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# The status of the conditional evolutionarily stable strategy

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**The conditional evolutionarily stable strategy (ESS) has proven to be a versatile tool for understanding the production of alternative phenotypes in response to environmental cues. Hence, we would expect the theoretical basis of the conditional strategy to be robust. However, Shuster and Wade have recently criticized the conditional ESS based on Gross's 1996 proposal that most alternative reproductive tactics are conditional and have evolved by 'status-dependent selection.' We critically assess Gross's status-dependent selection model and Shuster and Wade's critique. We find shortcomings and misconceptions in both. We return to the findings of the strategic models behind the conditional ESS and demonstrate how environmental threshold models use a reaction norm approach and quantitative genetic theory to understand the evolution of conditional strategies.**

## Introduction

Arguably, the most influential model for understanding the occurrence of alternative reproductive tactics within the sexes, having been cited over 400 times (http://portal.isiknowledge.com/ on Ref. [1]), is the status-dependent selection model (SDS) (Box 1) proposed by Gross [1]. Gross notes that most of the examples of alternative male-reproductive tactics appeared to be conditionally expressed in response to status or some surrogate thereof, such as body size, and, therefore, fall under the umbrella of what is known in evolutionary game theory as the conditional strategy (see Glossary) [2–4].

In spite of its wide currency, especially in the behavioural ecology literature, the value of the SDS specifically, and game theory models for conditional strategies in general, have been recently questioned. In their book *Mating Systems and Strategies*, Shuster and Wade [5] strongly criticize the SDS, believing its premise to be flawed and its explanatory power to be 'more apparent than real'. This high-profile criticism of such a widely adopted theoretical framework requires detailed consideration, particularly because conditional strategies have been reported in a wide range of taxa, are seen increasingly as common adaptations and might be the most common form of discrete variation within species (for reviews, see [6–10]). The many examples now known encompass a broad swathe of evolutionary ecology and include induction of defences against predators [11], trophic polymorphisms [12], protective polymorphisms [13], seasonal polyphenisms [14], sex-ratio investment [15], alternative male-reproductive tactics [16,17], investment in adaptations to sperm competition [18–20] and numerous behavioural traits associated with competitive interactions [21]. Consequently, understanding how these strategies evolve and are maintained by natural selection is important.

Here, we review the SDS and the criticisms by Shuster and Wade [5] and then we show how other theoretical models reveal problems in both positions. Using an approach both Gross and Shuster and Wade advocate, we then show how the current understanding of the evolution of the conditional strategy has a greater depth than is generally recognized [1,22–24].

## The SDS and Shuster and Wade's critique

Shuster and Wade's [5] critique is related to two particular characteristics of the SDS (Box 1): the population is genetically monomorphic in its response to status (tactic switchpoint); the average fitnesses of the alternative tactics are

### Glossary

**Alternative strategies**: The occurrence in a population of a stable mixture of different, genetically based decision rules (e.g. strategy $a$ = always sneak and strategy $b$ = always guard).
**Conditional strategy**: A decision rule containing a conditional clause (e.g. fight if larger than opponent, sneak if smaller than opponent).
**Environmentally cued threshold trait**: A threshold trait in which the value of the threshold is a function of environmental cues.
**Evolutionarily stable strategy (ESS)**: A strategy or combination of strategies that cannot be invaded by any other mutant strategy.
**Mixed strategy**: A decision rule with a probabilistic basis (e.g. play 'sneak' with a probability of 0.25, play 'guard' with a probability of 0.75).
**Monomorphism**: The occurrence in a population of a single genetically based decision rule; monomorphism is synonymous with a pure strategy.
**Polymorphism**: The occurrence in a population of alternative phenotypes or strategies reflecting genetic differences at a single gene; polymorphism is synonymous with alternative strategies.
**Pure strategy**: When a population is composed of a single strategy (i.e. the conditional strategy and the mixed strategy are pure strategies).
**Strategy**: A genetically based decision rule [1] (e.g. fight if larger than x, sneak if smaller than x).
**Switchpoint**: The equivalent of liability for an environmentally cued threshold trait; the value of an environmental cue necessary to switch development from one phenotypic alternative to another.
**Tactic**: The phenotype generated by the decision rule [1] (e.g. sneaking male behaviour).
**Threshold**: The point on a normal distribution of liabilities or switchpoints delimiting the proportions of alternative phenotypes in a population. In the liability model, the threshold has a fixed value on the underlying liability scale, whereas, in the ET model, the threshold simply delimits the proportion of the emergent phenotypes at each value of the environmental cue.
**Threshold trait**: A trait with discontinuous emergent phenotypes whose expression is dependent on the liability or switchpoint of an individual relative to some threshold value (the threshold).

