CONDITIONAL EVOLUTIONARILY STABLE STRATEGIES*

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Under the concept of natural selection, individuals should respond to their environment in such a way as to increase their fitness. Not every individual in a population may respond the same way to the same environmental conditions. In the past, individuals that behaved differently from the most common pattern of behavior were considered mutants of low fitness (Alcock, 1984). However, it is now recognized that there may often be alternative, equally adaptive responses to selection pressure.

One aspect of natural selection, sexual selection, deals with acquiring mates. In frequency-dependent selection, the cost and benefits associated with a given mating behavior depend on what the other individuals do. This paper uses game theory to address male-male competition for mates. In evolutionary game theory, mating phenotypes are treated as alternative mating strategies (Maynard Smith, 1982). The importance of alternative strategies is the hallmark of the game theory approach to natural selection.

The chief theoretical novelty of this paper is the formalization of a class of games called <u>conditional</u>. A game is conditional when the payoff matrix varies systematically with conditions in the environment, even though the strategies available to the players do not. We extend the classical notion of ESS from games within a single condition (unconditional games), to the wider class of conditional games. This extension is called the Conditional ESS or CESS. A word of caution is in order here. Dawkins (1980) has already used the term "conditional" in a narrower sense to refer to the various role situations which may arise in an asymmetric game. Hopefully, no confusion will result from our adoption of the same term. In describing the mating behavior of a species, it has been noted that behavior may vary between populations and within a population between seasons (Emlen and Oring, 1977), and within seasons. So far, game theory has been used in studies of frequency-dependent variance in behavior within a population. This paper takes within-population variance a step further, and looks at the coexistence of alternative strategies in a fluctuating environment. Unconditional games can help us understand the coexistence of alternative strategies when it is adaptive to respond to the average condition. However, many <u>important</u> factors that affect the fitness of mating behavior change drastically between seasons, even within seasons. The conditional games allow us to examine mating strategies in a much wider and more realistic way, as they allow us to follow a strategy through more than one environmental condition.

Perhaps the richest supply of examples of alternative male mating strategies comes from the order of anuran amphibians (Wells, 1977). The typical male mating behavior is to signal, in which males congregate at the breeding site and attract females vocally. Alternative male behaviors include satellite, parasite, search, call-and-mill, and pass (descriptions in Nelson, et al., 1985). Several investigators have noted that for anurans, the density of males at the breeding site seems to effect the type of mating behavior observed (Wells, 1977). Other factors that might influence a male's behavior include availability of territories, varying costs to calling, synchrony of female arrival (or operational sex ratio) and the male size distribution.

Dawkins (1980) states that conditional strategies are advantageous because they allow the male to be more flexible, therefore able to obtain the highest reproductive benefit in each condition. CESS as we have defined them, formalize this advantage and apply it to a much wider class of games than has been considered before.

I. Conditional ESS: the symmetric game case

Let i be an index of conditions, i = 1, 2, ..., n. Let $E_i(I, J)$ denote the payoff in condition i to playing strategy I against strategy J. The strategy set available to each player does not vary across conditions. Each condition i arises with probability p(i). One can think of conditions as features of the environment, such as availability of territories or population density, which do not depend on the strategic interaction of the game. A conditional strategy is a vector of strategies (I_i) , i = 1, 2, ..., n.

One can now define a conditional ESS as follows. A conditional ESS is a conditional strategy satisfying the equilibrium property and the stability property component-by-component. Let (I_i) be a conditional ESS.

<u>Equilibrium Property</u>. In each condition i, $E_i(I_i, I_i) \ge E_i(J_i, I_i)$, for all strategies J_i .

<u>Stability Property</u>. In each condition i, if $E_i(J_i, I_i) = E_i(I_i, I_i)$, then $E_i(I_i, J_i) \ge E_i(J_i, J_i)$.

Notice that in the case of a single condition, this is equivalent to the classical notion of an ESS.

