

PROVIDING OR HIDING INFORMATION: ON THE EVOLUTION OF AMPLIFIERS AND ATTENUATORS OF PERCEIVED QUALITY DIFFERENCES

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ABSTRACT

In many coevolutionary systems members of one party select members of a second party based on quality differences existing among members of the latter (e.g., predators and prey, pollinators and flowers, etc.). We examined the fate of characters that increase (amplifiers) or decrease (attenuators) the perceived amplitude of differences in the quality upon which choice of the selecting party is based. We found that the evolution of such characters depends on (i) the relationship between the cost of the character and the relative benefit it gives to the high quality individuals (if an amplifier) or low quality individuals (if an attenuator), and (ii) the frequency, among members of the selected party, of the quality sought by the selecting party.

KEY WORDS: Communication, information, amplifiers, attenuators.

1. INTRODUCTION

Many coevolutionary systems are comprised of two parties, where members of one party (the selecting party) select among members of the other (selected) party. Members of the two parties can be of the same or different species (e.g., females and males or predators and prey, respectively). In such systems, there is a certain quality (or qualities) that varies among members of the selected party, and benefits those selectors that are able or lucky enough to make a correct choice. Whether the choice is precise or not, selected individuals either always lose or always benefit, depending on the particular coevolutionary system in question (for example, males benefit from being selected by females, whereas prey lose when selected by predators).

An important question in evolutionary biology is whether members of the selected

party should provide information to selectors about the quality that the latter seek (Dawkins & Krebs, 1978). Here, we are specifically interested in the situation where the selecting party is already using a certain cue to help determine quality in the selected party. Consequently, we focus on the question whether evolution in the selected party favours increased or decreased clarity of this cue, thereby increasing or decreasing the precision of choice made by the selecting party.

Using a genetic model, this question was first examined in the sexual selection system (Hasson, 1989). Here, we extend the logical solution of Hasson's model to some other coevolutionary systems, such as the following three examples:

1. *Pollination*: Pollinators are attracted to flowers, usually to find nutritional rewards such as nectar and pollen. Within populations, flowers vary with respect to the availability of these resources as a function of both productivity and previous visits. Flower productivity of nectar and pollen may be correlated with visual cues such as flower symmetry (e.g., Hasson, Shmida and Cohen, unpublished), size or physical damage, and previous visits may be recognized by pollen scattered over the petals.

2. *Predator-prey*: Predators select the more rewarding prey, usually the sick, weak, injured or young, or, alternatively, the unaware prey (Curio, 1976), and avoid unprofitable prey by using cues that indicate alertness or high escape potential (Hasson, 1991a).

3. *Rivalry*: When two individuals are engaged in a fight, they decide whether to continue the fight or to withdraw, based on the fighting ability (and motivation) of their opponent (Enquist, 1985). Cues that indicate likelihood of winning, such as size and vigour, increase the tendency of opponents to withdraw. In this system, unlike in the previous ones, there can be a complete symmetry of roles between the two parties, and each rival simultaneously belongs to both the selecting and selected parties.

Because of its complexity, the sexual selection model assumed a haploid genetic system (Hasson, 1989). Here, we use a diploid model and show the qualitative differences that arise as a result. Finally, Hasson's previous model considers only the evolution of characters that expose information. Here we also examine the evolution of those that conceal information, compare the two evolutionary strategies, and use this comparison to make important generalizations.

1.1. Amplifiers and attenuators

Fitness of individuals in the selected party can be described as a function of (i) their expected basal fitness (F-component), and (ii) the effect of the selector's decision (S-component) on the F-component. A simplifying assumption made here is that fitness is computed by taking the product of these components. This is the case, for example, if the F-component is defined as the expected basal fitness when the selected party receives the highest possible rewards from the selecting party (for flowers - pollination, for prey - avoidance, etc.), and the S-component as the proportion of the F-component that the individual member of the selected party actually receives due solely to the response of the selecting party.

It is important to note that via the selection process (i) selectors benefit if their choice is correlated with the value of the selected party's F-component (either positively or negatively, depending on the system), and (ii) selectors reward individuals of the selected party whose F-component is high (thus, pollinators benefit by selecting the most

productive flowers and predators by selecting weak prey. In both cases, fitness of individuals within the selected party whose F-component is high, increases). As a result, the S-component becomes positively correlated with the F-component. For example, an individual's vigour and size determine its potential to survive, win combats, and reproduce (the F-component), but may also determine how often it deters rivals (the S-component). Similarly, both the flower's fertility (F-component) and reward to pollinators (determining success in the S-component) may be affected by the same physical damage to the flower or to the branch upon which it sits, or by the same deficiency of resources available to a part or to the whole plant (whether the ultimate causes are phenotypic or genetic).