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### Box 1. The SDS model

The SDS [1] is concerned with how the conditional ESS occurs when status-dependent decision rules are used. The SDS model is said to have five characteristics: '(1) the tactics involve a 'choice' or 'decision' by the individual; (2) the decision is made relative to some aspect of the individual's status; (3) individuals are genetically monomorphic for the decision; (4) the average fitnesses of the tactics are not equal, but the fitnesses of the alternatives at the switchpoint are equal; and (5) the chosen tactic results in higher fitness for the individual' [1]. Hence, the model assumes that individuals differ in their competitive ability or status (Figure I) and that differences in status or some associated trait, such as body size, influence the fitness and expression of the alternative tactics of the conditional strategy (denoted as X and Y in Figure I).

If the fitness functions of X and Y are linear in relation to status and have different slopes (e.g. the fitness of Y increases with status more rapidly than does the fitness of X), then the fitness functions will intersect at some value of status (s*). At s*, the fitnesses of the two tactics are equal, thus defining the 'evolutionary stable strategy switchpoint' (ESSs*) [1].

According to the SDS model, switching tactics at the ESSs* is the decision rule that will maximize fitness and, as a result, is the decision rule to which the population evolves. The result will be a single genetic strategy (so-called 'monomorphism') with two status-dependent alternative tactics. The tactics are status dependent because those individuals of status greater than ESSs* will adopt Y and those with a status lower than ESSs* will adopt X. According to the SDS, the frequency distribution of status has no effect on the ESSs*. However, changes in ESSs* and in the distribution of status will alter the frequency of individuals adopting each of the alternative tactics (shaded arrows in Figure I); if frequency-dependent selection is important, this could reduce the ability of the SDS to predict the ESSs* (but see Ref. [24]).

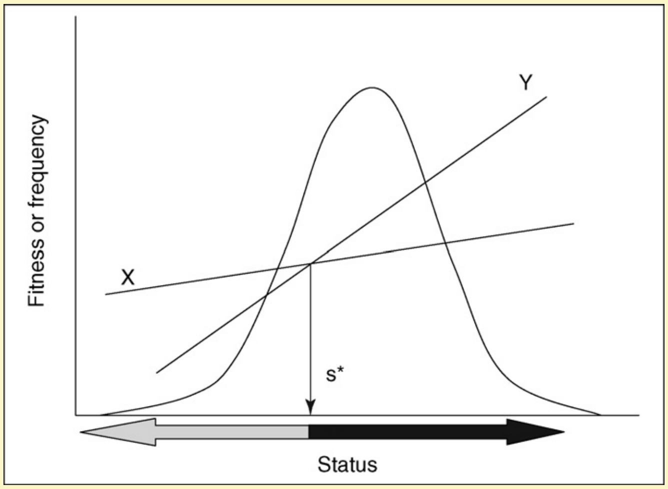

**Figure I.** The SDS model [1]. Fitness functions for the alternative tactics X and Y overlay a normal distribution of status for individuals in a population. The fitness functions intersect at the status s*. Filled arrows indicate the proportion of the population adopting tactic X (grey) versus tactic Y (black).

unequal. Although Gross' use of the term 'monomorphism' is misleading, the term monomorphism is in keeping with the terminology of game theory, in which it is used to distinguish the conditional strategy from a mixture of equally successful alternative strategies (a genetic polymorphism). The assumption of game theory with respect to conditional strategies is that different switchpoint genotypes compete with one another, with selection favouring those that match the current ESS. The SDS proposes that the current ESS will be genotypes that switch between alternative tactics at the status where the fitness functions for the tactics intersect. However, as Shuster and Wade correctly point out, by assuming that there is no heritable variation in switchpoint, the SDS cannot quantify the effects of selection on switchpoints.

