheritance Theorem, namely the stability of the equilibrium. This means that if the tactics are perturbed from their equilibrium proportions, they will return across generations to their equilibrium proportions. An example is provided in mites. We have therefore established an Inheritance Theorem which includes both the existence of an equilibrium and its stability for alternative tactics in a conditional strategy.

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Introduction

Natural selection will often favor a single best or optimal phenotype in a population. However, biologists have uncovered hundreds of examples of organisms that exhibit alternative behavioral, morphological and life history phenotypes, such as the complex foraging morphs of many vertebrates (e.g. Skulason & Smith, 1995), the alternative developmental life cycles of many insects and fishes (e.g. Gross, 1984; Roff, 1996; Henson & Warner, 1997; Wiegmann *et al.*, 1997), and the widespread occurrence of fighters (α) and sneakers (β) in animal mating systems (e.g. Gross, 1996). How such phenotypic diversity evolves under natural selection remains a difficult theoretical problem (Bell, 1997; Roff, 1997).

Gross (1996) identifies several important empirical patterns that must be accommodated by the theory. First, the alternative phenotypes typically result from

individuals expressing choice based on their individual state, for example, “if big fight and if small sneak”. The term “phenotypic plasticity” can be applied to this flexibility and decision process (e.g. McNamara & Houston, 1996). Second, in most cases the alternative phenotypes do not have equal average fitnesses. Fighters, for example, may have higher average fitness than do sneakers, or, in other species, the reverse may hold. Third, the alternative phenotypes may show genetic inheritance, for example, α individuals may overproduce α progeny and β overproduce β progeny, and this inheritance acts in concert with the phenotypic plasticity in which individuals are choosing their phenotype based on their state.

A widely used theoretical framework for studying alternative phenotypes was developed by Maynard Smith (1982). He suggested that the alternative phenotypes are explained by frequency dependent

selection, and he developed the concepts of the mixed Evolutionarily Stable Strategy (mESS) and the Evolutionarily Stable State (ESSt) based on principles from game theory (e.g. Binmore, 1992; Dugatkin & Reeve, 1998). These two game theoretic models have been very influential; however, they do not fully accommodate the three important biological empirical patterns described above. For instance, they do not readily address the common situation where individuals choose among alternative tactics based on their individual state (however, see Parker & Sutherland, 1986; Houston & McNamara, 1988). The alternative phenotypes of the mESS are typically generated by genetically pre-programmed frequencies—a randomization strategy for tactics that is state-independent. The ESSt is a model in which competing genotypes are maintained through negative frequency-dependent selection—individuals express the phenotype of their genotype. Another limitation is that the game-theoretic models usually postulate the same average fitnesses for the alternative phenotypes. These fitness equalities define the equilibrium frequencies of the alternative phenotypes: the set-point for tactic frequencies in the mESS and the frequencies of alternative strategies in the ESSt. Third, the game-theoretic models have largely overlooked important biological processes such as inheritance and phenotype development: they do not accommodate the observation of inheritance of alternative phenotypes, when inheritance works in concert with state-dependent individual choice.

A new theoretical framework for alternative phenotypes is therefore needed, one that incorporates state-dependent decision making, unequal average fitnesses, and tactic inheritance through the heritability of state. This heritability of state may be genetic, cultural or environmental in origin, although we usually refer to additive genetic variance. Gross (1996) proposed the use of the concept of the “conditional strategy”, a term coined by Dawkins (1980) and refined by Gross (1984, 1996), and he provided a model of the conditional strategy that incorporates state-dependent decision making and unequal average fitnesses. Repka & Gross (1995) have proven that a conditional strategy has a unique switchpoint when both status and frequency determine fitnesses. The third important pattern, inheritance, was incorporated by Gross & Repka (1998). They proved that the alternative tactics of a conditional strategy can remain in equilibrium across generations even with tactic inheritance and unequal fitnesses. They also established the structure of the conditional strategy, giving the relationships among tactic proportions, tactic fitnesses and tactic inheri-

tances that are imposed by the requirement that the strategy be at equilibrium.

We now build on the work of Gross & Repka (1998). We show here that a conditional strategy with state-dependent decisions, unequal average tactic fitnesses, and tactic inheritance will accommodate perturbations to the tactic frequencies. In other words, when tactic frequencies are perturbed from their equilibrium, the conditional strategy will return the tactics to their equilibrium. Thus, the conditional strategy can provide a robust theoretical framework for understanding phenotypic diversity. We provide an example of the application of our model to the α and β males in the mite system of Radwan (1995).

The Conditional Strategy

The conditional strategy is a relatively new concept for which we are attempting to build a theoretical framework (e.g. Gross, 1984; Repka & Gross, 1995; Gross, 1996; Gross & Repka, 1998). The key characteristics of a conditional strategy are: (1) the tactics involve a choice or decision by the individual; (2) the decision is made relative to some aspect of the individual’s state or status; (3) all individuals in the population have the same genetically-based strategy and the genes for expressing the tactics; (4) the average fitnesses of the tactics are unequal (typically); and (5) the chosen tactic results in higher fitness for the individual.