In these and in other equivalent systems, characters may arise that either diminish or enhance the perception of the cues upon which the choice of the selecting party is based. For example, pollen and corolla (and anthers) in contrasting colours improves the perception of pollen on the flower, thereby adding information regarding both pollen quantities (on anthers) and previous visits (pollen on petals). If the perception of the cue is further enhanced, previously recognized differences in quality are amplified. Consequently, the resolving power of the selecting party increases with respect to the chosen quality. We use the term *amplifiers* to denote such amplifying characters (Hasson, 1989; see also Hasson, 1991b, for other examples of potential amplifiers). By the same token, we use the term *attenuators* to denote characters that conceal the revealing cue and attenuate the previously recognized differences in quality of the selected party.

We restrict the definition of the terms amplifiers and attenuators to characters that bear zero or positive costs to the F-component of fitness. The importance of this restriction is made clear later on.

Based on the definitions above we rephrase our question to ask: under what conditions will amplifiers or attenuators evolve, and what determines their equilibrium values?

2. THE MODEL

2.1. Assumptions

1. Selection is assumed to operate on the selected party only. In particular, we discuss only selection at the amplifier/attenuator (A) locus. At the evolutionary stage discussed here, the effect of the selecting party on the selected party's fitness is assumed to change only as a result of changes at the A locus.

2. We assume two levels of quality, and denote the frequency of high quality individuals by q . For simplicity we assume that differences in quality among members of the selected party are purely phenotypic. Also, because we take the standpoint of the selected party, and for convenience of terminology, the term "quality" is hereafter regarded as being positively correlated with the F-component (thus, predators tend to avoid high quality prey).

3. An individual's fitness is computed as the product of the two fitness components, and thus the population's average fitness is measured by $qFS + (1-q)fs$, where F and f denote the expected basal fitness (F-component) of the high and low quality individuals, respectively; similarly, S and s denote the effect of the selecting party (the S-component) on the high and low quality individuals, respectively (see Appendix 1 for mathematical

compatibility with the above biological systems).

4. Because we use relative fitnesses and assume the F-component to be fixed for a given environment, we use $F=1$ and assume $f<1$. In contrast, we assume some inherent error in the selector's choice as a result of incomplete information, and therefore $S<1$ (by definition, $S=1$ would be the S-component of high quality individuals, given the best possible choice in each system, unconstrained by lack of information). Consequently, we assume $s<S<1$.

5. We introduce a new allele, A, to this system, which leads to a character affecting both the F-component and the S-component. When A is expressed, the F-component decreases by ω , regardless of whether A produces an amplifier or an attenuator. Thus, ω represents the cost involved in expressing the A character, and is a result either of resources devoted to producing the character, or of costs involved in maintaining it (by becoming less efficient in feeding, escaping predators, avoiding parasites, etc.). In contrast to the F-component, the effect of the new character on the S-component is a function of the individual's quality and of its effect on the selector's perception. If we define $\sigma>0$ (increased clarity) when A is an amplifier, and $\sigma<0$ (decreased clarity) when A is an attenuator, then A causes σ to be added to S but subtracted from s.

6. Because the intensity of selector's choice is a function of variance among members of the selected party with respect to the F-component, σ should be a function of q , and become zero when $q=1$ or $q=0$ (for example, we might assume $\sigma = \alpha q(1-q)$, or any other related expression, where α is a coefficient that associates σ and q). For simplicity, however, we consider σ to be independent of q . This is indeed the case whenever q is fixed, as a *force majeure*, in any given environment. Consequently, although q varies between environments, we assume it to be fixed within each during the evolutionary stage discussed here (e.g., if we use $\sigma=\alpha q(1-q)$ then, because q is constant throughout each evolutionary scenario, there is a fixed value of σ that corresponds to each fixed value of α , and remains the same throughout the simulation).

7. Nevertheless, although q is assumed to be fixed within populations (or environments), it is treated below as a variable because it varies between populations (or environments). This enables us to examine the effect of q on the evolution of amplifiers and attenuators. However, it also creates a quantitative error regarding the value of σ (see assumption 6), albeit a small one when σ is very small. This error is greatest when q is either very small or very large (the solution changes qualitatively when we allow $q=0$ or $q=1$, but these two cases are of no biological interest anyway). One should keep this in mind when considering extreme values of q .

8. In order to keep the model simple, we assume an equal additive effect of A, ω , on F and f , and an equal absolute additive effect of A, σ , on S and s (equal in magnitude, opposite in signs). Simulations show that the alternative assumptions, (i) that the effect of ω and σ is multiplicative, or (ii) that the additive effect of A on F and f is not symmetric, do not alter any of the qualitative conclusions of the model.

9. We assume no effect of social structure.

Based on these assumptions, we can now define an amplifier as a character whose effect on its carrier's fitness (here, additive) is ($\omega \geq 0$, $\sigma > 0$), and an attenuator as a character whose effect on its carrier's fitness is ($\omega \geq 0$, $\sigma < 0$).