Shuster and Wade's second criticism of the SDS is related to the fitnesses of the alternative phenotypes in an equilibrium population (Box 2). The SDS model maintains that the average fitness of the tactics will differ at equilibrium and the tactic switchpoint will be the status at which their fitness functions intersect [the evolutionary stable strategy switchpoint (ESSs*)]. By contrast, Shuster and Wade contend that the average fitness of the alternative tactics will be equal. This implies that when the expression of the alternatives is conditional, the tactic switchpoint will result in equal average fitness for the two tactics. Their view is based on the opinion that 'general evolutionary theory describes four conditions that are necessary for the persistence of any phenotype in a population'. One of these conditions is that 'to persist in a population at a stable frequency, the average fitness of the alternative phenotype at equilibrium must equal the average fitness of the conventional phenotype'.

## Problems with the SDS and Shuster and Wade's critique

The major problem with the SDS and Shuster and Wade's critique is that arguments for the equality or inequality of fitnesses of the alternative phenotypes are not supported mathematically. Shuster and Wade do produce what is essentially a game theoretic model for the evolution of alternative mating phenotypes. However, the modelled alternative phenotypes are genetic, rather than phenotypes that are expressed conditionally. Consequently, and contrary to their thesis, Shuster and Wade's model does not address their contention that alternative phenotypes expressed conditionally are expected to have equal fitness.

One model that does address the question of the fitnesses of conditionally expressed alternative phenotypes is that of Lively [11], who modelled the evolution of a conditional strategy given a coarse-grained, two-patch environment, a fitness trade-off for the alternative tactics in the different environments and a reliable environmental cue correlated with the environments [11]. The model has the essential ecological features of the SDS model, with variation in status and intersecting fitness functions in the SDS being equivalent to coarse-grained environmental variation and fitness tradeoffs, respectively. Indeed, Lively's model goes one step further than the SDS by specifying how reliable the environmental cue must be for the conditional ESS to evolve [11]. For the conditional strategy to be the ESS, cues must be more reliable than random and one of the alternative phenotypes must have greater fitness in one environment and vice versa (see also [4]). When these conditions are met, the fitness of the conditional strategists (which is a function of the average fitnesses of the two phenotypes they produce) is greater than that of

## Box 2. The environmental threshold model

The ET model is based on the notion that there is genetic variation among organisms in the response of an all-or-none trait to some environmental cue(s), such as status or body size (i.e. there is genetic variance in reaction norm switchpoints). Similar to the liability model, there are two emergent phenotypes or tactics (X and Y in Figure I) but their expression is influenced strongly by an environmental cue. For each switchpoint phenotype, there is a value for the environmental cue (i.e. the switchpoint) above which phenotype Y is produced and below which phenotype X is produced. Therefore, in a sense, each reaction norm is a different conditional strategy. Although only seven switchpoint phenotypes are shown in Figure Ia, the frequency distribution of switchpoints in the population is assumed to be continuous and normal, which is typical of a polygenic or quantitative trait (Figure Ib). At any specific value of the environmental cue (e.g. the threshold, e,* in Figure Ib), some individuals have switchpoints that are greater than the value of the cue; thus, their switches are untripped and they adopt tactic X (white arrow, Figure Ib), whereas others have switchpoints that are less than the value of the cue and so are tripped and thus adopt the other tactic, tactic Y (black arrow, Figure Ib). The position of the threshold, e*, is a function of the environmental cue, hence the label 'environmentally cued threshold model'.

