

The role of amplifiers in sexual selection: an integration of the amplifying and the Fisherian mechanisms

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Summary

In a non-Fisherian genetic model I have shown that sexual displays can evolve even if displays are not directly and unconditionally preferred by females (a basic requirement in any Fisherian model), provided that they amplify previously recognized differences in male quality. Here I show how this amplifying mechanism interacts with the traditional Fisherian mechanism of sexual selection. The theory that integrates these two mechanisms provides a more robust, entirely selective scenario of the evolution of mating preferences and sexual displays.

Keywords: Sexual selection; Fisher's runaway; amplifiers; quality cues; quality indicators; effects of mating systems.

Introduction

Models of sexual selection show that male sexual display can evolve when females prefer displaying males over non-displaying males. The theoretical basis for most models of sexual selection is provided by Fisher (1958), who recognized that female heritable preferences that are based on variance in the display's expression (henceforth, a 'direct' choice for the display) become associated with the male display at later generations. As a result, even if their preferences give females no additional offspring, they may nevertheless evolve via selection that operates on the females' male descendants. If male fitness increases as a result of having a sexually preferred character, then female choice will evolve together with the male sexual character, in a 'runaway' fashion (Fisher's terminology for describing this feedback mechanism).

Therefore, in any scenario based on Fisher's process, a basic requirement for the evolution of both female choice and male sexual display is that on the average the display increases the fitness of its male carrier. In order to fulfil this requirement, the frequency of female choice must be greater than a threshold value, so that any reduced male viability will be compensated for by sufficiently intense female preferences (Maynard Smith, 1978, 1985; O'Donald, 1980; Kirkpatrick, 1982, 1986a, 1986b; Pomiankowski, 1987a, 1987b). A major difficulty in sexual selection theory is to explain the evolution of female choice before it is sufficiently common to benefit displaying males. Theorists commonly overcome this difficulty by explaining the origin of female choice by either non-selective evolutionary forces, like pleiotropic effects (Kirkpatrick, 1982) or genetic drift (Lande, 1981; Kirkpatrick, 1982), or by an initial association of female choice with 'good genes' (Fisher, 1958; Heisler, 1984, 1985).

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All the Fisherian type models of sexual selection are based on the assumptions that: (a) certain or extreme values of the male sexual display are preferred by females; and (b) that this preference is unconditional on other male characters (although a number of these models propose that the expression of the male sexual display may be a function of other male characters). In contrast, a non-Fisherian model of sexual selection (Hasson, 1989) shows that under specific, simple conditions, male sexual displays can evolve even if not attractive to females, as long as the displays expose cues that are informative about male quality. In other words, conspicuous male characters such as colour or morphological patterns, elaborated behavioural displays or vocalizations (Hasson, ms) can evolve if they amplify previously recognized differences in male quality.

Theoretical aspects of the Fisherian mechanism have been extensively studied (O'Donald, 1980; Lande, 1981; Andersson, 1982; Kirkpatrick, 1982, 1985, 1986a, 1986b; Nur and Hasson, 1984; Pomiankowski, 1988). Therefore, the possible existence of a second mechanism of sexual selection requires attention to the nature of the relationship and possible interactions between the Fisherian and the 'amplifying' mechanisms. I show below how the integration of these two evolutionary mechanisms provides a general theory that explains the evolution of female choice and male sexual display in a gradual, entirely selective evolutionary scenario.

In the following I first review possible selective scenarios of the evolution of female choice and male display based on Fisher's process. I then describe a possible evolutionary scenario that is based on the amplifying mechanism by: (a) reviewing the conditions necessary for the evolution of amplifying male sexual displays; (b) explaining evolutionary causes for phenotypic variations in the expression of amplifying displays in response to variance in male quality; and (c) showing that these variations provide conditions that favour the evolution of female preferences that are based on such variations. At this stage, the existence of two types of female choice results in interactions between the Fisherian and the amplifying mechanisms. Depending on the intensity of female choice and on cost of displays, the Fisherian mechanism may either dominate the system and lead to a runaway process or be inhibited by the amplifying mechanism.

Because both mechanisms are likely to affect the evolution of male display and female choice, and operate either simultaneously or successively, I describe here a theory that does not replace Fisher's theory, but rather complements it. This theory overcomes the theoretical difficulty of explaining the initiation of the pure Fisherian process, and shows a new possible starting point for the initiation of a runaway.

The initiation of Fisher's runaway process

Initial definitions

Terms used in discussions of sexual selection are not always clear about the evolutionary forces that are underlined. This might be especially confusing here, when several evolutionary forces are discussed. Therefore, in order to avoid ambiguity, I define each term in a manner that is useful for the discussion that follows.