Figure 1 depicts the conditional strategy based on the underlying state of the individual. We deliberately do not specify the precise nature of the “state”; in some cases it will be closely related to size or growth rate. The fitnesses of the alternative tactics α and β vary with individual state, and the switchpoint s^* exists where their fitnesses are equal (West-Eberhard, 1979; Parker, 1982; Charnov, 1993; Repka & Gross, 1995). Individuals whose state is above s^* will choose tactic α , while those with state below s^* will choose β . A useful example to keep in mind is the fighter/sneaker system in which larger males adopt the “fighter” tactic (α) and smaller males adopt the “sneaker” tactic (β). For the purposes of our analysis we assume that the switchpoint is fixed throughout the population, though of course in reality it would be reasonable to expect some variance.

It is important to emphasize the distinction between “tactics” and “strategy”. The tactics are the two alternative phenotypes which individuals may adopt (α and β). Each tactic will have behavioral, morphological and other components that comprise the tactic. The underlying genetic makeup for each tactic will be present in each individual, although only

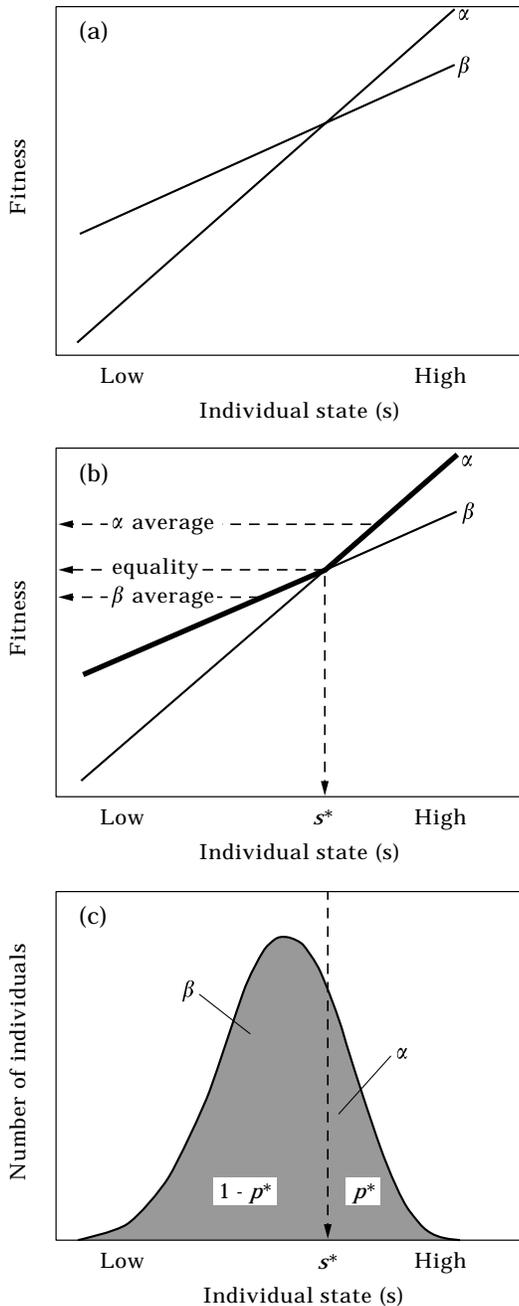


FIG. 1. The conditional strategy. Part (a) shows the fitness functions of the alternative phenotypes α and β across the range of individual states (e.g. individual body sizes). Part (b) shows the conditional strategy. The switchpoint s^* occurs where the fitness functions of the alternatives are equal. Individuals of state less than s^* choose tactic β and those of state greater than s^* choose tactic α , thereby maximizing their success. The heavy line is the resulting fitness function for the conditional strategy. Part (c) shows the population distribution of the resulting tactics across the distribution of individual states. The proportion of α individuals in the population is p^* (at equilibrium).

one set of tactic genes will be expressed. The strategy, also present in each individual, is the genotype which codes for making the choice of which tactic

to adopt, according to the switchpoint. The two tactics are regulated by the same strategy genotype, and although individuals compete with each other by using their tactics, the tactics do not compete with each other in an evolutionary sense because they belong to the same conditional strategy. The conditional strategy evolves as a means of maximizing the fitness of the individual, essentially by allowing each individual to maximize its potential among alternative tactics. The less able individuals adopt a less desirable tactic at which they do better than they would if they used the alternative tactic but had to compete directly with the high-state individuals.

The fitness of the strategy is at the population level, while the fitness obtained by each individual is through the expression of its tactic. The fitness of the strategy is not determined by either tactic alone but by how the strategy allocates individuals in the population to the two tactics. Each tactic contributes to fitness but their average fitnesses are unlikely to be equal. The overall fitness of the strategy is maximized through the appropriate allocation of tactics such that each individual does the best that it can, given its state. This, of course, also benefits the individual.

