

## The Evolutionarily Stable Strategy Under Individual Condition and Tactic Frequency

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A proof is presented to show that, when fitnesses from alternative tactics within a population depend on both their frequency and the phenotypic condition of individuals, there will be a unique ESS switchpoint  $s^*$  that determines both the condition at which an individual will switch between tactics and the resulting frequency of the tactics in the population. For an individual at the ESS  $s^*$ , the fitnesses of the alternative tactics will be equal. When fitness is averaged over the population, however, the average fitnesses of the alternative tactics will not be equal.

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### Introduction

In the original Evolutionarily Stable Strategy (ESS) concept of Maynard Smith (1982), the fitnesses of alternative tactics depend solely or primarily on their frequency in the population. For example, an individual may obtain greater fitness from a fighting tactic when fighting is rare in the population, and greater fitness from a sneaking tactic when sneaking is rare in the population. In many real-life situations, however, an individual's phenotypic condition may also affect the fitnesses it will obtain from its alternative tactics. For instance, an individual may obtain greater fitness from the fighting tactic when the individual is large in size, and greater fitness from the sneaking tactic when it is small in size (Krebs & Davies 1993). Insufficient theoretical research has gone to finding the ESS solution when alternative tactics depend on both their frequency in the population and the phenotypic condition of the individual.

West-Eberhard (1979) and Parker (1982) provide some of the first discussions of how individual phenotypic condition will affect alternative tactics. In general, selection should favour individuals who play

the alternative which provides the highest possible fitness given their condition. Most importantly, the switchpoint should exist at a point where the fitnesses from the alternatives are equal. Parker (1984a: 58) formalizes the ESS parameters for this switchpoint and then (1984b, 2(a) and 2(b): 131) merges frequency dependence with the condition-dependent switchpoint where the fitnesses of the alternatives depend both on frequency and condition. Although his analysis states some necessary mathematical conditions that must hold at an ESS, he does not discuss sufficient mathematical conditions that would guarantee the existence and uniqueness of an ESS. Therefore, there is no accounting for whether an ESS will arise in any given situation. The same is true of Malinski & Parker (1991). Charnov (1993) describes a relationship between phenotypic condition, fitness and a corresponding ESS, but not what situations will give rise to an ESS.

In the present paper we write the fitnesses of alternative tactics as functions of both their frequencies in the population and the phenotypic condition of the individual. We propose some mild properties which these fitness functions should satisfy, and show that with these properties there will always

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exist a unique ESS for switching between tactics. We feel that the properties we propose encompass many alternative tactic situations in nature.

### Population Parameters and Fitness Functions

We consider a large, stationary population with stable age distribution and constant population size that occupies a given environment. Individuals in this population have some measure of phenotypic condition, such as size, weight, etc., which we will denote by  $x$  ( $x \geq 0$ ). The population distribution according to  $x$  is given by the population density function  $D(x)$ , normalized to  $\int_0^\infty D(x) dx = 1$ . Subpopulations corresponding to increments in condition can therefore be read as proportions of the total population. It is important to note that the population density function links condition and frequency together. We make the technical assumption that  $D(x) > 0$ .

We consider two phenotypes:  $P$ , the primary tactic such as fighting; and  $A$ , the alternative tactic such as sneaking. We let  $p$  be the proportion of the population which adopt tactic  $P$  and  $q = 1 - p$  be the proportion of the population which adopt tactic  $A$ .

We also assume that in the population at large the decision by individuals as to which tactic to adopt is made according to their individual condition. In particular, we assume that individuals in the population have a strategy based on a ‘‘switchpoint’’,  $s^*$  so that individuals with condition  $x > s^*$  will choose tactic  $P$  and that individuals for whom  $x < s^*$  will choose tactic  $A$ . For example, large individuals adopt fighting while small individuals adopt sneaking. With this assumption, the proportion  $q$  of the population using tactic  $A$  is (c.f.(2c) in Parker 1984b):

$$q = \int_0^{s^*} D(x) dx. \quad (0)$$

Suppose that the fitnesses for a particular individual from the two tactics depend on both the individual's condition  $x$  and the frequency  $q$  of the tactic  $A$  in the population. We write  $F_P(x, q)$  and  $F_A(x, q)$  for the fitness functions of tactics  $P$  and  $A$ , respectively, for an individual of condition  $x$ , in a population in which the proportion adopting tactic  $A$  is  $q$ . We make the minor technical assumptions that these fitness functions are continuous and have continuous first partial derivatives (the graphs are without jumps or abrupt changes in direction).