Fitness of males can be conveniently divided into two components (which, depending on their assigned units, can often be treated as multiplicative:

- (1) A component that evolves in response to natural selection only, and is not affected by female choice. We can refer to this component as the male basal fitness, or *quality*. Most genetic models of sexual selection assume no heritable variation in: (a) paternal care; (b) the physiological component of male fertility; and (c) the social component of male fertility that determines accessibility to females (i.e. social rank and male-male competition; for some purposes, like discussions of sexual dimorphism as a result of such interactions, this sub-

component may be put together with the next component). Therefore, quality is represented in such models by viability (survivorship through the age of breeding).

(2) The social component of male fertility that is a function of female mating preferences in its broad sense, including post-mating decisions (Burley, 1985). Such preferences are based on variance in either male quality or in male sexual displays. We can refer to this component as the male *mating success*.

I define *sexual displays* (or, simply, displays) as characters that decrease the individual's quality, but nevertheless evolve as a consequence of their effect on mating decisions of potential mates. Therefore, I exclude any intrasexual effects as well as characters that are preferred by mates but also add to the individual's quality (e.g. Kodric-Brown and Brown, 1984). The latter can be classified as quality cues (see below).

I use the term *mate choice* to indicate a character whose primary effect is to induce non-random mating of its carriers with respect to perceived features in mates, when social or environmental effects (that determine accessibility to mates) are already accounted for (see Pomiankowski, 1988). The actual behavioural mechanisms or psychological states that are involved are not important for the discussion below. For simplicity of the presentation (only) I assume that only females are choosing and only males develop sexual displays. However, when males choose mates, regardless of whether females exhibit mate choice or not, sexual displays may evolve also in females.

I use the term *adaptive choice* to refer to the type of female choice that increases the number or the quality of the female's offspring (Trivers, 1972; Zahavi, 1975, 1977; Andersson, 1982, 1986; Heisler, 1984; Kodric-Brown and Brown, 1984; Nur and Hasson, 1984; Pomiankowski, 1987a). The term 'adaptive' is not meant to imply that this type of choice is more adaptive than others. It is used here merely to indicate that the ultimate basis of this choice is male quality. If quality is inherited (as genes, status or resources), choice becomes associated with it in later generations, and evolves as a correlated response to the success of individuals with high quality. The 'good genes' model is a special case of adaptive choice, in which male quality is genetically heritable (Heisler, 1984; Pomiankowski, 1988). In contrast, both the proximate and ultimate bases of *aesthetic choice* are variance in male display only. Therefore, by definition, aesthetic choice becomes associated with the purely attractive, *aesthetic display* (Burley, 1985; Pomiankowski, 1988) but not with any component of quality.

The evolution of adaptive choice

I divide adaptive female choice into two types, depending on their proximate basis of choice:

(1) Choice that is based on assessment of displays. In order that the choice based on variance in displays will become associated with quality (a) the mating benefits donated by females should be positively correlated with the degree of expression of male display; and (b) the display's expression should be correlated with male quality and, therefore, be an *indicator* of male quality. Most of the theoretical discussions assume that this correlation is maintained either by differential survivorship of displaying males (Zahavi, 1975, 1977; Eshel, 1978; Maynard Smith, 1978, 1985) or by an expression of displays that is conditional on male quality (Zahavi, 1977; Maynard Smith, 1978, 1985; Andersson, 1982; Pomiankowski, 1987a; Michod and Hasson, 1990).

Because the display's cost is an important feature that maintains the correlation between male quality and the display's expression (Zahavi, 1975, 1977; Andersson, 1982; Nur and Hasson, 1984; Michod and Hasson, 1990), such quality indicators are frequently termed *handicaps*, following Zahavi (1975). However, I show below that optimizing displays as a

consequence of costs to male quality and benefits in mating success, is not the only mechanism that results in a positive correlation between the display's expression and male quality. Therefore, handicaps are only a special case of quality indicators. Genetic models that simulate Fisher's mechanism show that the evolutionary potential of the combination of adaptive choice and quality indicators is greater than that of aesthetic choice and aesthetic displays (Pomiankowski, 1987a,b).

(2) Choice that is based on assessment of *quality cues*, an integral part of male quality, independently of the existence of displays (Fisher, 1915; 1958; Heisler, 1984; 1985). Unlike quality indicators, which evolve in response to female choice (and are sexual displays), quality cues are defined as characters that evolve in response to natural selection only, but maintain sufficient variance to indicate quality.