Gross & Repka (1998) consider the likely existence of at least some heritability of state (e.g. through additive genetic variance). If there is heritability of the underlying state, then there must be some inheritance across generations of the expressed tactics. It follows that high-state individuals will have disproportionately many high-state offspring, which of course will choose the α tactic, while low-state individuals will have disproportionately many low-state offspring, which choose the β tactic. The inheritance of tactics in this manner is problematic because of their different fitnesses. It seems that the higher fitness tactic should “run away” with the strategy due to its inheritance. However, Gross and Repka’s model provides a new “Inheritance Theorem” showing that the conditional strategy has an equilibrium that can accommodate the inheritance. Specifically, they prove that under a specified set of conditions, involving tactic proportion, tactic recruitment (fitness), and tactic inheritance, a conditional strategy can exist at which the tactic proportions will remain unchanged across generations. Thus, the conditional strategy has a unique equilibrium.

We have shown that a conditional strategy with tactic inheritances can have an equilibrium, but it remains to be shown that the equilibrium is stable. An equilibrium means that the proportions of each tactic will remain the same across generations. Stability means that the proportions will return to the

equilibrium if they are perturbed away from the equilibrium. For instance, if for whatever reason (e.g. drift, environmental fluctuation) the α phenotype was reduced in its frequency, would it later increase to its original equilibrium proportions? We now proceed to establish a second property in the Inheritance Theorem, namely that there is stability with inheritance in the conditional strategy.

The Single-sex Model

We follow the modeling framework of Gross & Repka (1998). We consider only the individuals of one sex, which we will refer to as males. We suppose the males behave according to the conditional strategy shown in Fig. 1. For simplicity we assume non-overlapping generations. We assume that there is heritability of underlying state and thus inheritance of the tactics: on the average, a proportion i_α of the (male) offspring of an α individual are themselves α , and a proportion i_β of the (male) offspring of a β individual are α , with $0 < i_\beta < p < i_\alpha < 1$ (p is the proportion of α individuals in the population). These inheritances take into account the female contribution to inheritance by assuming that each male mates with an “average” female (as explained below, relaxation of this assumption does not change our results). We assume that the α and β tactics produce the same ratios of sons and daughters. We write r_α (respectively r_β) for the average recruitment of offspring of an α (respectively β) individual into male adults in the next generation, and assume that $0 < r_\beta < r_\alpha$. Gross & Repka (1998) show that it is possible for an equilibrium to exist in such a population. The proportion of α individuals at equilibrium is denoted p^* .

Is the equilibrium proportion p^* stable? Will the proportions of each tactic be corrected by the conditional strategy if the proportions are perturbed, such as by any natural environmental factor that temporarily impacts one tactic more than the other? We now suppose that the parameters r_α , r_β , i_α , and i_β are fixed, and consider what happens when p , the proportions of α individuals, is not equal to p^* , the equilibrium proportion of α individuals. We do not explicitly model frequency-dependent selection since its effects do not alter the conclusions here and only reinforce the stability that we demonstrate. Our analysis of equilibrium stability is carried out in terms of tactic proportions and the stability of the underlying population distribution across state will be shown elsewhere. The total number of (male) offspring is

$$pr_\alpha + (1 - p)r_\beta, \tag{1}$$

while the total number of α offspring is

$$pr_\alpha i_\alpha + (1 - p)r_\beta i_\beta, \tag{2}$$

and the total number of β offspring is

$$pr_\alpha(1 - i_\alpha) + (1 - p)r_\beta(1 - i_\beta). \tag{3}$$

Dividing (2) by (1), we find that the proportion of α offspring in the next generation is

$$\frac{pr_\alpha i_\alpha + (1 - p)r_\beta i_\beta}{pr_\alpha + (1 - p)r_\beta}. \tag{4}$$

For the Inheritance Theorem, we will now show both the equilibrium property, that there is exactly one tactic proportion p^* at which the population is at equilibrium, and the stability property, that the tactic proportions will return to p^* if perturbed to any other value of p (where $0 \leq p < p^*$ or $p^* < p \leq 1$).

To say that the population is in equilibrium means that the proportion of each tactic is unchanged from one generation to the next, or

$$\frac{pr_\alpha i_\alpha + (1 - p)r_\beta i_\beta}{pr_\alpha + (1 - p)r_\beta} = p. \tag{5}$$

Collecting terms, we find that this is

$$(r_\alpha - r_\beta)p^2 + (r_\beta + r_\beta i_\beta - r_\alpha i_\alpha)p - r_\beta i_\beta = 0. \tag{6}$$

The population is in equilibrium at those values of p that satisfy (6). Since we assumed that $r_\alpha > r_\beta$, we find that the coefficient of p^2 is positive and the left side of (6) is an upward-opening parabola [Fig. 2(a)]. Its value when $p = 0$ is negative ($-r_\beta i_\beta$), while its value when $p = 1$ is $(r_\alpha - r_\beta) + (r_\beta + r_\beta i_\beta - r_\alpha i_\alpha) - r_\beta i_\beta = r_\alpha - r_\alpha i_\alpha = r_\alpha(1 - i_\alpha)$, which is positive. The parabola must therefore cross the p axis exactly once between $p = 0$ and $p = 1$, so there is only one solution to (6). This reveals that there is exactly one equilibrium proportion p^* .