Our model is based on three assumptions about the fitness functions. First, we consider the relative change in fitness with change in frequency. We expect

that as  $q$  increases, that is as more individuals adopt tactic  $A$ , the fitness  $F_A(x, q)$  decreases relative to the fitness  $F_P(x, q)$  for each fixed  $x$ . More precisely, when larger numbers of individuals adopt tactic  $A$ , the value of tactic  $A$  decreases more quickly than (or relative to) the value of tactic  $P$ . This, our first assumption, can be formally expressed as:

$$\partial/\partial q(F_P(x, q)) \geq \partial/\partial q(F_A(x, q)). \quad (1)$$

These partial derivatives represent the rate of change of fitness in  $F_P$  or  $F_A$  with respect to  $q$ , holding  $x$  constant.

Second, we consider the relative change in fitness with change in condition. We expect that as  $x$  increases, the fitness  $F_P(x, q)$  increases more quickly than (or relative to) the fitness  $F_A(x, q)$  for each fixed  $q$ . In other words, with increasing individual condition, for example body size, the value of the tactic  $P$  increases relative to the value of tactic  $A$ . This, our second assumption, can be formally expressed as:

$$\partial/\partial x(F_P(x, q)) > \partial/\partial x(F_A(x, q)). \quad (2)$$

The absence of an equal sign in inequality (2) reflects the importance in our model of a differential fitness effect due to condition  $x$ . These partial derivatives represent the rate of change of fitness in  $F_P$  or  $F_A$  with respect to  $x$ , holding  $q$  constant.

Third, we consider the effects of tactic choice at extremes of low and high condition. We assume that for some low switchpoint,  $s_L$ , and the corresponding value

$$q_L = q(s_L) = \int_0^{s_L} D(x) dx,$$

we have

$$F_A(s_L, q_L) > F_P(s_L, q_L). \quad (3a)$$

This means that if few individuals adopt tactic  $A$ , then individuals of low condition can obtain higher fitness through tactic  $A$  than  $P$ .

Similarly, we assume that for some high switchpoint,  $s_H$ , and the corresponding value

$$q_H = q(s_H) = \int_0^{s_H} D(x) dx,$$

we have

$$F_P(x_H, q_H) > F_A(x_H, q_H) \quad (3b)$$

This means that if many individuals adopt tactic  $A$ , then individuals of high condition obtain higher fitness through tactic  $P$  than  $A$ . Therefore, the fitness functions  $F_A$  and  $F_P$  intersect at some intermediate point.

We believe that properties (1) through (3) are robust enough to include many biological systems of interest.

### Theorem

In a population satisfying properties (1) through (3) there will always exist a unique ESS for the population. The ESS is described by a switchpoint  $s^*$  with individuals of condition  $x < s^*$  adopting tactic  $A$ , and those with condition  $x > s^*$  adopting tactic  $P$ . The frequency of individuals adopting tactic  $A$  in a population at ESS is given by the equation:

$$q^* = \int_0^{s^*} D(x) dx. \quad (4)$$

The ESS switchpoint  $s^*$  is determined by the equation:

$$F_P(s^*, q^*) = F_A(s^*, q^*). \quad (5)$$

Equation (4) defines the relationship between population frequency  $q^*$  and the corresponding individual phenotypic condition switchpoint  $s^*$ ;  $q^*$  is the proportion of the population with condition below  $s^*$ . Equation (5) says that the ESS occurs where the fitnesses are equal (c.f. Parker, 1984a, b).

### PROOF

To prove the theorem we begin by thinking of the switchpoint as varying, label it  $s$ , and as above define the corresponding value of  $q$  by

$$q = q(s) = \int_0^s D(x) dx.$$

This  $q(s)$  represents the proportion of the population adopting tactic  $A$  if the switchpoint is  $s$ .

By the Fundamental Theorem of Calculus,

$$dq/ds = D(s).$$

In other words, the rate of increase in the proportion of the population with condition less than  $s$  is given by the density function  $D(s)$ .

Now consider the function of the single variable  $s$  which is defined by

$$f(s) = F_P(s, q(s)) - F_A(s, q(s)).$$

By the Chain Rule, its derivative is

$$\begin{aligned} f'(s) &= d/ds(f(s)) = \partial/\partial s(F_P(s, q(s))) \\ &\quad - F_A(s, q(s)) + \partial/\partial q(F_P(s, q(s)))dq/ds \\ &\quad - \partial/\partial q(F_A(s, q(s)))dq/ds \\ &= \partial/\partial s(F_P(s, q(s)) - F_A(s, q(s))) \\ &\quad + (\partial/\partial q(F_P(s, q(s)))D(s) \\ &\quad - \partial/\partial q(F_A(s, q(s)))D(s)). \end{aligned}$$

Both terms are non-negative, according to our assumptions. Indeed,  $\partial/\partial s(F_P(s, q(s)) - F_A(s, q(s)))$  is positive by property (2). Also  $\partial/\partial q(F_P(s, q(s))) - \partial/\partial q(F_A(s, q(s)))$  is non-negative by property (1), and since we have assumed  $D(s) > 0$ ,  $\partial/\partial q(F_P(s, q(s)))D(s) - \partial/\partial q(F_A(s, q(s)))D(s)$  is non-negative. Combining these two observations, we find that  $f'(s) > 0$ .