The establishment of a character whose effect is ($\omega < 0$, $\sigma > 0$) is equivalent to the extinction of the attenuator ($\omega > 0$, $\sigma < 0$), and, similarly, the establishment of a character

whose effect is ($\omega < 0$, $\sigma < 0$) is tested by examining the extinction of the amplifier ($\omega > 0$, $\sigma > 0$). Therefore, no further definitions are required.

2.2. Basic equations

Given the assumption of a diploid model, the genotypes considered are AA, Aa, and aa, where A stands for an amplifier or attenuator allele, and a for neither. Therefore, the fitnesses of the different genotypes are described by

$$W_{aa} = qS + (1-q)fs \quad (1a)$$

$$W_{Aa} = q(1-h\omega)(S+h\sigma) + (1-q)(f-h\omega)(s-h\sigma) \quad (1b)$$

$$W_{AA} = q(1-\omega)(S+\sigma) + (1-q)(f-\omega)(s-\sigma) \quad (1c)$$

h being the degree of A's expression in the heterozygote ($0 \leq h \leq 1$).

Let t be the allele frequency of A. The change in t from one generation to the next, Δt , is therefore calculated by

$$\Delta t = \frac{t^2 W_{AA} + t(1-t)W_{Aa}}{\bar{W}} - t \quad (2)$$

where $\bar{W} = t^2 W_{AA} + 2t(1-t)W_{Aa} + (1-t)^2 W_{aa}$.

2.3. Analysis

The model is a standard one-locus, two-alleles model. Its complexity arises from the facts that (i) the alleles at this locus may have opposite effects on each of the two fitness components, and (ii) the direction of the effect (positive or negative) of A on the S-component depends on the value of the F-component. As a result of the latter, we are interested in the dependence of the evolution of A on q (the frequency of high quality individuals). Ultimately, we also want to know how the evolution of the amplifying or attenuating characters would be affected by their cost to the F-component, ω , and by the intensity or direction of their amplifying effect, σ .

States of equilibrium are given by $\Delta t = 0$ (because polymorphism can occur, we do not use the standard analysis $W_{Aa} > W_{aa}$ and $W_{AA} > W_{Aa}$, which (i) is not much simpler here than a complete analysis, and (ii) overlooks frequency dependent effects). By rearranging equation (2) and solving it for $\Delta t = 0$, we get two simple states of equilibrium, $t = 0$ and $t = 1$. We present the third state of equilibrium, for the sake of later biological interpretation, in terms of q' :

$$q' = \frac{(f\sigma+s\omega)T_1-\sigma\omega T_2}{[\sigma(1+f)-\omega(S-s)]T_1-2\sigma\omega T_2} \tag{3}$$

where q' is the value of q that gives an equilibrium, $T_1=t+h(1-2t)$ and $T_2=t+h^2(1-2t)$. Note that $h=0$ or $h=1$ (or $t=1/2$) results in $T_1=T_2$. Under these conditions equation (3) is significantly simplified and, as a result, q' represents an equilibrium that is independent of t .

An important conclusion of equation (3) is that an amplifier can evolve only if $q > q'$, and an attenuator only if $q < q'$ (Appendix 2.1). When we solve equation (3) for σ , given the constraint $0 < q' < 1$ (for $q=1$ or $q=0$, we define $\sigma=0$, see assumption 6), we get two distinct solutions, depending on whether σ is positive or negative:

If $\sigma > 0$, then both $\Delta t > 0$ and $0 < q' < 1$ are possible only if

$$\sigma > \frac{\omega s T_1}{T_1 - \omega T_2} = \sigma' \tag{4}$$

and if $\sigma < 0$, then both $\Delta t > 0$ and $0 < q' < 1$ are possible only if

$$\sigma < -\frac{\omega s T_1}{f T_1 - \omega T_2} = -\sigma'' \tag{5}$$

(see Appendix 2.2).

When q' , σ' and σ'' are constant and independent of t (i.e., if $h=0$ or 1) the conditions for the evolution of an amplifier can simply be presented as

I. $\sigma > \sigma'$ and

II. $q > q'$,

which are different from, although not the exact opposite of, the conditions for the evolution of an attenuator:

I. $\sigma < -\sigma''$ and

II. $q < q'$.

When $0 < h < 1$, the threshold values of q' , σ' and σ'' become functions of t , thereby allowing for polymorphism at the A locus.