To see if p^* is stable, namely that the proportions of each tactic will return to p^* if perturbed, consider formula (4) again. The denominator is positive for $0 \leq p \leq 1$, while the value of (4) at $p = 0$ is $(r_\beta i_\beta)/r_\beta = i_\beta$. The value of (4) at $p = 1$ is $(r_\alpha i_\alpha)/r_\alpha = i_\alpha$. Both of these values are between 0 and 1. By calculating the derivative, it is possible to check that (4), which is also the left side of (5), is an increasing function for $0 \leq p \leq 1$. The right side of (5) is the straight line which is 0 at $p = 0$ and 1 at $p = 1$. The function on the left side is above the line at $p = 0$ and below the line at $p = 1$, but increasing. This makes the equilibrium stable, because if p is below p^* , the proportion of α in the next generation, given by (4), will be larger than p but less than p^* , while if p is

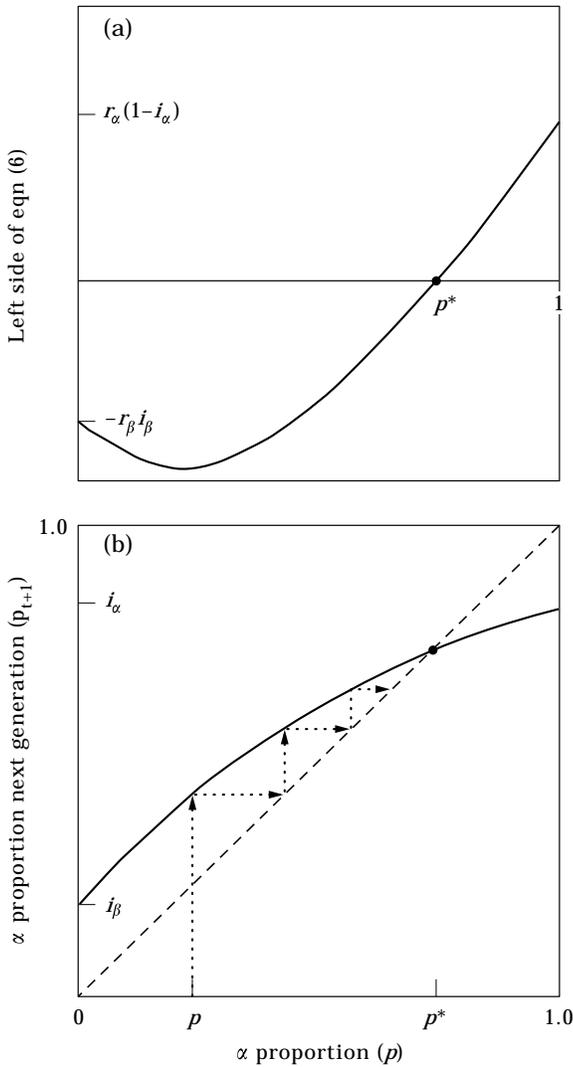


FIG. 2. The equilibrium and stability of the conditional strategy as shown by the behavior of eqns (4) and (6). Part (a) shows the existence and uniqueness of the equilibrium by plotting the parabola given by the left side of eqn (6). It is below the axis at $p = 0$ (i.e. drops to $-r_\beta i_\beta$) and above it at $p = 1$ (i.e. reaches $r_\alpha(1 - i_\alpha)$), crossing the axis exactly once. The corresponding value of p on the axis is a solution of (6), so it is also a solution of (5), which means that it is the equilibrium frequency p^* . Part (b) shows the stability by plotting the change in p after it is perturbed from the equilibrium p^* . The left side of eqn (5) is the solid curve and the right side is the dashed diagonal line; they intersect at the equilibrium frequency p^* . If the population is perturbed to a frequency p which is less than p^* , as shown, it will make its way back across generations to p^* . The same happens if p is greater than p^* . This demonstrates that the equilibrium is stable.

above p^* , the proportion of α in the next generation will be less than p but greater than p^* . Therefore, if the tactic proportions are perturbed away from equilibrium, they will return to equilibrium.

The stability is illustrated in Fig. 2(b). If $p = 0$, that is the population consists entirely of β individuals,

then because of inheritance, the next generation will include some α individuals. The proportion of α individuals in the next generation is exactly i_β . At the opposite extreme, if $p = 1$ and the population consists entirely of α individuals, then because of inheritance, the next generation will include some β individuals. The proportion of α individuals is thus reduced to exactly i_α . Therefore, at either extreme the behavior of the system is to move the next generation back toward the equilibrium, and the closer to the equilibrium, the more gradual the return. We know from Fig. 2(a) that there is in fact only one equilibrium to which the tactic proportions will return, p^* .

The Two-sex Model

We now develop a more complex two-sex model. In the two-sex model we explicitly incorporate inheritance of tactics through the females as well as the males. Having high or low state does not result in tactic differences for females because we assume they do not express these tactics. However, female state does influence through heritability the state of their sons and thus their son's tactics. We show that the two-sex model, which incorporates the complexity of dual inheritance (through mother and father), confirms the stability of the conditional strategy equilibrium. Moreover, it reduces to the same solutions as the single sex model, and therefore validates the use of the simpler model.