Since  $f(s)$  has a positive derivative it is an increasing function. By properties (3a) and (3b), we see that  $f(s) = F_P(s, q(s)) - F_A(s, q(s))$  is negative for  $s = s_L$  and positive for  $s = s_H$ . By the Intermediate Value Theorem there is a value  $s = s^*$  between  $s_L$  and  $s_H$  at which  $f(s^*) = 0$ , and since  $f(s)$  is increasing, there is exactly one such value. At this value,  $q^*$  is given by eqn (4). This completes the proof of the existence and uniqueness of a switchpoint  $s^*$  satisfying eqn (5).

There are two possible approaches for demonstrating that a population at  $s^*$  is in ESS: (i) Maynard Smith's (1982) original global stability; and (ii) to establish both local mutant stability and local population stability (discussed in Taylor, 1989, 1995). We will use the second approach.

It is necessary to distinguish three switchpoints:  $s^*$ , the evolutionary equilibrium;  $s_{\text{pop}}$ , the switchpoint of the population; and  $s_{\text{mut}}$ , the switchpoint of a rare mutant. The proportion of the population adopting tactic  $A$  is

$$q_{\text{pop}} = \int_0^{s_{\text{pop}}} D(x) dx.$$

The requirement for the local mutant stability is

$$\partial^2 M / \partial s_{\text{mut}} < 0 \quad \text{when } s_{\text{mut}} = s_{\text{pop}} = s^* \quad (6)$$

where  $M$  is the fitness of the mutant (Taylor, 1995). This means that in a population at evolutionary equilibrium, i.e. with  $s_{\text{pop}} = s^*$ , a rare mutant with switchpoint  $s_{\text{mut}} \neq s^*$  cannot invade.

The fitness of the mutant with switchpoint  $s_{\text{mut}}$  is the integral of individual fitnesses, weighted by the

population density:

$$M = \int_0^{s_{\text{mut}}} F_A(x, q_{\text{pop}})D(x) dx + \int_{s_{\text{mut}}}^{\infty} F_P(x, q_{\text{pop}})D(x) dx.$$

(We assume that the mutant population differs only in the location of the switchpoint and therefore has the same density function  $D(x)$  as the wild population. This means that we are modelling only an effect of change in switchpoint, not in growth rate, size, etc.) It follows that:

$$\begin{aligned} \partial M / \partial s_{\text{mut}} &= F_A(s_{\text{mut}}, q_{\text{pop}})D(s_{\text{mut}}) \\ &\quad - F_P(s_{\text{mut}}, q_{\text{pop}})D(s_{\text{mut}}) \\ &= (F_A(s_{\text{mut}}, q_{\text{pop}}) - F_P(s_{\text{mut}}, q_{\text{pop}}))D(s_{\text{mut}}), \end{aligned}$$

and

$$\begin{aligned} \partial^2 M / \partial s_{\text{mut}}^2 &= \partial / \partial s_{\text{mut}} ((F_A(s_{\text{mut}}, q_{\text{pop}}) \\ &\quad - F_P(s_{\text{mut}}, q_{\text{pop}}))D(s_{\text{mut}})) \\ &= \partial / \partial s_{\text{mut}} (F_A(s_{\text{mut}}, q_{\text{pop}}) \\ &\quad - F_P(s_{\text{mut}}, q_{\text{pop}}))D(s_{\text{mut}}) \\ &\quad + (F_A(s_{\text{mut}}, q_{\text{pop}}) \\ &\quad - F_P(s_{\text{mut}}, q_{\text{pop}}))\partial / \partial s_{\text{mut}} (D(s_{\text{mut}})). \end{aligned}$$

If we let  $s_{\text{pop}} = s^*$ , then  $q_{\text{pop}} = q^*$ , and if we also let  $s_{\text{mut}} = s^*$  in this formula, we see that the last half equals zero, by condition (5). Since  $D(s^*)$  is positive, inequality (2) shows that the first half is negative.

We have shown that  $\partial^2 M / \partial s_{\text{mut}}^2 < 0$  when  $s_{\text{mut}} = s_{\text{pop}} = s^*$ , which establishes the local mutant stability (6).

To establish the local population stability we need to show (Taylor 1994) that:

$$\partial^2 M / \partial s_{\text{mut}}^2 + \partial^2 M / \partial s_{\text{mut}} \partial s_{\text{pop}} < 0$$

when

$$s_{\text{pop}} = s_{\text{mut}} = s^*. \quad (7)$$

This means that in a population not at evolutionary equilibrium, i.e. with  $s_{\text{pop}} \neq s^*$ , a rare mutant with  $s_{\text{mut}}$  between  $s_{\text{pop}}$  and  $s^*$  has greater fitness than the wild population.