The distribution of switchpoints in a population can be estimated by the cumulative frequency distribution of the individuals adopting one of the alternative tactics (Figure Ic) over a gradient of cue values. The range of variation in switchpoints (solid line in Figure Id) will usually be small relative to the variation in the cue to which the population is exposed (broken line in Figure Id). Therefore, the cumulative frequency distribution of tactic expression (dotted line in Figure 1d) can estimate the mean and variance in switchpoint. The mean switchpoint can therefore be estimated as the cue value at which there is an equal frequency of the two alternative tactics. Populations with little variance in switchpoints will have a relatively steep cumulative normal curve; those with more variation will have shallower curves [33]. Formally, the standard deviation in switchpoints is one-half of the difference in cue values that produce 16% and 84% of tactic Y.

In the ET model, selection can affect the distribution of switchpoints only through the fitnesses of the alternative tactics. Because tactic frequency is dependent on the switchpoint distribution and the cue distribution, both are taken into account in determining how tactic fitness influences the evolution of switchpoints (Box 3). Hence, the ET model provides a quantitative mechanism that can tie variation in switchpoints to ecological differences that affect selection on the alternative tactics [44].

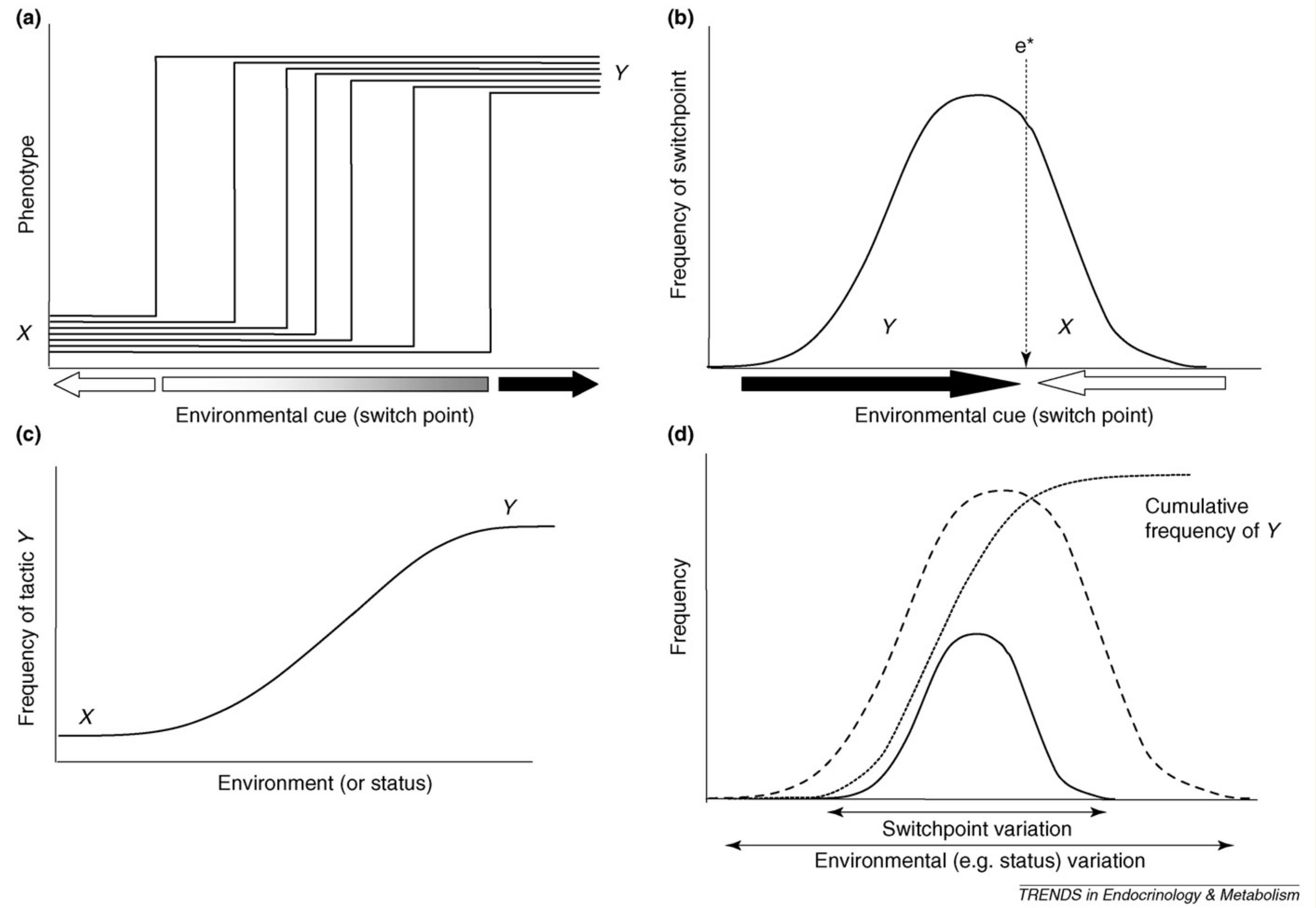

**Figure I.** The environmental threshold model [32,33]. **(a)** The average reaction norms (phenotypes) for seven switchpoint genotypes plotted against a gradient of the environmental cue (e.g. status). Arrows show the change in tactic expression with increasing cue strength from tactic X (open arrow) to increasing expression of tactic Y (filled arrow). **(b)** The mapping of the frequencied of emergent alternative phenotypes, X and Y, on a normal distribution of switchpoint phenotypes in environment e*. Arrows show switchpoints that are tripped (filled arrow) and untripped (open arrow) for this value (e*) of the environmental cue. **(c)** Cumulative frequency distribution of switchpoints as revealed by the frequencies of the alternative tactics X and Y over a range of cue values. **(d)** The variance in switchpoints (solid line) will usually be small relative to the total variance in environmental cue to which the population is exposed (broken line). Therefore, the cumulative normal curve of tactic expression (in this case Y) reveals (dotted line) the mean and variance in the underlying switchpoint.

competing unconditional strategists, but the average fitness of the two phenotypes produced by the conditional strategists can be equal or unequal.