To show this definition captures the notion of a population stable against invasion by a mutant, suppose that mutant with frequency e arises in the population. The mutant plays an alternative conditional strategy (Ji). The payoff to a member of the population playing the conditional ESS is given by

(1)
$$\sum_{i} p(i) E_i(I_i, (1-\varepsilon)I_i + \varepsilon J_i)$$

whereas the payoff to a mutant is given by

(2)
$$\sum_{i} p(i) E_i(J_i, (1-\epsilon) I_i + \epsilon J_i).$$

The mutant is selected against if (1) is greater than (2). Using the bilinearity of the E_i 's, selection against the mutant occurs when

(3)
$$(1-\varepsilon)\sum_{i}p(i) (E_i(I_i, I_i) - E_i(J_i, I_i)) + \varepsilon \sum_{i}p(i)(E_i(I_i, J_i) - E_i(J_i, J_i))>0.$$

(3) will not hold for all small positive ε , all p(i), and all alternative strategies J_i unless the equilibrium property holds--the first half of the expression on the left would otherwise be negative. Suppose then that in condition i, J_i is a best reply to I_i so that $E_i(I_i, I_i) = E_i(J_i, I_i)$. Then, unless the stability property holds, the second half of the expression on the left will be negative. Thus, the equilibrium and stability properties characterize a conditional ESS.

Define $E = \Sigma p(i)E_i$ to be the payoff function of the average condition. Suppose I is an ESS for this unconditional game. Then I is a conditional ESS if and only if I satisfies the equilibrium and stability properties for each condition. Otherwise, I can be invaded by a mutant playing a conditional strategy which is the same as I in every condition except condition i, and better in condition i.

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It is useful to know when a conditional ESS is unique. Clearly, what is required is that a unique strategy satisfy the equilibrium and stability properties in each condition i. One condition for this is given by Bishop and Cannings (1978), Theorem 3. If strategy I satisfies the equilibrium and stability properties, and every pure strategy is a best reply to I, then I uniquely satisfies the equilibrium and stability properties. Another condition for this is as follows. Let I and J be pure strategies. Strategy I <u>dominates</u> strategy J in the game with payoff function **E if E(I,I)** \geq E(J,I) E(I,J) \geq E(J,J)

and at least one of the two inequalities is strict. If in condition i there is a strategy Ii which dominates all the others (there can be at most one strategy which does this), then it is the only strategy satisfying the equilibrium and stability properties for that condition.

Here are some biological examples. Suppose there are two phenotypes and two conditions. In condition 1, the payoff matrix is

while in condition 2, the payoff matrix is

There is a unique conditional ESS, which is phenotype 1 in both conditions. This follows since phenotype 1 is a dominant strategy in both conditions.

Here is a more complicated example. The payoff matrix in condition 1 is

 $\begin{pmatrix} 2 & 0 \\ 0 & 1 \end{pmatrix}$

while in condition 2 it is

$$\begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}.$$

There are two conditional ESS's, namely (strategy 1, strategy 1) and (strategy 2, strategy 1). Now suppose that the population is currently playing the unconditional game with the average payoff matrix

$$\begin{pmatrix} 2p(1) + 1p(2) & 0 \\ 0 & p(1) \end{pmatrix}.$$

Then this population will either be at the unconditional ESS strategy 1, or the unconditional ESS strategy 2. If the population is at the ESS strategy 1, then it is also at the conditional ESS (strategy 1, strategy 1) and is therefore stable against invasion by a conditional mutant. However, if the population is at the unconditional ESS strategy 2, then it can be invaded by a conditional mutant. In this case, though, only a conditional mutant playing the conditional strategy (strategy 2, strategy 1) can invade. This shows that not every conditional ESS can be reached from an initial population at an unconditional ESS. This case also shows that in general the CESS payoffs (3) differ from the payoffs in the game averaged across conditions.

We show below that conditional ESS models are generally suited to analyzing systems where phenotypic plasticity and threshhold effects are important. Phenotypic plasticity makes possible the playing of conditional strategies, while threshholds are often important in distinguishing conditions.