To simplify, we refer to high and low state individuals as α and β in either males or females. We assume that the proportions of α and β individuals are the same among males and females. We assume that from a pair of parents, one of whom is α and the other β , the same proportions of α and β offspring arise, no matter which parent is α and which is β . Finally, we assume that the average ratio of sons and daughters is the same from any combinations of α and β parents.

Let p be the proportion of α individuals and q be the proportion of β individuals ($q = 1 - p$). Let $i_{\alpha\alpha}$, $i_{\alpha\beta}$ and $i_{\beta\beta}$ represent the proportions of α individuals among the offspring of parents who are $\alpha\alpha$, $\alpha\beta$ and $\beta\beta$, respectively. Let $r_{\alpha\alpha}$ be the recruitment parameter so that the number of male offspring from α fathers mating with α mothers is $r_{\alpha\alpha}p^2$. Similarly, the number of male offspring from α fathers mating with β mothers is $r_{\alpha\beta}pq$, from β fathers with α mothers is $r_{\beta\alpha}qp$, from β fathers with β mothers is $r_{\beta\beta}q^2$. Note that we do not assume that $r_{\alpha\beta} = r_{\beta\alpha}$. We assume that

$$i_{\alpha\alpha} > i_{\alpha\beta} > i_{\beta\beta}, \tag{7}$$

and

$$r_{\alpha\alpha} > r_{\alpha\beta} > r_{\beta\beta}, \quad (8a)$$

and

$$r_{\alpha\alpha} > r_{\beta\alpha} > r_{\beta\beta}. \quad (8b)$$

Under the above assumptions, the total number of male offspring is

$$r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2, \quad (9)$$

and the total number of male offspring of type α is

$$r_{\alpha\alpha}i_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})i_{\alpha\beta}pq + r_{\beta\beta}i_{\beta\beta}q^2. \quad (10)$$

Dividing (10) by (9) we find that the proportion of α offspring in the next generation is

$$\frac{r_{\alpha\alpha}i_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})i_{\alpha\beta}pq + r_{\beta\beta}i_{\beta\beta}q^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2}. \quad (11)$$

The condition for the population to be at equilibrium is

$$\frac{r_{\alpha\alpha}i_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})i_{\alpha\beta}p(1-p) + r_{\beta\beta}i_{\beta\beta}(1-p)^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})p(1-p) + r_{\beta\beta}(1-p)^2} = p. \quad (12)$$

From this result [eqn (12)], it is possible to show that the two-sex model has exactly one value p^* for which the population is at equilibrium, and that the tactic frequencies return to p^* if perturbed to any other value p (where $0 \leq p < p^*$ or $p^* < p \leq 1$). The proof is given in Appendix A.

Moreover, it can be shown that the predictions of the two-sex model correspond with those of the single-sex model. Specifically, the equilibrium frequency p^* is the same for both models. We demonstrate this in Appendix B.

We have therefore shown that the single-sex model and the two-sex models are compatible representations of the dynamics of the conditional strategy. The single-sex model can therefore be used in lieu of the more complicated two-sex model in calculating many problems of interest.

A Biological Example

We now apply our single-sex model to a specific biological example. This shows how a conditional strategy with tactic inheritance will respond to the perturbation of its tactics from their equilibrium frequency.

Radwan (1995) provides a valuable case study of alternative phenotypes in mites. Male polymorphism occurs in several species of the mite family Acaridae; one male phenotype, the fighters (α), has a thick and

sharp third pair of legs which are used to puncture and kill other males, while the other male phenotype, the non-fighters (β), has unmodified legs and does not attack other males. In *Rhizoglyphus robini*, 66.9% of males in his population are the α phenotype. Radwan demonstrates through breeding studies that 76% of the male progeny of α males mature into the α phenotype, while only 35% of the male progeny of β males mature into the α phenotype, a statistically significant bias in production of the α phenotype. This finding suggests that the two phenotypes are a genetic polymorphism. However, mites that were fed on a poor diet during development were less likely to develop into the α phenotype. This suggests that the decision is state-dependent where state is determined by both heritability and environmental input.

Radwan's research provides a set of empirical parameters for our conditional strategy model. Let $p^* = 0.669$, $i_\alpha = 0.763$ and $i_\beta = 0.351$. Knowing these three values, we can calculate the recruitment r for each phenotype using the eqns (13) and (7) in Table 2 of Gross & Repka (1998): $r_\alpha = 1.15$ and $r_\beta = 0.69$. This shows that the α phenotype has 67% greater recruitment into the next generation than the β phenotype $((1.15 - 0.69)/0.69 = 67\%)$. Since the alternative phenotypes have both inheritance and unequal fitnesses, one might think that an equilibrium cannot exist. However, the model of Gross & Repka (1998) establishes allowability conditions for an equilibrium to exist. Inspection of their Table 3 shows that these parameter values are in fact allowable. With the observed male proportions, the observed inheritances, and the calculated recruitments, an equilibrium of the two tactics, α and β , can persist across mite generations.