## Quantitative genetic models of threshold traits under status-dependent selection

Both Gross [1] and Shuster and Wade [5] suggest that the concept of phenotypically plastic threshold traits is an accurate conceptualization of the genetics of alternative reproductive tactics and strategies; both cite Ref. [25] in an identical context. The threshold trait concept was first developed by Wright [26] to explain all-or-none phenotypic differences that were not inherited as simple Mendelian alternatives. Subsequent papers by Dempster and Lerner [27] and Falconer [28] built on Wright's original work. The basic quantitative genetic models for threshold inheritance assume that the expression of an all-or-none character depends on some underlying, normally distributed and heritable phenotypic variable, 'liability' [29]. If liability exceeds some threshold value, then one of the all-or-none phenotypes is expressed; if it fails to exceed the threshold value, the other phenotype is expressed [29]. Evolutionary changes in the frequency of the alternative phenotypes arise from shifts in the liability distribution with respect to a single static threshold.

The liability model can be adapted to conditional strategies by modelling populations as having genetic variation for switchpoints, such that individuals respond to different values of some environmental cue. The cues that affect the switch between alternative phenotypes are, by definition, environmental, under the conditional strategy (Box 2). The environmentally cued threshold model (ET) was proposed 30 years ago to explain the genetic basis of the environmentally cued production of cryptic green and brown pupae in butterflies [30,31]. The model was formalized mathematically in 1990 and 2004 [32,33]. In the ET model [32–34], the distribution of liabilities has become a distribution of tactic switchpoints and the position of the threshold depends on environmental cues (i.e. the proportions of the alternative phenotypes change depending on the cue). Variation in switchpoints means that the proportion of individuals expressing each tactic depends on both the distribution of variation in switchpoints and the distribution of cues experienced by the population at the time. Tactic frequency can change in the short term as a result of changes in cue distribution; for example, in the case of status-dependent alternative phenotypes, owing to dietary effects on body size, [35–39], ecological conditions [40] or changing social conditions [21] (Box 2). Evolutionary changes arise through changes in the distribution of switchpoints [39,41–45].