2.4. Polymorphism

The threshold q' is a monotonic function of t . However, q' is a positive function of t only if $0 < \sigma < \omega(S+s)/(1-f)$, and a negative function of t , otherwise. Figure 1a shows two curves of q' , one at $t=0$, the other at $t=1$. When $\sigma > 0$, the curves $q'(t=0)$ and $q'(t=1)$ intersect at $\sigma = \omega(S+s)/(1-f)$. Given the assumption of symmetrical effects of σ and ω (assumption 8), this occurs at exactly $q=0.5$ (if ω is smaller for high than for low quality individuals, or if σ is smaller for low than for high quality individuals, or both, the value of q at the point $q'(t=0)=q'(t=1)$ is higher than 0.5).

Therefore, when $\sigma < \omega(S+s)/(1-f)$ (and either $\sigma > \sigma'$ or $\sigma < -\sigma''$), the effect of t on q' creates a limited option for polymorphism. If $\sigma' < \sigma < \omega(S+s)/(1-f)$, we find three possible states that affect the evolution of A:

- (i) $q < q'(t=0)$ always results in $\Delta t < 0$; thus the extinction of A.
- (ii) $q > q'(t=1)$ always results in $\Delta t > 0$; thus the fixation of A.
- (iii) $q'(t=0) < q < q'(t=1)$ gives a state of stable polymorphism: when t is small, $q > q'$ (t =small), t increases, and therefore $q'(t)$ also increases. Nevertheless, t continues to increase only until $q'(t)=q$. Similarly, when t is large, $q < q'$ (t =large) and both t and $q'(t)$ decrease until $q'(t)=q$.

If $\sigma < 0$, q' is a negative function of t , and therefore, polymorphism is possible for any $\sigma < -\sigma''$, depending only on the value of q . In contrast with q' , σ' and σ'' are always positive functions of t . If $\sigma(t=0) < \sigma' < \sigma(t=1)$ then $q'(t=1) > 1$, A cannot be fixed, and can only exist in a polymorphic state. Similarly, if $\sigma(t=0) > -\sigma'' > \sigma(t=1)$ then $q'(t=1) < 0$ and again, A can only exist in a polymorphic state.

Equations (1a-c) show that fitness of the selected party is a function of q . An important observation here is that when $q'(t=0) < q < q'(t=1)$ for an amplifier, or $q'(t=0) > q > q'(t=1)$ for an attenuator (i.e., the states that lead to polymorphism), the fitness of the heterozygote is greater than that of the homozygotes. The relationship between the fitnesses of the homozygotes provides the equilibrium frequency of allele A, t .

Polymorphism of amplifiers is intuitively explained as follows: when q is small, the second expression of the fitness equations is dominant in determining fitness, most individuals lose by having an amplifier, and therefore $W_{AA} < W_{aa}$. When q is large, the first expression dominates the fitness equations, most individuals benefit by having an amplifier, and therefore $W_{AA} > W_{aa}$. Within a limited range of parameter values, the intermediate expression of an amplifier (determined by h) as found in the heterozygote Aa, gives the highest fitness. Similarly, when $\sigma < 0$, values of q and σ that are just below their corresponding threshold values, q' and $-\sigma''$, can also lead to heterozygote superiority and stable polymorphism.

An alternative way of fine-tuning the intermediate expression of amplifiers is an assumption that their cost, ω , is lower in the high than in the low quality individuals. If one assumes a sufficiently low cost of amplifiers confined to the high quality individuals, one gets, at the intermediate range values of q , heterozygote inferiority rather than superiority, with no stable polymorphism.

2.5. Exposing or hiding information about quality

The above model assumes that selectors can evaluate members of the selected party, and examines the conditions for the evolution, in that party, of amplifiers or attenuators of the cues that selectors use during this evaluation process. At least during the evolutionary stage described here, amplifiers or attenuators are assumed to be neither preferred nor rejected *per se* by the selecting party. Their effect on the selected party's fitness is assumed to be derived from their direct cost on the one hand, and from their effect on selector resolving power on the other.

Because, by definition, amplifiers and attenuators never increase the F-component of their carriers, they must increase the S-component of at least some individuals in order to evolve. If we assume $h=1$ or $h=0$, equations (4) and (5) can be rearranged and presented as $(1-\omega)(S+\sigma) > S$ (for $\sigma > 0$) and $(f-\omega)(s-\sigma) > fs$ (for $\sigma < 0$), correspondingly. Thus, in its simplest form condition I states that an amplifier cannot evolve unless it improves overall fitness of its high quality carriers (note that we assume $F=1$), and an

attenuator cannot evolve unless it increases fitness of its low quality carriers. In this form, condition I for the evolution of an amplifier is identical to condition I in Hasson's haploid sexual selection model (Hasson, 1989).