II. Conditional ESS: the asymmetric game case

This section extends the notion of conditional ESS developed above to asymmetric games. Let (A,B) denote a situation with roles A and B which may appear in a game. For instance, A may be a large animal and B a smaller animal, or A may hold a territory on which B intrudes. For the sake of simplicity, attention will be restricted to a single role situation, although the results generalize to multiple role situations (large territory holder vs. small intruder, e.g.). Moreover, only the perfect information case is considered here; that is, each player is assumed to know the role situation (A,B) and the role he is playing. This assumption is substantive, although more general information settings have been studied (Selten, 1980).

Let $I_{A,i}$ represent a strategy played by role A in condition i; ^JB,i, a strategy played by role B in condition i. EA,i(IA,i,JB,i) is

the payoff for role A in condition i when played against strategy J by role B in condition; likewise $E_{B,i}(I_A, i, J_B, i)$ is the payoff to role B in this situation. Strategy $I_{A,i}$ is a <u>best reply</u> to $J_{B,i}$ if

(4)
$$E_{A,i}(I_{A,i}, J_{B,i}) \ge E_{A,i}(I'_{A,i}, J_{B,i})$$
 for all $I'_{A,i} \neq I_{A,i}$.

The definition of J_B , i as best reply to $I_{A,i}$ is analogous. The pair $(I_{A,i}, J_{B,i})$ is a <u>strong equilibrium</u> if $I_{A,i}$ is a unique best reply to $J_{B,i}$ and conversely.

For unconditional asymmetric games, one can show that an ESS must be a pure strategy (Selten, 1980). Moreover, in the case of perfect information, every ESS must take the form of a strong equilibrium pair of strategies for each role situation (Hammerstein, 1981). To apply these results to the class of conditional games, notice that the role situation (A,B) in condition i, for i = 1, 2, ..., n can be reinterpreted as a sequence of role situations (A_i, B_i), each appearing with probability p(i) in an unconditional game. Under either interpretation, the payoff of an animal playing the strategy ($I_{A,i}$) for each i against the strategy ($J_{B,i}$) for each i is given by

(5)
$$E_A((I_A, i), (J_B, i)) = \sum_i p(i) E_{A,i}(I_A, i, J_B, i).$$

This formal isomorphism establishes the following characterization of a conditional ESS in a conditional asymmetric game: a conditional ESS is a vector of strong equilibrium pairs $(I_{A,i}, J_{B,i})$, with one such pair for each condition i.

A necessary and sufficient condition for a unique conditional ESS in an asymmetric game is that there be exactly one strong equilibrium in each condition i. For a given condition i, a sufficient condition for a unique condition strong equilibrium is that each role have a dominant strategy. Unlike in the symmetric case however, the dominant strategy needn't be the same for both players.

For the case of two phenotypes, a necessary condition is that at least one player have a dominant strategy.

We now consider some examples. Suppose that in condition 1, the payoff matrix is

with the upper entry referring to role A. In this condition, the first strategy is dominant for role A, while the second strategy is the best reply for role B. In condition 2, the payoff matrix is

Strategy 1 is still dominant for role A, but now strategy 1 is also the best reply for role B. The conditional ESS is therefore the vector

Moreover, this conditional ESS is unique. The payoff to role A at the ESS, substituting these values into (5), is 1, while the payoff to role B is .5. Note that, as in any asymmetric game, there is no reason for the payoffs to the different roles to be equal.

Now suppose that the payoff matrix in condition 1 is as before, while the payoff matrix in condition 2 is

In condition 2 there are two strong equilibrium pairs. The conditional ESS's now are (6), as before and

(7) (IA, 1 = strategy 1, JB.1 = strategy 2,1A, 2 = strategy 2.JB.2 =
strategy 2).

As in the symmetric case, if there are multiple conditional ESS's, which one is reached will depend on the unconditional behavior that is first invaded by a conditional mutant. For instance, if the unconditional behavior is strategy 1, then it is more likely to be invaded by an unconditional mutant following (6) than (7), since a smaller change in behavior will presumably require fewer mutations. By the same token, an unconditional behavior of strategy 2 is more likely to be invaded by (7).

Asymmetric games are especially rich in conditional effects, as we shall show in section IV.

III. Evolutionary Models of Mating Strategies

This section constructs several models of the evolution of mating strategies. All of these models are based on the argument for male dimorphism in Gadgil (1972). Two male phenotypes are posited, one involving the emission of a strong signal to attract a mate, the other involving the emission of a weak signal (perhaps no signal). Such a signalling model has previously been studied by Rubinstein (1980).