We now illustrate the stability of this equilibrium, namely that the proportion of α males in the population will return to the equilibrium proportion ($p^* = 0.669$) if the α proportion is increased or decreased. Figure 3 shows the results from perturbing the proportion of α males to a p of 0 (100% β males), 0.335 (midway between 0.669 and 0), 0.835 (midway between 0.669 and 1), and 1 (100% α males). The results are calculated by substituting the parameter values i_α , i_β , r_α and r_β from the preceding paragraph into formula (4). We assume that the recruitment r and inheritance i parameters are fixed, and consider what happens with different values of p . The results show that across generations the tactic proportion of α males returns to the equilibrium. The return is relatively rapid, and virtually indistinguishable from the equilibrium in 5 to 10 generations. This is true even for the extreme cases of complete loss of one or other of the male phenotypes ($p = 0$ or 1), provided

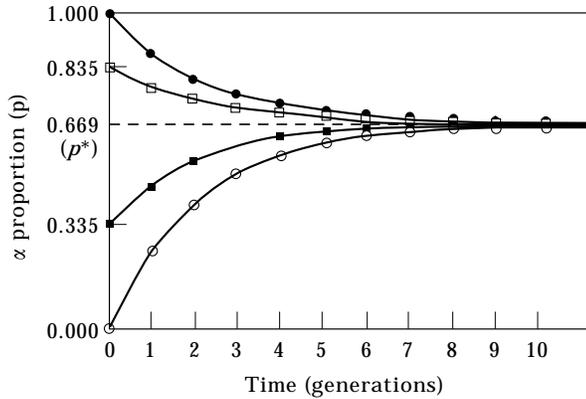


FIG. 3. A graphical demonstration of the stability of the conditional strategy in the phenotypic polymorphism of mites. Male mites have two phenotypes: α (fighters) and β (non-fighters). We show here the response of the population to perturbations of the α 's to a new proportion $p = 1$ (100% α males in the population), 0.835 (half-way between p^* and $p = 1$), 0.335 (half-way between p^* and $p = 0$), and 0 (100% β males in the population). In all cases, the proportion of α males in the population returns to the equilibrium p^* after just a few generations.

that the recruitment and inheritance parameters remain constant.

Discussion

Phenotypic diversity is widespread within populations in nature. The game theoretic approach to understanding this diversity (e.g. Maynard Smith, 1982) imposes restrictions which do not accommodate some of the important biological properties found in many examples. The conditional strategy can incorporate these properties and therefore offers an alternative perspective. Since the tactics in a conditional strategy do not have equal fitnesses, it has been thought that a conditional strategy cannot exist in the presence of heritability of its tactics. In Gross & Repka (1998) and in the present paper we have developed the following result.

Inheritance Theorem

A conditional strategy with heritable alternative tactics can be in equilibrium. Moreover, the equilibrium is stable.

The Inheritance Theorem demonstrates that the inheritance of tactics does not prevent the evolution of a conditional strategy.

Gross & Repka (1998) developed a model defining the structure of the conditional strategy in terms of the inheritances, recruitments (fitnesses), and proportions of the tactics. Their model describes the allowable relationships among these parameters under which a conditional strategy can be in equilibrium,

establishing the first assertion of the theorem. The second assertion, about the stability of the equilibrium, is the subject of the present work. The first paper explored conditions under which the population would not change from one generation to the next, that is, be at equilibrium, while the current paper explores the response of the population to a perturbation.

We have introduced some minor terminology changes. In Gross & Repka (1998) the underlying cue for the conditional strategy was called "status", with the intention of emphasizing that it might depend on the relative positioning of the individual within a population. In this paper we use the simpler and more familiar term "state", but no change in meaning is implied. We have also changed our tactic labels from the suggestive F (fighter) and S (sneaker) to the more generic α and β .

Gross & Repka (1998) modeled the conditional strategy looking at only one sex (males). Here we use a similar approach which we call the single-sex model. However, in addition, we develop a two-sex model to capture the interactions between the two sexes and to allow for inheritances through either. We found that the equilibrium predictions of the two-sex model reduce to those of the simpler single-sex model, thus confirming the approach of Gross & Repka (1998) and validating the use of the simpler model for subsequent research.

The conditional strategy provides a new theoretical framework that explains phenotypic diversity while incorporating three important empirical patterns: state-dependent decision making, unequal average fitnesses, and tactic inheritance. Evolutionary game theory has implied that the presence of heritability suggests a genetic polymorphism and Evolutionarily Stable State (ESS) with equal average fitnesses and frequency-dependent selection. Our work, however, demonstrates that the empirical observation of heritability is compatible with the conditional strategy. We used the mite system studied by Radwan (1995) as an example of the use of the conditional strategy approach to explain the presence of heritability.

Our modeling procedure for examining the stability of the equilibrium in the conditional strategy assumes that the parameters for recruitment and inheritance of the tactics are constant even when the tactic proportions are perturbed. We recognize that extreme shifts in tactic proportions would likely affect recruitment, for example through frequency- or density-dependent selection, and inheritance, for example through loss of additive genetic variance or the alleles from the ends of the state distribution. In

Fig. 3 we included calculations for the extreme perturbations of $p = 0$ and 1 to aid in visualization although in a real situation such drastic perturbations may alter the parameters, resulting in a different equilibrium.