An amplifier allele benefits by being associated with high quality individuals (because it adds to their S-component of fitness) and loses when associated with low quality individuals. This creates a threshold in the frequency of high quality individuals (q') above which the amplifier will evolve and below which it will go extinct. Similarly, because an attenuator allele benefits when associated with low quality individuals, it will evolve when the frequency of the high quality individuals is sufficiently low (below q'). This is described by Condition II for the evolution of amplifiers or attenuators, respectively. Condition II for the evolution of amplifiers is qualitatively similar to Condition II for the evolution of amplifiers in Hasson's model of sexual selection (Hasson, 1989). Again, assuming $h=0$ or $h=1$ (i.e., ignoring the complexity created by the diploid structure of the model), we can rearrange equation (3) to state that an amplifier or an attenuator will evolve if the marginal fitness of allele A is greater than the marginal fitness of the alternative allele, a (i.e., $q(1-\omega)(S+\sigma) + (1-q)(f-\omega)(s-\sigma) > qS + (1-q)f$; see also Hasson, 1989).

Mathematically, stating condition II in terms of marginal fitnesses is trivial, not requiring complicated mathematical models. Condition II as presented here and in Hasson (1989), however, deviates from this basic formulation because each model adds a different biological complexity (incomplete dominance here; linkage disequilibrium in the sexual selection model).

Another complexity that is maintained here, for biological rather than for mathematical reasons, is the distinction between conditions I and II. In fact, condition I is included within condition II: equations (4) and (5) are mathematical derivations of equation (3), and given the assumptions of the model, condition I is necessary, but not sufficient for the evolution of amplifiers and attenuators, whereas condition II is both necessary and sufficient. Nevertheless, by setting up the mathematics in a way that separates between conditions I and II in the form of equations (3), (4) and (5), we conveniently address two biological factors that are important for the evolution of amplifiers and attenuators. They are, cost to the F-component (assumed to be correlated with the character's expression, and thus also with its amplifying effect) and conditional expression of amplifiers and attenuators.

2.6. Cost of amplifiers or attenuators

If an amplifier or an attenuator confers no cost (i.e., $\omega=0$), then σ' or σ'' , respectively, become zero. Consequently, condition I becomes $\sigma > 0$ for the evolution of an amplifier, and $\sigma < 0$ for an attenuator. Because this is true by definition, the evolution of a cost-free amplifier or attenuator depends only upon the population's q value (condition II).

When an amplifier is cost-free, its alternative allele is a cost-free attenuator. It is only at this point that the evolution of an amplifier is identical to the extinction of an attenuator, and *vice versa* (Fig. 1c).

In contrast, when $\omega > 0$, there is a range of σ values, $-\sigma'' \leq \sigma \leq \sigma'$, in which neither an amplifier, nor an attenuator will evolve. In this case, the extinction of an amplifier is not identical to the evolution of an attenuator. Our definition of an amplifier or an

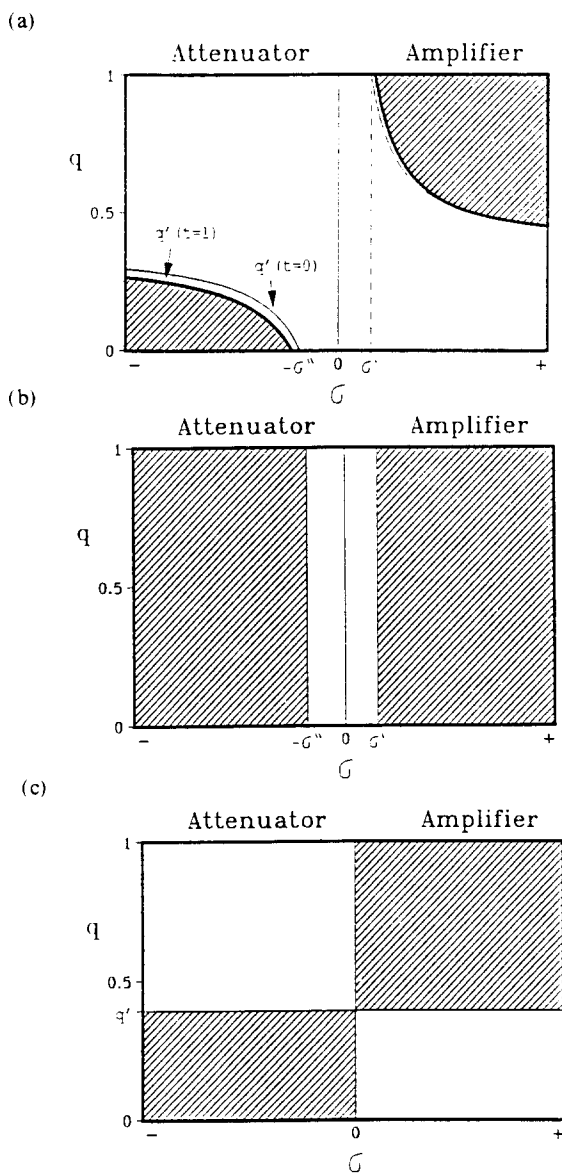


Fig. 1. A graphical illustration of conditions I and II. Shaded areas indicate the range of parameter values that lead to the fixation of amplifiers or attenuators (the exact curve shapes are functions of ω , S , s and f). The range that leads to polymorphism is shown (in **a**) between $q'(t=0)$ (marked with a thin line) and the shaded area.; **a** - Amplifiers or attenuators confer cost ($\omega > 0$) and are expressed in all individuals; **b** - Amplifiers are expressed only in high quality individuals, and attenuators only in low quality individuals; $\omega > 0$. **c** - Amplifiers or attenuators confer no cost ($\omega = 0$) and are expressed in all individuals.

attenuator as a character whose ω cannot be negative, is useful for making this distinction.