In their discussion of threshold traits, Shuster and Wade come close in their Figure 12.8 to describing the ET model. However, in their version, the threshold is fixed and environmental variation, which includes variation in the cue, shifts the distribution of liabilities relative to the threshold, owing to environmental effects. In the ET model, only non-cue environmental effects and genetic differences influence phenotypic variation in switchpoints, whereas the position of the threshold shifts, relative to the distribution of switchpoints, owing only to differences in the environmental cue that influences the expression of the alternative phenotypes. This partitioning of cue and non-cue environmental variation in the ET enables selection on switchpoints to be weighted by the distribution of the cue (e.g. social context). The weighting of selection by social context is something that Shuster and Wade suggest is lacking in the SDS but did not resolve with their threshold model.

In terms of specifying the conditions favouring a conditional strategy, the ET model produces almost identical results to those of Lively's ESS model [11] but does so using quantitative genetic theory [32,33] (Box 3). The model, which has the advantage of accommodating any distribution of environmental cue, as well as multiple cues, is potentially applicable to any situation in which alternative phenotypes are produced in response to an environmental cue, including those that the SDS was proposed to explain.

When applied to status-dependent selection, how do the expectations of the ET model compare with those of Gross' SDS model [1] and what do they reveal about Shuster and Wade's [5] objections? First, because the ET model is a quantitative genetic model, the effect of selection on the distribution of switchpoints is quantified as a selection differential that determines where the mean switchpoint ultimately evolves. The ET is similar to game-theory models, in that it seeks to determine the ultimate outcome of selection, in which each switchpoint is a conditional strategy. However, instead of using invasion criteria, it searches for the stable mean of a normal distribution of switchpoints where the selection differential is zero. The selection differential is a function of three sets of variables: the differences in slopes of fitness functions of the two tactics for males of different status (i.e. the slopes of fitness plotted on status for each tactic); the frequency distribution of status (the assumed environmental cue); and the variance in the distribution of switchpoints in the population. These variables, along with the current switchpoint mean, interact to determine the sign and magnitude of the selection differential. This approach differs from the SDS in which only the intersection of the fitness functions is assumed to determine the outcome of selection on variation in switchpoint. According to the ET model, the population will have evolved to its equilibrium switchpoint mean when the selection differential on switchpoint is zero (Box 3).

One of the most important observations of the ET model is that nothing in the mathematics of how the fitness functions influence the selection differential links the equilibrium mean of the switchpoint distribution explicitly to the intersection of the fitness functions of the alternative tactics (condition four of the SDS model). In other words, the intuitively appealing notion that the point at which the fitness functions cross is the point to which the population switchpoint will evolve is, in fact, false. However, neither does the mathematics support the view that the average fitnesses of the alternative tactics will be equal at equilibrium, as proposed by Shuster and Wade. In the ET model, the equilibrium switchpoint can be at the status where the fitness functions of the alternative tactics intersect (Box 3), as expected by the SDS; and the average fitnesses of the alternative tactics can be equal at

### Box 3. Predicting the mean switchpoint of a population

The ET model uses quantitative genetic techniques to identify the mean switchpoint to which a population will evolve by searching for the mean switchpoint at which the overall selection differential is zero. Close agreement between this expected value and the observed mean switchpoint (i.e. the body size at which a 1:1 ratio of the two tactics exists) suggests that the mean switchpoint is being stabilized by selection. Disagreement would suggest that the population is under either directional or disruptive selection and additional observations could quantify the response to such selection.

The selection differential on switchpoint is calculated as it would be for any quantitative trait selected in different directions or intensities in a variety of environments. Hence, for a population with a given mean and variance for a trait that is distributed randomly among environments, the effect of selection in each environment is weighted by the frequency of the environment. In the case of the ET, the different environments are the different values of the environmental cue (assumed here to be body size) and the direction and intensity of selection in those cue environments is based on the values of the fitness functions for the alternative phenotypes. Because the fitness functions, cue values and switchpoints are continuous, integration is used (Equation I).