The possibility that female choice can evolve when it is based on assessment of quality cues has been disputed less (Fisher, 1958; O'Donald, 1980; Heisler, 1984, 1985; Maynard Smith, 1985; Hasson, 1989; but see Kirkpatrick, 1985), but also less discussed than assessment of indicators. This is probably because it has not been appreciated as an important factor in the evolution of male display, except for providing the initial conditions for the evolution of aesthetic male displays in Fisher's scenario (Fisher, 1958; Heisler, 1984, 1985).

Quality cues and Fisher's runaway

Once female choice is based on variance in quality cues (as a consequence of the association of choice with quality), quality cues become attractive, and mutations that increase the expression of quality cues may further evolve. Assuming natural selection had already carried quality cues to an equilibrium, such mutations would only decrease the males' quality because they shift the expression of quality cues away from this equilibrium. Nevertheless, if the mating benefits of mutant males are sufficiently high to compensate for their costs in quality, they will spread in the population (Fisher, 1958; Heisler, 1984, 1985).

Quality cues may indicate quality under the following two conditions, each with its own set of constraints that may limit further development of the quality cues in response to female choice:

(1) The correlation between quality and the expression of its cue is maintained because the cue is an evolutionarily unstable character, under the regime of natural selection. Therefore, either a certain value of the cue or its mere existence reflects quality (Fisher, 1958; Heisler, 1984).

The constraints that limit a runaway of such quality cues depend on two possible states:

(a) The quality cue is conferred by a single allele. Therefore, it is doubtful whether the process of selection will last long enough (until the allele is fixed) for the appropriate mutation of female choice to both arise and raise its frequency above the threshold required for a runaway. Furthermore, even if female choice arises, it is doubtful whether it will maintain its high frequency until another mutation of the male character evolves and increases its expression to a value beyond that preferred by natural selection (to form a display).

(b) The quality cue is a quantitative character. Although directional selection may exhaust heritable variations quite rapidly (but more slowly than in the single allele case), a certain level of variations can be maintained as a result of mutation load (Lande, 1976). This may be sufficient for the evolution of female preferences for a certain optimal value that undergoes a stabilizing selection (Heisler, 1984). However, if the environment is unstable, the character's optimal value changes frequently and unpredictably. Consequently, the association with quality of the female choice that is based on variance in its expression will decrease (Hasson, ms).

(2) The correlation between quality and the expression of the cue is maintained because the cue's expression is affected by many characters. Consequently, low variance in each character,

as a result of mutation load (Lande, 1976; Manning, 1984) or environmental changes (e.g. Hamilton and Zuk, 1982), may accumulate to produce higher variance in the expression of such quality cues. Usually, quality is reflected by extreme values of such cues (Hasson, ms).

When females show preferences that are based on quality cues, a runaway process will proceed until: (a) additive genetic variance in the display's expression is exhausted; or (b) balanced by the opposing force of natural selection, which becomes increasingly stronger as the display's expression develops (Fisher, 1958; O'Donald, 1980; Lande, 1981; Kirkpatrick, 1982; Pomiankowski, 1987a). If natural selection that opposes further development of quality cues is initially strong, a runaway process may be very limited, resulting in no noticeable changes of the quality cues.

It is probably for this reason that Fisher (1915) and Heisler (1985) assume that quality cues are only correlated with quality, but are not directly exposed to strong natural selection. However, when considering characters that may qualify as quality cues it appears that most are likely to be both mechanistically affected by many characters, and exposed to strong natural selection (Hasson, ms). Therefore, further development of quality cues in response to female choice may often be rather limited.

Amplifiers

The evolution of amplifiers

Female choice that is based on variance in an attractive male character can result in an evolutionary change in its expression via Fisher's process. However, a population genetic model that is not based on Fisher's process (Hasson, 1989) using a different mechanism for the evolution of male sexual displays shows that male sexual displays can evolve even if they are not directly and unconditionally preferred by females, provided that they amplify previously perceived differences in quality cues. In other words, amplifying displays, amplifiers hereafter, are assumed to increase the resolution power of females with respect to male quality. This assumed amplifying effect of displays is implicit in Zahavi's verbal theory of sexual selection (Zahavi, 1975; and especially 1978), although not explicitly isolated from other elements. Previously to Hasson (1989), formal models of sexual selection had overlooked it.