Let strategy 1 be the emission of a strong signal; strategy 2, the emission of a weak signal. Consider the strategic interaction of two males competing for females. Suppose that the emission of a strong signal will attract an extra female, but at an increase in cost. For instance, a strong signal may attract increased predation or weaken a male energetically. Let z be the probability of surviving to mate after signalling. Then z measures the net increase in fitness due to the emission of a strong signal. Now emission of a weak signal imposes no such extra costs, but does not attract an extra female.

Let 1-m be the probability that a male emitting a weak signal will nevertheless succeed in mating with the extra female attracted by a strongly signalling male. Finally, normalize all the data so that the emission of a weak signal by both males gets payoff 0. Bishop and Cannings (1978, Theorem 5) show that such a normalization can always be made without loss of generality. Then one has the following payoff matrix for the unconditional symmetric game:

strong signal weak signal strong signal z mz weak signal l-m O

Two types of unconditional ESS are possible. If z > 1-m, there is a monomorphic ESS with all males issuing a strong signal. If z < 1-m, then there is a polymorphic ESS with signallers of both types present. At the polymorphic ESS, the ESS frequency of each phenotype is such that both mating strategies receive equal payoff. A population genetic model of such a situation is worked out in the appendix.

To make the model conditional, suppose that the cost parameter z actually depends on a condition such as density. In condition 1, high density, predation risk is less than it is at low density:

 $(8) _{Z1} > _{Z2}$.

However, the probability m is assumed not to vary with **condition**. Then one has the conditional symmetric game:



Three types of conditional ESS are possible in such a model:

(9)	<u>Condition</u> 1	Condition 2				
	(strong signal,	strong signal)	when	z 2 :	>	1-m
	(strong signal,	polymorphism)	when	z 1 :	>	1-m
			but	z2 -	<	1-m
	(polymorphism,	polymorphism)	when	z 1 ·	<	1-m.

:

In the last ESS, the proportion of males emitting the strong signal will be higher in condition 1 than in condition 2. The discussion section considers some biological systems to which this symmetric conditional model appears to apply.

Two asymmetric models can be derived from the above conditional model, depending on whether the role asymmetry (A,B) is payoff-relevant or not. The role asymmetry could be (large, small) in a population with size asymmetry or (owner, intruder) in a population with size asymmetry or (owner, intruder) in a population with a territorial asymmetry.

If the role asymmetry is payoff irrelevant, one has the asymmetric conditional game



Three types of conditional ESS are possible in such a model:

(10) Condition 1 Condition 2 Role A Role 1 Role A Role В when strong signal, strong signal strong signal, strong signal Z2 > 1-m strong signal, strong signal weak signal, strong signal $z_{1>}$ l-m and strong signal, strong signal strong signal, strong signal Z2 < 1-m weak signal, strong signal strong signal, weak signal z1 < 1-m weak signal, strong signal weak signal, strong signal strong signal, weak signal strong signal, weak signal strong signal, weak signal weak signal, strong signal

The role asymmetry therefore serves to determine which of the two males will emit the strong signal.

Finally, the role asymmetry may be payoff relevant. To discuss this case, some further notation is needed. Let zA,i be the probability of surviving the predation risk to role A in condition i, and similarly zB,i. The payoff relevant asymmetric conditional game then is



The analogue of condition (8) in this case is

(8)' $z_{A,1} > z_{A,2}$ $z_{B,1} > z_{B,2}$

The predation risk differential allows for unequal payoffs, even when behavior is the same. If role A is more advantageous than role B, one also has that

(11) $z_{A,i} > z_{B,i}$ for all i,

which we shall also asssume.