To use the ET model, one needs estimates of the variables that affect the sign and magnitude of the selection differential (Equation 1) (see [53] for derivation):

$$S(\mu) = \left(\frac{\sigma^2}{D(\mu)}\right)\int_{-\infty}^{\infty}[w_X(t) - w_Y(t)]g(t)\, f(t;\mu)dt \qquad \text{[Eqn 1]}$$

where $S(\mu)$, is the selection differential on switchpoint with tactic fitness functions $w_X(t)$ and $w_Y(t)$, body size distribution $g(t)$ and switchpoint distribution $f(t)$ with variance $\sigma^2$ and mean $\mu$. Field studies would be necessary to generate estimates of the fitness functions (e.g. by regressing tactic fitness on body size) and the frequency distribution of body sizes, $g(t)$. The variance, $\sigma^2$, and mean, $\mu$, of the distribution of switchpoints are estimated from the cumulative frequency distribution of switchpoints (Box 2, Figure Ic). $D$ normalizes the selection differential [32] and is always positive. Given these estimates, a plot of the selection differential for different values of the mean switchpoint ($\mu$) will result in a graph similar to that in Figure I, if the conditional strategy is favoured. The value of the mean switchpoint at which the selection differential is zero is a stable equilibrium if mean switchpoints above and below this value produce negative and positive selection differentials, respectively. If variation in switchpoint is heritable, selection will move the switchpoint mean to this equilibrium.

The ET model differs from the SDS in that, in addition to tactic fitness functions, it takes into account both variance in switchpoints ($\sigma^2$) and the distribution of the cue. Their combined effect on the selection differential in most cases will result in the equilibrium mean switchpoint not corresponding to the intersection of the fitness functions. Likewise, when the mean switchpoint is at its equilibrium value, the average fitness of the alternative tactics will usually not be equal.

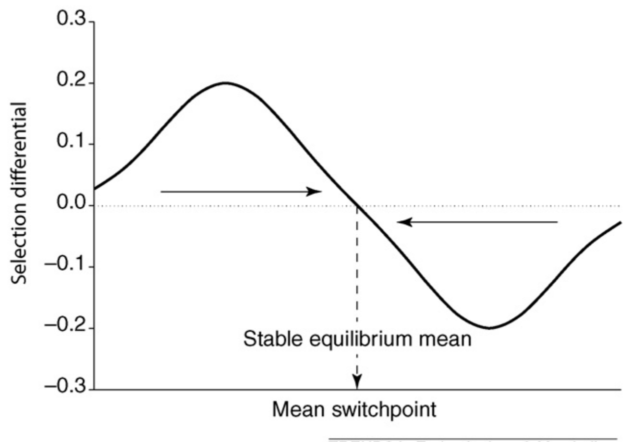

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**Figure I.** A graphical solution to the equilibrium mean switchpoint. Solid arrows indicate the direction of shift in the mean tactic switchpoint towards a stable equilibrium (broken arrow) where the selection differential equals zero.

equilibrium, as expected by Shuster and Wade (and Ref. [46]), although neither result is guaranteed. In short, the ET model, which incorporates the phenotypic plasticity and threshold-evolution approaches suggested by both Gross and Shuster and Wade for studying conditional strategies, does not provide support for Gross' or Shuster and Wade's position.

## Future directions: empirical approaches to studying alternative reproductive tactics

Unlike the SDS, the ET model can: (i) model both the trajectory and ultimate outcome of selection on a conditional strategy; (ii) accommodate both discrete and continuously distributed environmental cues and variation in cue reliability; and (iii) take into account major genetic effects, such as epistasis, as well as frequency-dependent selection [33]. Neither the SDS nor the alternative proposed by Shuster and Wade has similar explanatory power.