By definition, an amplifier is advantageous to the preferred, high quality males, but is disadvantageous to males of poor quality (because their poor quality is better recognized). Contrary to the traditional (Fisherian) view of the evolution of male display, females give mating benefits to displaying males only if they also bear a certain quality, and deprive them of mating benefits if their quality is poor. Therefore, the primary association of female choice is with quality rather than with male sexual display. Nevertheless, the genetic model shows two simple conditions for the evolution of amplifiers:

- (1) The total change in fitness (reduced viability, higher mating success) to the high quality males as a result of having an amplifier, must be positive.
- (2) The average fitness benefit to the amplifier's carriers via high quality males should be higher than the average costs in both viability and mating success via the less viable, less preferred males.

Condition (2) indicates that the evolution of amplifiers depends on a threshold frequency of the preferred, high quality males: the higher their frequency, the higher the average fitness of the amplifier's carriers. This frequency dependent condition is relaxed by a genetic association that is built up between genes for amplifiers and genes for high viability, as a result of female choice and

the amplifying effect (Hasson, 1989). Furthermore, if the expression of the amplifier is conditional on male quality (Hasson, ms), costs to the amplifier allele via the poor quality males, both in quality and in mating success, decrease. If amplifiers are expressed only in high quality males, the evolution of amplifiers depends on condition (1) only (Hasson, 1989).

The evolution of amplifiers provides conditions that enable a sequence of important evolutionary changes. In the following I describe the evolutionary steps that are likely to follow the evolution of amplifiers. Fig. 1 may be used as an easy reference throughout the description of this evolutionary scenario.

Further accentuation of the amplifier

Once an amplifying mutation evolves, the pattern of the quality cue becomes accentuated (Hasson, ms). This process may repeat itself in a sequence of mutations that continue to accentuate the quality cue's pattern, as long as conditions (1) and (2) are satisfied. Consequently, amplifiers may become quantitative characters that progressively amplify the previously perceived differences in the quality cue.

This process of accentuation may come to an end, even in the presence of additional mutations, when; (a) the contrast between the pattern and its background has reached its maximum (Hasson, ms); (b) any further change in the pattern's shape decreases its amplifying effect (Hasson, ms); or (c) further development of the amplifier may decrease male quality such that condition (1) is not satisfied.

Conditional expression of amplifiers

An amplifier increases mating success of high quality males, but decreases mating success of low quality males. Therefore, the conditions for the evolution of an amplifier are relaxed if its expression is limited to the high quality males. Nevertheless, amplifiers can evolve even if they are expressed equally in all males (Hasson, 1989).

When the expression of an amplifier is initially fixed, then selection should favour, subject to developmental constraints (Hasson, ms), genetic modifiers in males that reduce the expression of the amplifier when associated with the low quality males (see also Michod and Hasson, 1990). These modifiers benefit their low quality carriers by reducing the amplifier's costs (in both quality and mating success), but have no effect on the high quality males. Therefore, it seems that at a stable state the expression of amplifiers becomes conditional on male quality (Fig. 1). Note that in such cases the correlation between the amplifier's expression and male quality is maintained primarily because of the display's amplifying effect (on male mating success), not because of antagonism between costs in quality and benefits in mating success (as is required for a handicap).

Assessment of displays

Once an amplifier becomes also an indicator of male quality, a mutation of female choice that is based on variance in the expression of the amplifier/indicator also becomes associated with quality. Consequently, unless it is too costly, direct and unconditional female preferences for extreme expressions of the male amplifier/indicator should evolve (Pomiankowski, 1987b, 1988).

Female choice usually incurs costs like increasing risks or loss of time and energy. On the other hand, choice that is based on variance in the amplifier's expression is likely to reduce costs of the (original) choice that is based on the variance in the quality cue: instead of examining and evaluating quality cues of all males encountered, females look first for differences in the expression of the probably more conspicuous amplifier (e.g. feather colourations; Hasson, ms). After exhibiting the first screening procedure, having already better than average males, females