The ESS possibilities in this model are rather more complicated:

(12)	Condition 1 (h	igh density)	Condition 2 (1	ow density)	when
	<u>Role</u> <u>A</u>	<u>Role</u> <u>B</u>	<u>Role</u> <u>A</u>	<u>Role</u> <u>B</u>	

strong signal, strong signal strong signal, strong signal $z_{B,2} > 1-m$ strong signal, strong signal strong signal, weak signal $z_{B,2} < 1-m$

but other z's > 1-m strong signal, weak signal strong signal, weak signal $z_{B,i} < 1-m$

both i

but $z_{A,i} > 1-m$

strong signal, weak	signal	weak signal, strong	signal	only $z_{A,1} > 1$ -	·D
strong signal, weak	signa l	strong signal, weak	signal		
strong signal, weak	signal	strong signal, weak	signal	z _{A,1} < 1-m	
strong signal, weak	signal	weak signal, strong	signal		
weak signal, strong	s igna l	strong signal, weak	signal		
weak signal, strong	signal	weak signal, strong	signal		

Thus, the payoff-relevant model offers a welter of conditional ESS's. This model is particularly relevant for the study of sexual parasitism, when the role playing a parasitic strategy is at a definite disadvantage.

IV. Examples and Discussion

In this section we discuss three biological examples of the conditional models. Evidence for some of the examples is more

complete than for others. Exploring these systems makes it evident that conditional games are useful in many situations. All cases assume that the strategies are discrete and that a pairwise game applies.

Conditional ESS: the symmetric game case

Example A.

The green treefrog Hyla cinerea provides a good example of a symmetric contest. Perrill et al. (1982) have shown that males will switch mating strategies within a given evening. Some males call, while others termed satellites, sit quietly near a caller and attempt to intercept the females attracted to the calling male. In this study, males were induced to switch strategies by either removing the calling male from a satellite-caller association (satellite switched to calling in 11 out of 19 trials), or presenting a calling male with a recorded conspecific call (caller switched to satellite in 5 out of 8 trials). The probability that a male switched strategies was not correlated with size, suggesting that the biology fits a symmetrical model. It is always difficult to prove that a game is symmetrical, since the game could be asymmetrical based on some variable not yet detected. For anurans, however, male size is the variable most often considered to determine role asymmetries.

This game may become conditional if we consider the contests at high and low densities of males. At higher densities, a male is more likely to encounter other callers. Perrill et al. state that a calling male is much more prone to shift strategies from call to satellite if he has first been exposed to several encounter calls

(Perrill, et al., 1982). Increased encounters at higher densities could increase the cost to calling, thus making the satellite strategy more viable. Encounter calls would be energetically costly and probably increase the probability of being preyed on by making a male more conspicuous (Howard, 1978). Therefore, the CESS is pure call in condition #1 (low density, lower cost to calling), while in condition #2 (high density, higher cost to calling) one encounters the mixed ESS of call-satellite. The CESS is thus a phenotypically plastic strategy that responds to density in such a way as to procure a higher fitness than a strategy based on the average density.

Asymmetrical conditional (payoffs relevant)

Most pairwise contests are likely to be asymmetric, in the sense that some perceived difference between the contestants will be used as a cue to settle the contest (Maynard Smith, 1982). The best evidence of an asymmetrical conditional game in anura comes from Howard's work with bullfrogs (Rana catesbeiana). Some areas around a pond provide higher survival and faster development for egg masses. Howard has shown that more females are attracted to the larger males on the better sites (Howard, 1978). Smaller males will either defend suboptimal territories or parasitize a larger male. A parasite will sit quietly near a calling territorial male and attempt to intercept the females the larger male attracts. Females can detect larger males as they make deeper, more resonant calls as compared to the higher, relatively hollow calls of the smaller males (Howard, 1978). The question then becomes, when should a small male defend a territory as compared to behaving as a parasite? In Howard's study, there was an

absence of larger males in 1977, possibly due to increased overwintering mortality during the harsh winters of 1976 and 1977 (Howard, 1980) and small males joining the chorus adopted territorial behaviors for most of the season. In comparison, in 1978 the variance in male size was significantly greater, with two distinct size classes, and small males behaved as parasites for the entire season. Larger males attract more females and are more heavily parasitized. Smaller territorial males never have parasites. For a small male to have a higher probability of stealing a mate than attracting one, he needs to parasitize a male that is attracting a lot of females. If the variance in male size is low, then females will be more evenly distributed across the population of calling males, and it would be better for a small male to call. Therefore, the asymmetric CESS in condition #1 (low variance in male size) is pure call, while in condition #2 (high variance in male size) larger males call and smaller males behave as parasites. The CESS in this case is for larger males to call in both conditions, but for smaller males to play call in condition #1 and parasite in condition #2.