To differentiate  $\partial M / \partial s_{\text{mut}} = (F_A(s_{\text{mut}}, q_{\text{pop}}) - F_P(s_{\text{mut}}, q_{\text{pop}}))D(s_{\text{mut}})$  with respect to  $s_{\text{pop}}$ , we first note that

since  $q_{\text{pop}} = \int_0^{s_{\text{pop}}} D(x) dx$ , we have  $\partial q_{\text{pop}} / \partial s_{\text{pop}} = D(s_{\text{pop}})$ . Using this, we find that:

$$\begin{aligned} \partial^2 M / \partial s_{\text{mut}} \partial s_{\text{pop}} &= (\partial / \partial q_{\text{pop}} (F_A - F_P) \\ &\quad \times \partial q_{\text{pop}} / \partial s_{\text{pop}})D(s_{\text{mut}}) \\ &= \partial / \partial q_{\text{pop}} (F_A(s_{\text{mut}}, q_{\text{pop}}) \\ &\quad - F_P(s_{\text{mut}}, q_{\text{pop}}))D(s_{\text{pop}})D(s_{\text{mut}}). \end{aligned}$$

This is less than or equal to zero when  $s_{\text{mut}} = s_{\text{pop}} = s^*$  by inequality (1). This fact together with inequality (6) gives the local population stability property (7). Combined with the local mutant stability property (6), it completes the proof that the point determined by eqn (5) is an ESS. Therefore, under properties (1) through (3) there will always be an ESS.

## Discussion

Our proof shows that when individual phenotypic condition and population frequency jointly determine the fitnesses of alternative tactics there will be a unique ESS switchpoint  $s^*$  in the population. Our formulation explicitly relates the fitnesses to both the frequency of the phenotypes in the population and the phenotypic condition of an individual, and allows us to prove the existence and uniqueness of an ESS switchpoint affected by both. Our proof is based on assumptions about the fitnesses expressed in properties (1) through (3). These properties are sufficient to ensure an ESS, although we do not claim that they are necessary. Mathematical condition (5), that fitnesses are equal at the switchpoint, is a necessary condition that was also recognized by West Eberhard (1979) and Parker (1982).

There is a specific relationship between  $s^*$  and  $q^*$  at the ESS equilibrium. They are linked through the population density function because  $q^*$  is the proportion of the population with phenotypic condition less than  $s^*$ . Knowledge of  $s^*$  therefore allows the calculation of  $q^*$ , and vice versa, if the population density function is known.

If the fitness functions  $F_P(x, q)$  and  $F_A(x, q)$  are independent of the frequency variable  $q$ , then we have reproduced a model of fitness based purely on phenotypic condition (e.g. Ghiselin, 1969; West Eberhard, 1979). However, if the fitness functions are completely independent of phenotypic condition  $x$ , then it is not possible to have a switchpoint based on condition, and our model does not apply. The appropriate model then is based purely on frequency-dependent selection as in the original concept of Maynard Smith (1982).

The properties (1) through (3) which underly our

theorem are an attempt to abstract the common features of alternative tactic systems (e.g. Andersson, 1994). Although frequency-dependent models have been the common form of analyzing alternative tactics, it is also necessary to consider individual phenotypic condition. For example, in male salmon, success for the sneaker jack and fighter hooknose tactics is frequency dependent (Gross, 1985). However, jack males come from the larger juveniles in the population, while hooknose males come from the smaller juveniles thus condition must also be considered (Gross, 1991a). Properties (1) and (2) describe the manner in which the relative success of jacks and hooknose males varies with frequency and phenotypic condition respectively. The opposing effects of these two influences results in the ESS equilibrium described by our theorem. At the ESS equilibrium the average fitnesses of the alternatives in the population need not be equal, although the fitnesses will be equal for an individual at the switchpoint. Similar conditions will apply to sex determination in nematodes (Blackmore & Charnov, 1989), development of horns in beetles (Eberhard, 1982), and nest parasitism in ducks (Eadie & Fryxell, 1992).

Although the conditions leading to our theorem are robust they can of course be violated by an unusual natural history. One such case is the protandrous shrimp *Athanas kominatoensis* where the fitness functions  $F_p$  and  $F_A$  may intersect more than once with increasing condition (Nakashima, 1987). Another is the bluegill sunfish *Lepomis macrochirus* where  $F_A$  initially increases with frequency while the sneaking tactic is rare in the population (Gross, 1991b). In both cases, our approach can be adapted by considering a specific range of values for phenotypic condition  $x$  and tactic frequency  $q$  where our conditions are valid. Our proof will then show that there is a unique ESS point within that range.

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