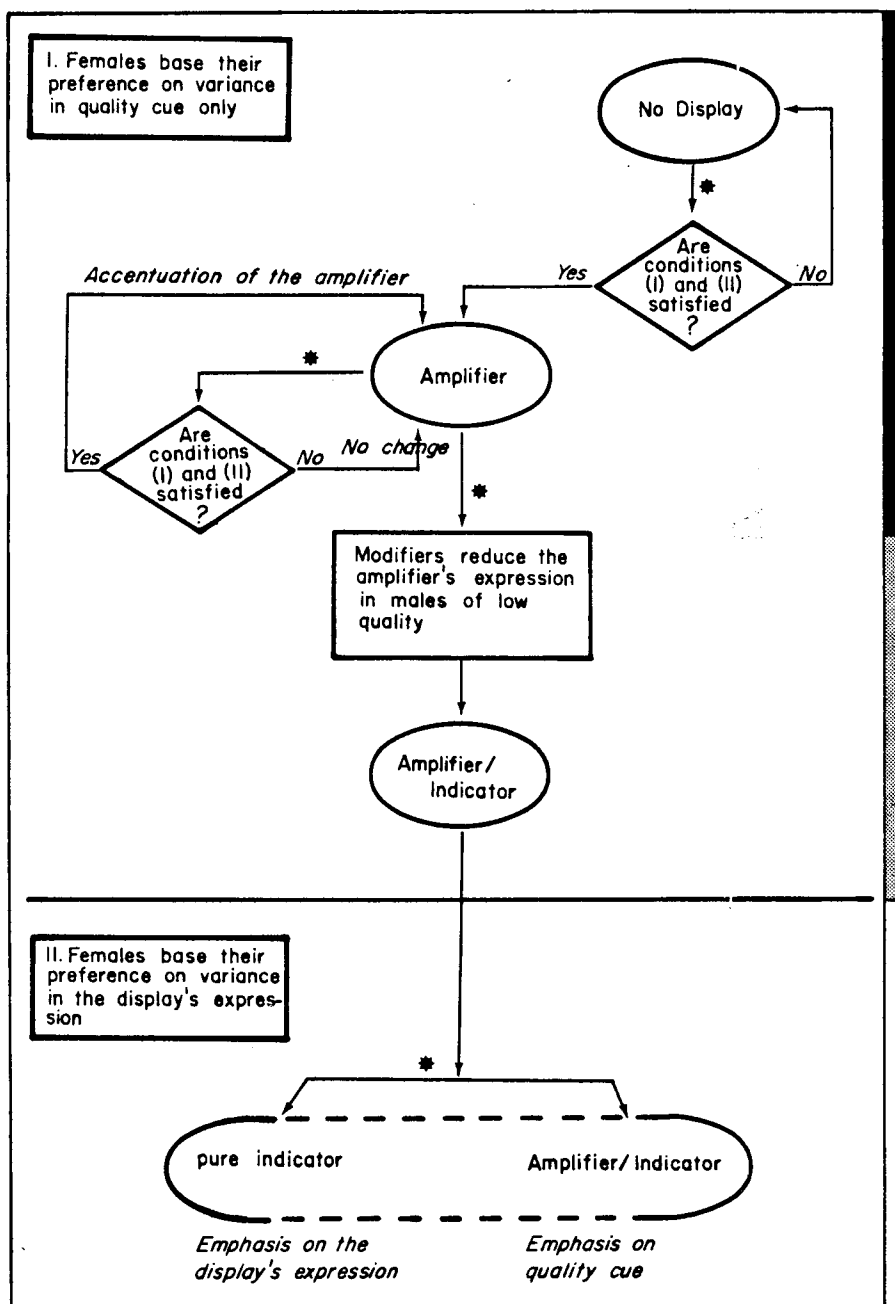


Figure 1. A flowchart of the evolution of male display by the amplifying theory. The upper box represents the stage where females base their choice on quality cues only, and the lower box, on both quality cues and amplifier's expression. Asterisks mark the stages at which the appropriate genetic variation is required before proceeding to the next evolutionary step. The column on the right shows, in black, the stage that is based on a genetic model (Hasson, 1989); in grey, the stage that can be inferred from this model although not explicitly modelled, and in white, the steps that are further explained in the present paper.

may then examine the more subtle quality cue whose efficiency is (still) further enhanced by the amplifier.

Because females are selective anyhow, and because direct choice for displays may both speed up the mate selection process and increase its precision, the total costs of this choice may be low, or even negative. Consequently, the conditions for the evolution of choice that is based on the expression of amplifiers (hence, attractive amplifiers) should be met more frequently than for the evolution of choice that is based on the expression of handicaps (see Pomiankowski, 1987b, 1988).