Asymmetric conditional (irrelevant payoffs)

In the above example, the asymmetry of larger males attracting more females affected the payoffs in such a way that larger males always had a higher payoff. It is possible to have an asymmetry upon which a contest is decided, but which does not necessarily affect the payoffs. In the bullfrog example (Howard, 1978), the low variance in male size in 1977 could cause the payoffs for all calling males to be equal in condition #1. Although females have been shown to be able to

choose between males that vary greatly in size (Ryan, 1980), there will be a limit to any female's ability to discriminate between males that do not vary greatly in size. The asymmetry may have only been used by the contestants to pick their roles, but was irrelevant to the payoffs in the condition where the variance in size was small.

The last example makes clear the difficulty in interpreting conditional models: the theory takes as given an asymmetry independent of the conditions, when the condition itself may influence the asymmetry. Thus, the variance of the size distribution of males may itself be density dependent. One may have to refine further the notion of condition in order to better understand such relationships.

The CESS will differ from the unconditional ESS when a strategy that is phenotypically plastic, switching when necessary to obtain the highest fitness in each condition, has a higher fitness than a strategy based on the average condition. We would expect the evolution of phenotypic plasticity in populations which are regularly exposed to fluctuating environments.

Summary

Conditional ESS, or CESS, is an extension of the notion of ESS in games with a single condition to a wider class of games, conditional. A game is conditional when the payoff matrix varies systematically with conditions in the environment, even though the strategies available to the players do not. One example of conditionality is density-dependence. The CESS will differ from the unconditional ESS when a strategy that is phenotypically plastic, switching when necessary to obtain the highest fitness in each condition. We would expect the evolution of phenotypic plasticity in populations which are regularly exposed to fluctuating environments. CESS theory is illustrated in a sexual selection model. Selection acts on males alone, and two mating phenotypes are present. A population genetics result underlies the game theoretic analysis: in the one-locus, two-phenotype case with incomplete penetrance, a phenotypic equilibrium is a genotypic equilibrium. Appendix. A Genetic Model of the Evolution of Mating Strategies

O'Donald (1980) has argued strongly that game theoretic models of sexual selection be grounded in a genetic model. The purpose of this appendix is to exhibit such a model. Indeed, the model will be based on O'Donald's model of selection of males alone. Another closely related analysis for random mating is found in Lessard (1984).

Let A and a be alleles a a single locus. Genotype AA plays strategy 1 with probability 1; denote the frequency of this genotype by u. Genotype Aa plays strategy 1 with probability 1-k; denote the frequency of AA by v. Finally, genotype aa plays strategy 2 with probability 1; denote the frequency of this genotype by w. O'Donald considers the case of A dominant, in which k = 0. We allow for incomplete dominance as well.

Let p (respectively, q) represent the frequency of allele A (respectively, a). It follows from what has just been said that

p = u + v/2 q = w + v/2. Finally, let x be the proportion of males using strategy (phenotype)

2. Clearly,

x = w + kv.

Let g(x) be the probability that phenotype 1 mates, given x. (The functional dependence of g on x will be suppressed in the notation, when no confusion will result.) One can also see that g measures the proportion of all matings made by phenotype 1:

(proportion of phenotype 1)(probability of mating)/(proportion of population) = (u + (1-k)v)g/(1-x) = g.