The ET model can provide a general framework for advancing our understanding of the conditional strategy, although some key assumptions remain to be tested adequately. For example, the ET model is constrained genetically by the fact that the threshold phenotypes of different genotypes are assumed to have a genetic correlation of 1.0 across different cue values [47]. This assumption has empirical support from studies of wing polymorphic in insects [34,47] but is largely untested for alternative reproductive tactics. Such a correlation makes intuitive sense if the probability that a genotype will produce the induced phenotype increases monotonically with increasing cue strength and seems especially probable in conditional strategies that are not reversible and in which tactic choice is made during a sensitive period. Because of this correlation, the ET model predicts that the response to selection on switchpoint at one environmental cue value will be accentuated or reduced in a predictable manner when the population is reared at some other value of the cue [34]. Support for this prediction comes from the mite *Sancassania berlesei,* in which density influences the expression of the scrambler or fighter morphs; mites selected for either the scrambler or fighter morph at medium densities also yielded divergent switchpoints when individuals were reared alone [45].

Tactic fitnesses have been quantified only rarely for alternative reproductive tactics. The fitness functions for sneaking and fighting behaviours in coho salmon *Oncorhyncus kisutch* [16] and in the dung beetle *Onthophagus taurus* [17] show the fitness trade-off with status expected under the conditional ESS; however, further studies are required to verify this prediction. The prevalence of frequency-dependent selection is also an issue that requires further attention. Gross stated that frequency-dependent selection might or might not be important in the SDS [1] and, despite theoretical consideration [24], it has rarely been addressed in species with conditional tactic expression [48]. The ET model can accommodate frequency-dependent selection by incorporating tactic frequency in the tactic fitness functions, although this has only been done in the case of the conditional strategy of predator-induced defence [33]. In that case, frequency-dependent selection made the coexistence of conditional and unconditional phenotypes (mixed control) possible [33], a result that is consistent with ESS models [11] (see also Ref. [49]).

The genetic architecture of status and switchpoints also requires further study. Genetic variation is expected for both traits but the genetic correlation between these two traits is likely to be low, enabling each trait to be altered independently by selection. This view is based on the idea that, in theory, the phenotypic correlation between status or body size and tactic could result either from a genetic correlation between the two traits or from a tactic being conditional on body size. The conditional expression of the alternative tactics therefore implies a low genetic correlation between switchpoint and body size. Evidence for this pattern comes from the lack of correlated change in body mass in lines of the mite *Sancassania berlesei* that diverged dramatically in the position of the average switchpoint owing to artificial selection [45]. However, the phenotypic correlation between tactic expression and body size does suggest that selection on switchpoint also may have indirect effects on body size that reinforce the maintenance of conditional reproductive tactics. According to the ET model, the crossing fitness functions result in the maintenance of the conditional strategy because stabilizing selection places the mean switchpoint at a body size such that large individuals tend to exercise a defensive tactic, whereas small individuals exercise the sneaking tactic. Because intermediately sized individuals do poorly at both, selection on body size may be disruptive and, possibly frequency dependent [1]. As a result, the variation in status that makes the evolution of conditional reproductive tactics possible might be enhanced even more once the conditional strategy evolves.

At the proximate level, the mechanisms by which signals from cues related to status are used to control tactic expression require further study. For example, Emlen and Allen [50] have hypothesized that the regulation of growth rate and duration by the insulin pathway and other endocrine mechanisms could be responsible for trait scaling with body size. These mechanisms could similarly be involved in the scaling of behaviour and associated traits with body size [51,52].

## Conclusions

Gross's 1996 review of alternative reproductive tactics stimulated a large amount of research on variation in mating strategies. It was particularly influential in arguing that much of the variation in mating behaviour could be understood as alternative phenotypes expressed conditionally. However, as noted by Shuster and Wade, the model has several shortcomings, the most important of which is the lack of a genetic framework for understanding selection on alternative phenotypes. Using the genetic framework suggested by Gross and by Shuster and Wade, we have argued that, because it takes into account both genetic variation underlying phenotype expression as well as variation in the environmental cues that affect phenotype expression [32], the ET model is the best model available currently for understanding the evolution and maintenance of conditional strategies.

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