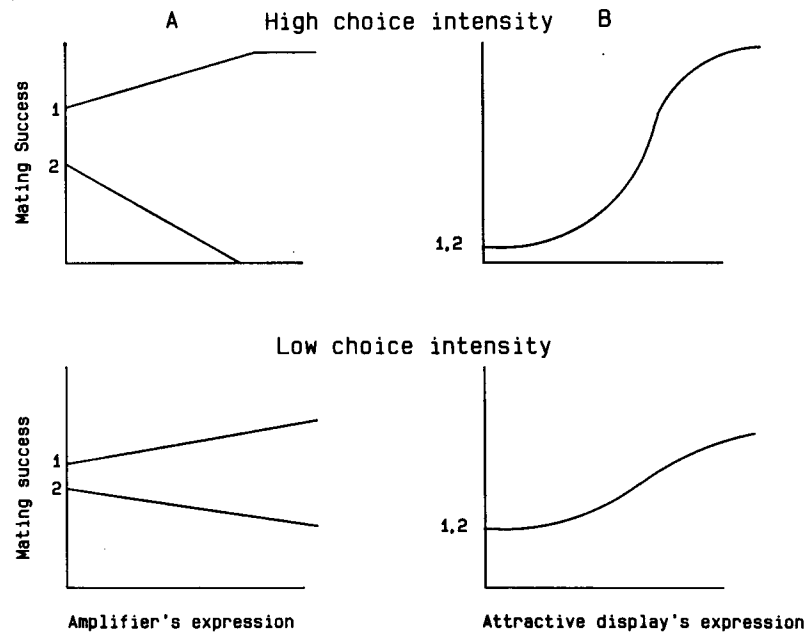


Figure 2. The effect of the expression of male display on his mating success. The column A represents amplifying displays and B attractive displays, when the intensity of female choice is low (bottom) and high (top). The amplifying effect is assumed, for simplicity, to be a linear function of the display's expression. Number 1 represents a high quality male and 2 a low quality male. A sigmoidal shape of the mating curve in column B is assumed (for reasons explained in Nur and Hasson, 1984).

Fisher's process and the amplifying mechanism

A runaway of amplifiers

When the two types of female choice coexist, male mating success is divided into two components: (a) the Fisherian component, which is a function of the amplifier's expression and is independent of male quality (Fig. 2b); and (b) the amplifying component, which is a function of both the quality cue's expression (and thus of quality) and the amplifier's expression (Fig. 2a). As a result, a mutation in males that increases the expression of an attractive amplifier, may have opposite effects on the two components of male mating success. This is illustrated with the following two options:

- (1) The amplifying pattern is further enhanced. Consequently, mating success of poor quality males increases as a result of female preferences for a greater display expression (the Fisherian

component), but decreases as a result of female preferences for quality cues that are better revealed (the amplifying component).

(2) Further enhancement of the display changes the amplifying pattern. Consequently, mating success of the better males increases due to the Fisherian component, but decreases due to lower precision or choice based on quality cues.

Under certain conditions, such mutations will evolve. However, it is clear from these examples that the extent of further development of an amplifier/indicator crucially depends on whether females put more emphasis on choice based on displays or on choice based on quality cues (affecting the Fisherian or the amplifying component of male mating success, respectively).

Fisher (1915), followed by Heisler (1985), argues that a character that is correlated with quality but is not mechanistically affected by other characters that are part of quality, has a strong potential to respond to female choice and initiate a runaway process. Amplifiers/indicators are correlated with quality but, unlike many quality cues (Hasson, ms), are not affected by many characters and therefore satisfy Fisher and Heisler's conditions for the initiation of a runaway. However, because there might be a conflict between the two components of male mating success, a runaway process will proceed more easily when females put more emphasis on the choice that is based on the display's expression. If a runaway process occurs, both the display and the choice that is based on its expression may lose their association with quality and become, at least temporarily (Michod and Hasson, 1990), aesthetic display and choice.

The final conclusion of the interactions between the amplifying and the Fisherian mechanisms depends on exact values of relevant parameters. In the following I present a simple model of optimization of the expression of male display, considering costs and benefits. Its implications on the expected nature of female choice and on the reciprocal effects on male display (via options for a runaway process) show a few possible evolutionary pathways. In particular, they indicate interesting effects of the intensity of female choice and of the display's cost on male sexual displays and on female choice.

The analysis is based on the assumption that the two components of male mating success are multiplicative. This would be the case if females assess amplifiers' expression first and quality cues later. Another important assumption is that male quality and mating success are multiplicative. Therefore, I assume that male mating success is optimized in a manner described in Nur and Hasson (1984; see also Andersson, 1982). Males of low and high quality are considered, and the range between their optimal display's expression, as well as their values, are assumed to affect female choice in the following manner:

- (1) The greater the amplifier's expression, the greater the amplifying effect, and the more precise is female choice that is based on quality cues. Consequently, the stronger becomes its association with quality.
- (2) The greater the difference between the optimal amplifier's expression of low and high quality males, the stronger the association with quality of the female choice that is based on the amplifier's expression.

The degree of association with quality of each type of choice should be positively correlated with its potential to evolve (Heisler, 1984; Pomiankowski, 1987b, 1988).

Fig. 2 shows each component of male mating success as a function of the expression of the male sexual display, and of quality. Male mating success, as a product of these two components, is shown in Fig. 3a. Figs 3b and 3c show male fitness, as a function of the expression of its sexual display, when the display confers low or high costs, respectively. Both Figs 2 and 3 assume two degrees of intensity of female choice, high (top) and low (bottom).