Likewise, 1-g is the proportion of all matings made by phenotype 2. Assuming an equal sex-ratio and random mating across females for a given male phenotype, one has the frequencies of matings:

	AA	Aa Aa (phenotype 1) (phenotype 2)		88	
	 1 - x	$\frac{(1 - k)vg}{1 - x}$	$\frac{kv(1 - g)}{x}$	$\frac{w(1 - g)}{x}$	
FEMALES			1		
AA u	$\frac{u^2g}{1-x}$	$\frac{(1-k)uvg}{1-x}$	$\frac{kuv(1 - g)}{x}$	<u>uw(1 - g)</u> x	
Aa v	$\frac{uvg}{1-x}$	$\frac{(1 - k)v^2g}{1 - x}$	$\frac{kv^2(1-g)}{x}$	<u>vw(1 - g)</u> x	
aa w	$\frac{uwg}{1-x}$	$\frac{(1 - k)vwg}{1 - x}$	<u>kvw(1 - g)</u> x	$\frac{w^2(1-g)}{x}$	

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This assumption rules out assortative matings between the sexes.

Using the frequency of matings data, one can compute the updated frequency of allele A, p':

$p' = \underline{pg} + \underline{px + kw} [\underline{1 - g} - \underline{g}]$ 1 - x = 2 = x = 1 - x

At a Hardy-Weinberg equilibrium, p' = p. A sufficient condition for this is that 1-g = x. We now show that 1-g = x also characterizes an ESS. From the matrix game

z mz 1-m o

one has the following payoffs to each strategy in a polymorphic ESS:

E (strong signal, x strong + 1-x weak) = xz + (1-x)mz. E (weak signal, x strong + 1-x weak) = (1-m)x.

At a polymorphic ESS, these payoffs must be equal. Moreover, each payoff represents the probability of mating for the given phenotype. Denote the common value of the payoffs E. Then one has

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phenotype 1 matings/all matings = (1-x)E/((1-x)E + xE) = 1-x = g,
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the proportion of phenotype 1. Thus, at a polymorphic ESS, each phenotype mates with a success probability equal to its frequency in the population. In case of a monomorphic ESS, one has either p' = p =1 when x = 1 and g = 0, or p' = p = 0 when x = 0 and g = 1. Thus, in every case as ESS corresponds to a Hardy-Weinberg equilibrium as well.

REFERENCES

- Alcock, J., 1984. Animal Behavior: An Evolutionary Approach. Sunderland: Sinauer.
- Bishop, D.T. and Cannings, C., 1978. A Generalized War of Attrition. J. theor. Biol. 70, 85-124.
- Dawkins, R., 1980. Good Strategy or Evolutionarily Stable Strategy. in Sociobiology: Beyond Nature/Nurture (Barlow, G.W. and J. Silverberg, eds.). Boulder: Westview Press.
- Emlen, S.T. and Oring, L.W., 1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. Science 198: 215-223.
- Gadgil, M., 1972. Male Dimorphism as a Consequence of Sexual Selection. Amer. Nat. 106: 576-587,
- Hammerstein, P., 1981. The Role of Asymmetries in Animal Contests. Anim. Behav. 29: 193-205.
- Howard, R.D., 1978. The Evolution of Mating Strategies in Bullfrogs, <u>Rana catesbiana</u>. Evo. 32: 850-871.
- Lessard, S., 1984. Evolutionary Dynamics in Frequency-Dependent Two-Phenotype Models. Theor. Pop. Biol. 25: 210-234.
- Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge, Cambridge University Press.
- Nelson, C., Morris, M. and Gardner, R., 1985. Evolutionary Stable Mating Strategies in Anuran Amphibia. Mimeograph.
- O'Donald, J.P., 1980. A General Analysis of Genetic Models with Frequency-Dependent Mating. Her. 44: 309-320.
- Perrill, S.A., Gerhardt, H.C., and Daniel, R.E., 1982. Mating Strategy Shifts in Male Green Treefrogs (<u>Hyla cinerea</u>): An Experimental Study. Anim. Behav. 30: 43-48.
- Rubenstein, D.I., 1980. On the Evolution of Alternative Mating Strategies, in Limits to Action: the Allocation of Individual Behavior (Staddon, J.E.R., ed.) New York: Academic Press.
- Ryan, M.J., 1980. Female Mate Choice in a Neotropical Frog. Science 209: 523-525.
- Selten, R., 1980. A Note on Evolutionary Stable Strategies in Asymmetric Animal Conflicts. J. theor. Biol. 84: 93-101.
- Wells, K.D., 1977. The Social Behavior of Anuran Amphibians. Anim. Behav. 25: 666-693.