Our modeling work shows that the knowledge of certain parameters in the conditional strategy is sufficient to derive the others. Gross & Repka (1998) show that only three of the following five parameters, r_α , r_β , i_α , i_β , and p , are necessary to calculate the other two. For example, from Radwan's (1995) data we were able to calculate the recruitments by knowing proportions and heritabilities. We now point out a further possible simplification. Note that eqns (4) and (5) are unchanged if the recruitments r_α and r_β are both multiplied by a constant. In other words, the equations depend on the *ratio* of the tactic recruitment values, not the actual values. This is useful because in practice it may often be easier to find this ratio than the actual values, and the ratio and two other parameters suffice to determine all the parameters. For instance, i_α , i_β and the ratio r_α/r_β may be the easiest to measure, or p , the ratio and one of i_α or i_β . Thus, calculating the empirical structure of a conditional strategy may be simplified.

In the two-sex model we assumed random mating by tactic. However, the model can easily be adapted to include non-random mating, such as through mate choice and environmental factors, by incorporating these effects into the recruitment values. This does not qualitatively change the Inheritance Theorem, although it may affect the location of the equilibrium.

The conditional strategy as a theoretical framework for understanding phenotypic diversity is very robust. It incorporates the empirical observations of state-dependent decision making, unequal fitnesses, and the potential for inheritances that are found in alternative phenotypes. The Inheritance Theorem strengthens the theoretical framework of the conditional strategy as a concept for explaining phenotypic diversity.

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APPENDIX A

Proof

The two-sex model has exactly one value p^* for which the population is at equilibrium, and the tactic frequencies return to p^* if perturbed to any other value p (where $0 \leq p < p^*$ or $p^* < p \leq 1$).

The denominator of (11) is positive whenever $0 \leq p \leq 1$. We claim that (11), the proportion of the offspring that are α , is an increasing function of p , for $0 \leq p \leq 1$. The presence of the pq “cross term” makes it difficult to prove, since as p runs from $p = 0$ to 1, the cross term $pq = p(1 - p)$ increases to a maximum

at $p = 1/2$ and then decreases. To prove this claim, we write (11) as

$$\begin{aligned}
 & \frac{r_{\alpha\alpha}i_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})i_{\alpha\beta}pq + r_{\beta\beta}i_{\beta\beta}q^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2} \\
 &= \frac{r_{\alpha\alpha}i_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})i_{\alpha\beta}pq + r_{\beta\beta}i_{\beta\beta}q^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2} - i_{\alpha\beta} + i_{\alpha\beta} \\
 &= \frac{r_{\alpha\alpha}i_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})i_{\alpha\beta}pq + r_{\beta\beta}i_{\beta\beta}q^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2} \\
 &\quad - \frac{r_{\alpha\alpha}i_{\alpha\beta}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})i_{\alpha\beta}pq + r_{\beta\beta}i_{\alpha\beta}q^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2} + i_{\alpha\beta} \\
 &= \frac{r_{\alpha\alpha}(i_{\alpha\alpha} - i_{\alpha\beta})p^2 + r_{\beta\beta}(i_{\beta\beta} - i_{\alpha\beta})q^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2} + i_{\alpha\beta} \\
 &= \frac{r_{\alpha\alpha}(i_{\alpha\alpha} - i_{\alpha\beta})p^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2} \\
 &\quad + \frac{r_{\beta\beta}(i_{\beta\beta} - i_{\alpha\beta})q^2}{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2} + i_{\alpha\beta}. \quad (\text{A.1})
 \end{aligned}$$

The third term in the final expression of (A.1), $i_{\alpha\beta}$, is a constant. The reciprocal of the first term in the final expression of (A.1) is

$$\begin{aligned}
 & \frac{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2}{r_{\alpha\alpha}(i_{\alpha\alpha} - i_{\alpha\beta})p^2} \\
 &= \frac{1}{r_{\alpha\alpha}(i_{\alpha\alpha} - i_{\alpha\beta})} (r_{\alpha\alpha} + (r_{\alpha\beta} + r_{\beta\alpha})(q/p) + r_{\beta\beta}(q^2/p^2)).
 \end{aligned}$$

Since $q = 1 - p$, we see that $q/p = (1 - p)/p$ and its square are both decreasing functions of p for $0 < p < 1$. Since $i_{\alpha\alpha} - i_{\alpha\beta} > 0$, by (7), the reciprocal of the first term in the final expression is a decreasing function so the first term itself is an increasing function.