The intensity of female choice is a function of morphological, physiological, environmental,

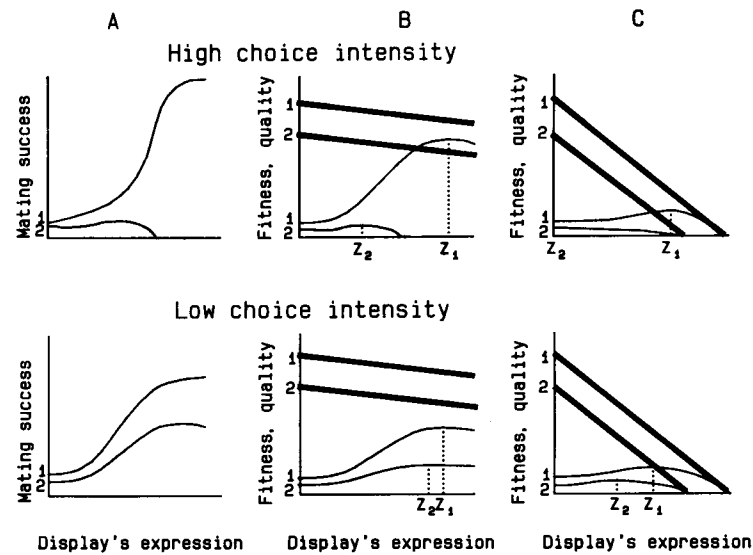


Figure 3. The effect of the amplifier's expression on male fitness. As in Fig. 2, 1 and 2 represent high and low quality males, respectively. Columns B and C show the male quality (thick lines) as a function of the display's expression, assuming low and high cost, respectively, and the total male fitness. For simplicity, quality is assumed to be a linear function of the display's expression, and is represented by two parallel, straight and monotonically decreasing lines, one for each type of male. Fitness of each male is calculated as the product of his mating success curve in column A, and his corresponding quality curve in column B or C. Quality is assumed to get values between zero and one (as viability, or as a relative fitness component), and mating success is the male's number of offspring. Z_1 and Z_2 represent the optimal display expression of high and low quality males, respectively.

and social factors, which affect the female perception of males and of their displays, accessibility to males and options for choice.

The results of Fig. 3 often depend on exact values of parameters, of which only a limited range is explored. Also, variance in the perceived expression of amplifiers and quality cues strongly depends on the specific nature of the quality cues and amplifiers: each pair of a quality cue and its corresponding amplifier is likely to have its own degree of perceived variations as a result of different biological constraints on both the amplifier-producing and the quality cue-perceiving systems. Consequently, a generalization of the results below should be taken in the appropriate perspective. Assuming everything else is equal, some conclusions can be drawn from Figs 2 and 3:

- (1) As a general rule, the trivial result is that the optimal display's expression increases with the intensity of female choice and decreases with the degree of cost conferred by the display. This result agrees with previous models of sexual selection that consider optimization of costs and benefits of attractive sexual displays (Andersson, 1982; Kodric-Brown and Brown, 1984; Nur and Hasson, 1984; Michod and Hasson, 1990).
- (2) However, higher intensity of choice increases the optimal display expression of only the high quality males (Fig. 3). In contrast, the optimal display expression of low quality males actually decreases. Therefore, this simple model supports the premises that: (a) the amplifying effect of a display can maintain the phenotypic correlation between its expression and male quality even when the amplifier becomes attractive; and (b) a runaway process that dissociates displays from quality, can be inhibited by the amplifying effect of displays.

The reason for this effect of amplifiers is that as the display's expression increases, so does its amplifying effect, and low quality is better recognized (Fig. 2a). Therefore, although females may have a greater tendency to approach males with more attractive displays (whether their quality is high or low), they may eventually reject the low quality males more often after examining their better exposed quality cues.

(3) The combination of high intensity of female choice with high cost conferred by an amplifier, even when attractive, may decrease to zero the optimal amplifier's expression of low quality males. This result is qualitatively different from the conclusions of previous models that considered male displays as attractive, but not amplifying. Such models show that even a slight chance to reproduce results in a greater than zero optimal expression of displays (not necessarily noticeable, if their costs are too high), even for low quality males (Nur and Hasson, 1984; Michod and Hasson, 1990).

(4) The range of optimal display's expressions between low and high quality males increases with the intensity of female choice and with the cost conferred by displays. Consequently, female choice based on the expression of male displays becomes more precise and better associated with both the display and quality. This increases the tendency of females to put more emphasis on expression of sexual displays.