2.7. Conditional expression of amplifiers and attenuators

An amplifier or an attenuator decreases the S-component of low or high quality individuals, respectively. Bearing this in mind, we further analyzed the model with the assumption that amplifiers are expressed only in high quality members of the selected party, or that attenuators are expressed only in low quality individuals. This argument follows several communication models dealing mostly with sexual selection (Andersson, 1982, 1886; Hasson, 1989; Michod & Hasson, 1990; Pomiankowski, 1987; Zahavi, 1977). The development of the equations is simple (technically, this is achieved by assuming $\sigma, \omega = 0$ at the second or first expressions of equations (1a-c) for amplifiers or attenuators, respectively). The conclusion of this model is similar to that of the sexual selection model (Hasson, 1989): for any given $0 < q < 1$ the evolution of conditionally expressed amplifiers or attenuators depends on condition I only (i.e., that $\sigma > \sigma'$ or $\sigma < -\sigma''$, respectively, and with no dependence on the value of q).

An intuitive understanding of this state for an amplifier is as follows (the arguments are reversed for attenuators): If individuals whose F-component is low do not express amplifying characters, then no cost is conferred on either their F-component or their S-component (otherwise, low quality individuals pay both costs and receive no benefits). Because high quality carriers are the only type that express condition-dependent amplifiers, the evolution of amplifiers depends only on their effect on those carriers. The F-component of high quality carriers decreases but, being better recognized as high quality individuals, their S-component increases. If A's total effect on them is positive (condition I) then amplifiers will evolve regardless of the density of low quality individuals (which do not determine success or failure of A). Furthermore, because (i) amplifiers always decrease the F-component, but (ii) always increase the high quality individuals' S-component, and because (iii) the degree of the positive change in the high quality carriers' S-component is a function of the amplifying effect, there is a positive correlation between ω and the threshold value of the amplifying effect, σ' (equation (4); see also Fig. 1b). In other words: the greater the cost in the F-component, the greater should be the benefit in the S-component, which is provided by further amplification of cues used by selectors.

When amplifiers and attenuators are costly and their expression is not condition dependent, q' becomes a function of the amplifying effect σ (Fig. 1a). Note that using the assumption of conditionally expressed A, allows for the possibility that both conditionally expressed amplifiers and attenuators of the same cue will evolve in a single population (Fig. 1b). If they are not conditionally expressed (Fig. 1a, 1c) then, depending on the q value of each population, either an amplifier or an attenuator of a cue can evolve, but not both.

3. DISCUSSION

An important question in behavioral ecology is whether signals have evolved to hide or reveal information. The answer given by the present model is that it depends on the parameter values determining the three thresholds, q' , σ' and σ'' . However, an interesting

generalization comes to light: all other things being equal, signals that expose information are more likely to evolve than signals that hide information (Fig. 1). This conclusion is derived from the fact that $\sigma' < \sigma''$, for any $\omega > 0$ (equations (4) and (5)). As a result, the range of parameter values above threshold for the evolution of an amplifier is broader than the equivalent range leading to the evolution of an attenuator.

The reason a lower threshold exists for the evolution of amplifiers is biologically very simple: amplifiers evolve via benefits they give to the high quality individuals, whereas attenuators evolve via benefits they give to the low quality individuals, whose F-component is initially lower. Therefore, all other things being equal, attenuators are at a relative disadvantage.

3.1. Polymorphism

In contrast to haploid models, our diploid model shows that polymorphism at the amplifier/attenuator locus is possible. However, this conclusion should be viewed in the appropriate perspective, in part because unless ω is very large, the range of parameter values within which polymorphism is possible is narrow. Furthermore, even if polymorphism does evolve, it is likely to have a negligible effect, for at least two possible reasons:

1. If an amplifier or attenuator evolves via the establishment of a sequence of mutations, each with a small effect, it eventually becomes a quantitative (metric) character. As long as each mutation's effect is small, polymorphism at each locus is less likely to occur (fine-tuning of the expression occurs, to a large extent, at the homozygous level). If polymorphism does occur in some loci of quantitative amplifiers or attenuators, its effect at any single locus may be negligible relative to the intensity of the character's overall expression, or to the additive genetic variance that is maintained in such characters as a result of mutation load (Lande, 1976).