Similarly, the second term in the final expression of (A.1) has reciprocal

$$\begin{aligned}
 & \frac{r_{\alpha\alpha}p^2 + (r_{\alpha\beta} + r_{\beta\alpha})pq + r_{\beta\beta}q^2}{r_{\beta\beta}(i_{\beta\beta} - i_{\alpha\beta})q^2} \\
 &= \frac{1}{r_{\beta\beta}(i_{\beta\beta} - i_{\alpha\beta})} (r_{\alpha\alpha}(p^2/q^2) + (r_{\alpha\beta} + r_{\beta\alpha})(p/q) + r_{\beta\beta}).
 \end{aligned}$$

We see that $p/q = p/(1 - p)$ and its square are both increasing functions of p for $0 < p < 1$. Since $i_{\beta\beta} - i_{\alpha\beta} < 0$, by (7), we see that the reciprocal of the second term in the final expression of (A.1) is a decreasing function so the second term itself is an increasing function. So we have proved the claim that (11), the proportion of the offspring that are α , is an increasing function of p for $0 \leq p \leq 1$.

Note that the value of (11) at $p = 0$ is $r_{\beta\beta}i_{\beta\beta}/r_{\beta\beta} = i_{\beta\beta}$, while the value of (11) at $p = 1$ is $r_{\alpha\alpha}i_{\alpha\alpha}/r_{\alpha\alpha} = i_{\alpha\alpha}$. Note that both of these values are between 0 and 1. This implies that there is exactly one solution of (12) with

$0 < p < 1$. The fact that (12) is an increasing function proves that the equilibrium is stable. The argument is the same as that at the end of the proof for the single-sex model.

APPENDIX B

Demonstration

The predictions of the two-sex model correspond with those of the single-sex model. Specifically, the equilibrium frequency p^* is the same for both models.

To compare the two-sex with the single-sex model we need to find the parameters of that model, r_α , r_β , i_α , i_β , in terms of the parameters of the two-sex model. Note that the parameter p is the same in both, so

$$r_\alpha = r_{\alpha\alpha}p + r_{\alpha\beta}(1 - p),$$

$$r_\beta = r_{\beta\alpha}p + r_{\beta\beta}(1 - p),$$

$$i_\alpha = \frac{r_{\alpha\alpha}i_{\alpha\alpha}p^2 + r_{\alpha\beta}i_{\alpha\beta}p(1 - p)}{r_{\alpha\alpha}p^2 + r_{\alpha\beta}p(1 - p)} = \frac{r_{\alpha\alpha}i_{\alpha\alpha}p + r_{\alpha\beta}i_{\alpha\beta}(1 - p)}{r_{\alpha\alpha}p + r_{\alpha\beta}(1 - p)},$$

and

$$\begin{aligned}
 i_\beta &= \frac{r_{\beta\alpha}i_{\alpha\beta}p(1 - p) + r_{\beta\beta}i_{\beta\beta}(1 - p)^2}{r_{\beta\alpha}p(1 - p) + r_{\beta\beta}(1 - p)^2} \\
 &= \frac{r_{\beta\alpha}i_{\alpha\beta}p + r_{\beta\beta}i_{\beta\beta}(1 - p)}{r_{\beta\alpha}p + r_{\beta\beta}(1 - p)}.
 \end{aligned}$$

Note that the total recruitment is

$$\begin{aligned}
 pr_\alpha + (1 - p)r_\beta &= r_{\alpha\alpha}p^2 + r_{\alpha\beta}p(1 - p) \\
 &\quad + r_{\beta\alpha}p(1 - p) + r_{\beta\beta}(1 - p)^2 = r_{\alpha\alpha}p^2 \\
 &\quad + (r_{\alpha\beta} + r_{\beta\alpha})p(1 - p) + r_{\beta\beta}(1 - p)^2, \quad (\text{B.1})
 \end{aligned}$$

which is the denominator of formula (11).

Also, the number of α male offspring is

$$\begin{aligned}
 p r_\alpha i_\alpha + (1 - p)r_\beta i_\beta &= p(r_{\alpha\alpha}p + r_{\alpha\beta}(1 - p)) \\
 &\quad \times \frac{r_{\alpha\alpha}i_{\alpha\alpha}p + r_{\alpha\beta}i_{\alpha\beta}(1 - p)}{r_{\alpha\alpha}p + r_{\alpha\beta}(1 - p)} \\
 &\quad + (1 - p)(r_{\beta\alpha}p + r_{\beta\beta}(1 - p)) \frac{r_{\beta\alpha}i_{\alpha\beta}p + r_{\beta\beta}i_{\beta\beta}(1 - p)}{r_{\beta\alpha}p + r_{\beta\beta}(1 - p)} \\
 &= r_{\alpha\alpha}i_{\alpha\alpha}p^2 + r_{\alpha\beta}i_{\alpha\beta}p(1 - p) \\
 &\quad + r_{\beta\alpha}i_{\alpha\beta}p(1 - p) + r_{\beta\beta}i_{\beta\beta}(1 - p)^2, \quad (\text{B.2})
 \end{aligned}$$

which is the numerator of (11).

The proportion of α offspring in the single-sex model, given by (4), is therefore the quotient (B.2)/(B.1). We have just shown this quotient is equal to (11), which is the proportion of α offspring according to the two-sex model. This shows that the two-sex model corresponds exactly with the single-sex model. Specifically, the equilibrium frequency p^* is the same for both models.