(5) An important effect of this association is that the stronger it is, the weaker becomes the association between quality and the choice based on quality cues. This is due primarily to the fact that after exhibiting a first, precise choice, differences in quality among the remaining males are small. Furthermore, when costs of displays are high, low quality males may display very little or not at all. This decreases further the expected correlation between quality and perceived expressions of quality cues, at the moment of the relevant choice. As a result, less emphasis should be put on choice based on quality cues, and the amplifying function of displays may not be important. Therefore, a runaway process becomes more feasible.

(6) In contrast, low choice intensity combined with low costs of displays results in high expression of displays, but low range of display's expressions. Therefore, choice based on expression of displays should not be strongly associated with displays or with quality. In contrast, a strong amplifying effect (as a result of high expression) combined with a low screening efficiency of the choice based on displays, should result in a strong association with quality of the choice that is based on quality cues. A runaway process should be limited or inhibited.

Discussion

This paper describes an evolutionary scenario that combines the two evolutionary forces operating on male sexual displays. One force is based on the traditional assumption that displays are attractive to females and may evolve further as a consequence of the additional mating benefits. At the same time, female choice may also continue to evolve either via attractive male descendants (Fisher, 1958; Lande, 1981; Kirkpatrick, 1982) or via high quality male and female descendants of the selecting females (Pomiankowski, 1987b; 1988). The second evolutionary force is concluded from the recognition that displays may reveal or expose quality in males (Zahavi, 1975, 1977, 1978; Hamilton and Zuk, 1982; Maynard Smith, 1985; Pomiankowski, 1988), and thereby amplify differences in male mating success (Hasson, 1989).

The integration of the Fisherian mechanism (further generalized by Pomiankowski, 1987b, by studying also the expected effects of costs conferred by female choice) with the amplifying mechanism enables an entirely selective scenario of the evolution of female choice and male display. It shows how amplifying displays may evolve even when not directly and unconditionally

preferred by females, how such preferences may arise later, and then the potential of a runaway of displays at this stage.

When experiencing a runaway process, attractive amplifiers may lose their amplifying effect (Hasson, ms) or their association with quality, and become aesthetic displays. This, however, is not an evolutionary stable state. Because displays confer costs, the optimal expression of males depends on their quality (Andersson, 1982; Nur and Hasson, 1984). Therefore, a mutation that modifies the expression of the sexual display to be closer to this optimum will evolve (Michod and Hasson, 1990). In other words, as long as quality differences exist among males, an evolutionary stable state of a runaway process is that male sexual displays become quality indicators (in fact, handicaps).

Therefore, at the end of the evolutionary process male sexual displays can be either: (a) only amplifiers (if, as a consequence of developmental constraints, its phenotypic expression cannot be modified to specific male qualities, Hasson, ms); (b) attractive amplifiers (amplifiers/indicators); or (c) only attractive (most likely, quality indicators).

Whether a sexual display that begins as an amplifier ends up as an attractive amplifier or as an attractive, non-amplifying display seems to depend on the costs that the display confers, and on the intensity of female choice. Therefore, it is possible to test the theory by examining general correlations of displays with factors that affect any of these two parameters.

For example, an important social factor that affects the intensity of female choice is the degree of polygyny, as it is represented in genetic models of sexual selection, i.e. variance in male mating success among genotypes. In this sense 'monogamy' implies no variance in male mating success (e.g. Bell, 1978; Andersson, 1986), and 'polygyny', some variance in male mating success, regardless of the males' social bonds. In other words, 'social' monogamy (with exclusive one male-one female pair-bonds or mating relationships; Gowaty, 1981) in which female investment in offspring is a function of the male's attractiveness (Burley, 1985) would be considered polygyny in genetic models of sexual selection, whereas promiscuity with no variance in mating success would be treated as a model of monogamy. Usually, though, the degree of 'social' polygyny will be positively correlated with variance in male mating success.

Therefore, other things being equal, it appears that social polygyny should lead more frequently to: (a) attractive non-amplifying displays; and (b) high variance in their expression (based on quality and age differences), whereas social monogamy should result in more frequently attractive amplifiers and lower variance in their expression.

Not all the evolutionary steps described here should always exist. For example, if the first mutation of a sexual display is both attractive and amplifying, or if amplifiers are expressed only in high quality males in the first place, a few evolutionary steps may be skipped. However, I present the full scenario here because it is more parsimonious and does not require two evolutionary steps at one time. One way or the other, the conclusion of this evolutionary process should probably not be affected.

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