2. If an amplifier or an attenuator evolves in one big step, polymorphism is more probable. However, it is also more likely to lead to the evolution of phenotypic variation in the character (i.e., its expression may become conditional on the individual's F-component; see Michod & Hasson, 1990). In turn, conditional expression may (i) diminish the density-dependent superiority of the heterozygote (thereby reducing the potential for polymorphism), and/or (ii) result in phenotypic variation that is greater than that created by polymorphism.

3.2. How much amplification or attenuation?

We have shown that amplifiers and attenuators can evolve provided that (i) the appropriate mutations arise, and (ii) the conditions for their evolution (I and II) are satisfied. Although we are, at this point, in no position to determine if these conditions are biologically realistic or not, they do seem to be both relatively simple and probable.

This, therefore, raises the following question: What are the biological constraints, if any, on the degree of amplification or attenuation (i.e., on the absolute value of σ) which are not expressed in the formal model? We can point to two such factors. One biological constraint, expressed mathematically by $0 \leq (S + \sigma) - (s - \sigma) \leq 1$ (giving the range of effective discrimination by selectors), is that there is an obvious upper limit to amplification or

attenuation (i.e., to precision or randomness of choice, respectively).

The second constraint is a result of limitations in the selecting party's perceptive mechanisms. It is very likely that as amplification increases, further amplification is possible only with exponentially increasing cost (ω). As a result, at a certain point condition I may no longer be satisfied. This constraint would often halt further amplification long before the previous constraint becomes effective.

3.3. Conditional expression

By decreasing cost, conditionally expressed amplifiers and attenuators have an obvious advantage over their fixed counterparts. Therefore, even if amplifiers and attenuators evolve initially as fixed characters, genetic modifiers that adjust their expression to the individual's quality, may arise later (Hasson, 1990; Michod & Hasson, 1990). Nevertheless, developmental constraints may inhibit the evolution of conditional expression in amplifiers and attenuators (Hasson, 1991b). This depends on which, in the selected party's ontogeny, develops and becomes fixed first, the quality itself or the amplifier (or attenuator):

If amplifiers (or attenuators) arise after the quality has already been determined, it is likely that they will be (or become) conditionally expressed. An extreme case is behavioral amplifiers (or attenuators) because they can be instantaneously turned on or off. For example, prey advertising alertness to predators are likely to do so only when they are really alert (Hasson, 1991a; Hasson *et al.*, 1989).

On the other hand, if amplifiers (or attenuators) are (ontogenetically) developed and become fixed before, or at the same time as the quality in question is determined, they cannot evolve conditional expression. Flowers are a good example of this, as their colours, size and patterns are largely determined during growth. Factors that determine nectar yield, such as physical damage, lack of water, etc. (and especially previous visits) may appear only later.

If the expression of amplifiers and attenuators become conditional on the selected party's quality, it might be useful as an indicator of quality. Consequently, the selecting party may develop a choice that is based, at least in part, on the expression of the amplifier or attenuator itself (Hasson, 1989). Some possible coevolutionary consequences of the evolution of such a criterion of choice are discussed elsewhere (Hasson, 1990, 1991b).

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APPENDIX 1:

APPLICATIONS TO DIFFERENT BIOLOGICAL SYSTEMS

This section of the appendix shows how the model fits the biological systems discussed in this paper. Specifically, it shows how the expression

$$qFS + (1-q)fs \quad (\text{A1.1})$$

can be used as a measure of average population fitness in different biological systems. Although the models presented below are merely simplifications of real biological systems, they link the latter with the important selective forces discussed here. To add more complexity and further generalization, the F and S functions can be further modified. This, however, is beyond the scope of the present paper.

1. *Flowers and pollinators:* One can divide this system into two simple cases:

Case I: All plants are identical, each having q high quality flowers, and $1-q$ low quality flowers. The total contribution to the plant's basal fitness of the former flowers is F , and of the latter, f . Pollinators reward the better flowers with S and the lesser flowers with s (rewards are assumed to be a positive monotonic function of visits by pollinators, whereas S and s describe the ratio between actual rewards and the maximum possible in a given system). Thus, fitness of each individual plant is expressed by equation (A1.1). Because all plants are assumed to be identical, this equation also describes the average population fitness.

Case II: The number of flowers per plant is fixed, and all flowers on an individual plant are of the same type. q plants have high quality flowers (whose F-component is F), and $1-q$, low quality flowers (whose F-component is f). S and s are defined as in the previous case. Fitness of high and low quality plants is FS and fs , respectively. Therefore, equation (A1.1) describes the population's average fitness.

2. *Prey and predators:* The simplest prey-predator system assumes that prey encounters predator only once in a lifetime, at the same age for all prey (to maintain the relationship between the F-component and the probability of escape), before reproduction. There are two types of prey, good escapers, whose F-component is F , and poor escapers whose F-component is f ($F > f$). When encountering prey, the predator initiates pursuit with a probability of $1-P_F$ for good escapers, and $1-P_f$ for poor escapers ($P_F > P_f$). If a predator pursues, prey either gets caught or loses energy. Consequently, the prey's F-component decreases, on the average, by ΔF or Δf for good or poor escapers, respectively ($\Delta F < \Delta f$). Therefore, one can define fitness of good and poor escapers by

$$w_F = F - (1 - P_F)\Delta F \quad (\text{A1.2})$$

and

$$w_f = f - (1 - P_f)\Delta f, \quad (\text{A1.3})$$

respectively.

Now define the relative costs of pursuit for good and poor escapers as $C_F = \Delta F/F$ and $C_f = \Delta f/f$, respectively (note that $C_F < C_f$). From this we obtain $\Delta F = C_F F$ and $\Delta f = C_f f$. Substituting ΔF and Δf in equations (A1.2) and (A1.3) and rearranging gives

$$w_F = F[1 - (1 - P_F)C_F] \quad (\text{A1.4})$$

$$w_f = f[1 - (1 - P_f)C_f] . \quad (\text{A1.5})$$

Defining the S-component of good and poor escapers as $S = 1 - (1 - P_F)C_F$ and $s = 1 - (1 - P_f)C_f$, respectively, we get $w_F = FS$ and $w_f = fs$. Using these definitions of S and s , equation (A1.1) describes the population's average fitness.

3. *Threatening rivals:* By substituting "rival" for "predator", "flight" for "pursuit", and "winning potential" for "escape potential", this case becomes similar to the former, with one major exception: here, both parties belong to the same gene pool and play the same role in the game. This can significantly complicate the model. However, as long as we assume that fighting ability is purely phenotypic (assumption 2), and that the proportion of stronger individuals, q , is fixed (assumption 6), fighting strategies do not evolve. Fights can then be assumed to occur over a fixed amount of resources that the winner (by a fight or a threat) gains. Consequently, any set of fighting rules that will give $\Delta F < \Delta f$ and $C_F < C_f$, will result in a derivation of equation (A1.1) which is similar to that in the prey-predator case.

APPENDIX 2: MODEL ANALYSES

1. *The relationships between q , Δt and the sign of σ*

Let N and M be the denominator and numerator of equation (3), respectively. When $N > 0$, $\Delta t > 0$ exists only if $q > q'$; when $N < 0$, $\Delta t > 0$ exists only if $q < q'$. Solving N for σ shows that $N > 0$ only if

$$\sigma > \frac{\omega(S-s)T_1}{(1+f)T_1 - 2\omega T_2} = B \quad (\text{A2.1})$$

Note that both the denominator and the numerator of B are positive. Therefore, when $\sigma > 0$, $\Delta t > 0$ exists only if $q > q'$ (i.e., if $\sigma > B$).

In contrast, any $\sigma < 0$ also gives $\sigma < B$, and therefore $\Delta t > 0$ exists for any $q < q'$.

2. *σ and the constraint $0 < q' < 1$*

a. $q > 0$: Again using N and M as the denominator and the numerator of equation (3), $q > 0$ is possible when either (i) $N, M > 0$ or (ii) $N, M < 0$.

(i) $N > 0$ if and only if $\sigma > B$ (equation A2.1), and $M > 0$ if and only if $\sigma > -\sigma''$ (see definition of σ'' in equation (5)). Because both the numerator and the denominator of σ'' are positive (equation (5)), $\sigma'' > 0$. In this case, any $\sigma > 0$ results in $M > 0$. Because $B > 0 > -\sigma''$, the condition $\sigma > B$, (equation (A2.1)), satisfied only by an amplifier, is both necessary and sufficient for satisfying the constraint $q' > 0$.

(ii) $N < 0$ if and only if $\sigma < B$ (equation (A2.1)), and $M < 0$ if and only if $\sigma < -\sigma''$. The more restrictive condition for satisfying the constraint $q' > 0$ is $\sigma < -\sigma''$, satisfied only by an attenuator ($\sigma < 0$).

b. $q' < 1$: If $N > 0$ (and thus $\sigma > B$), we obtain, by rearranging equation (3), $q' < 1$ only if $\sigma > \sigma'$ (σ' is defined in equation (4)), and if $N < 0$ (i.e., $\sigma < B$), then $q' < 1$ is obtained only if $\sigma < \sigma'$.

c. $0 < q' < 1$: Because $\sigma' \geq B \geq -\sigma''$, $0 < q' < 1$ is fulfilled either by (i) an amplifier that satisfies $\sigma > \sigma'$, or (ii) an attenuator that satisfies $\sigma < -\sigma''$.

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