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EVALUATING MODELS OF SEXUAL SELECTION: GENITALIA AS A TEST CASE

Current discussions of sexual selection by female choice include a variety of models of how female choice could evolve (O'Donald 1980; Bradbury and Andersson 1987; Hasson 1990; Ryan 1990; Balmford and Read 1991; Kirkpatrick and Ryan 1991; Maynard Smith 1991). A useful way to test theoretical models is to attempt to extend them to cases that differ from those for which the models were originally designed. The expectation is that some models will be strengthened by independent confirmations, while others may have to be modified or discarded. This note examines current models of sexual selection by female choice using data from comparative studies of animal genitalia.

Rapid divergent evolution in males, a hallmark of characteristics under sexual selection (Darwin [1871] 1960), probably occurs more often in male genitalia than in any other structure in the animal kingdom. It is apparently common in all major animal taxa in which males employ intromittent organs to fertilize females internally (Eberhard 1985). The morphological exuberance of male genitalia is every bit as dramatic as that of more traditionally discussed characters such as bird plumage or frog calls. And, since genitalia are seldom used in male-male aggressive interactions, their evolution has probably seldom been influenced by intrasexual selection.

Several lines of evidence indicate that many male genitalic characters are subject to sexual selection by female choice (Eberhard 1985). While direct experimental tests are still lacking for most species, several recent studies also support this conclusion. Male courtship behavior after copulation has already begun ("copulatory courtship") has proved more common in insects than previously appreciated (Eberhard 1991). This suggests that female discrimination even after copulation has begun may be widespread. Stimulation of the female that results from male genitalic movements has been shown to induce female responses that increase the male's chances of fathering the female's offspring in mammals (Dewsbury 1988), and species-specific genitalic structures (Otronen and Siva-Jothy 1991; O. von Helversen, personal communication) have also been demonstrated to stimulate female insects to discard sperm from previous mates (Otronen and Siva-Jothy 1991; von Helversen and von Helversen 1991). Closure of ducts within the female, which prevents insemination by males that have already achieved intromission, has been documented in additional groups with species-specific male genitalia (Eberhard 1990, 1993). A further prediction has also been

confirmed: the probability that a female primate will mate with more than one male during a given estrus is positively correlated with the complexity of both male genitalic structures and copulation behavior (Dixson 1987).

Hypotheses regarding the evolution of female choice can be classified by whether a female's choosiness provides her with better resources in addition to male genes (Maynard Smith 1991). If we set aside for the moment cases in which males provide resources, frequently mentioned benefits to selective females include the following:

A. Offspring are superior in their abilities to overcome environmental problems (the so-called good gene hypotheses). Proposed advantages include superior resistance to parasites and disease organisms (Hamilton and Zuk 1982), the ability to survive expression of otherwise disadvantageous characters (the handicap of Zahavi 1987), and other indicators of superior survival (see, e.g., Kodric-Brown and Brown 1984; Hasson 1990).

B. Offspring are superior not because they are better adapted to environmental contingencies but because the males are better able to attract mates and/or fertilize their eggs, giving rise to the classic "runaway process" of Fisher (1958), which could evolve, among other possibilities, via "sensory exploitation" (West-Eberhard 1983; Ryan 1990). Selection favors signaling ability per se in males (as opposed to honest signals).

C. Communication between the sexes is more effective (the species mate recognition system [SMRS] of Paterson 1985).

D. Hybridization with other species is avoided (Dobzhansky 1970).

This note evaluates the abilities of these four hypotheses to explain widespread rapid divergent evolution in intromittent male genitalia.

A. GOOD GENES

Good gene models suppose a direct or indirect association between expression of the male characters preferred by females and the ability of the male to survive disadvantages imposed by the characters themselves (handicap) or by the environment (e.g., parasites). Since male genitalic structures are usually carried retracted or otherwise hidden away except during copulation (see, e.g., Mayr 1963), and since the differences between species are often relatively small, it seems highly unlikely that the structures are costly to the male as supposed in the handicap model. This relative lack of cost also means that good gene explanations of evolutionary reduction (as opposed to elaboration; Balmford and Read 1991) of genitalic structures (e.g., in male spiders; Coddington 1990) are less convincing than they would otherwise be, since the balancing effects of cost are probably quite weak.

Similarly, there is no reason to suppose that genitalic characters are likely to be useful indicators of a male's ability to resist parasites (Hamilton and Zuk 1982), or any other aspects of male vigor (Kodric-Brown and Brown 1984; Hasson 1990). Limited data available show that genitalic size is correlated with male body size in some species (see, e.g., Coyne 1983) but not others (Eber-

hard 1985). Genitalic size is relatively less variant than other morphological characters in some species (Coyle 1985) but not others (Coyne 1983). In sum, good gene models provide relatively unlikely explanations of genitalic evolution.

B. SENSORY EXPLOITATION AND RUNAWAY PROCESSES

Sensory trap models suppose that male signals evolve to take advantage of preexisting female sensitivities and responses to particular stimuli (West-Eberhard 1983). Such models could account for the origin of sexual selection acting on male genitalia in different groups. Natural selection has apparently favored female responsiveness to stimuli from male genitalia during copulation, including triggering of such processes as gamete transport, gamete storage, oviposition, and suppression of further mating (see, e.g., Walton 1960 on mammals; Davies 1965 on insects). Other important stimuli, such as those of an egg passing down the oviduct, which induce movement of a previous male's sperm from storage sites to sites of fertilization, can also be mimicked by male genitalia (von Helversen and von Helversen 1991). Greater ability to trigger such female responses could increase a male's reproduction; male signals better at "playing to" such biases in the female's sensory abilities could result in more offspring.

Some authors have emphasized that sensory exploitation may mainly involve female preferences that were established by natural selection (the "pleiotropy" hypothesis; Kirkpatrick and Ryan 1991), but this weakens the model unnecessarily. As noted by Maynard Smith (1991) in discussing other characters, exploitation of preexisting female biases that arose by natural selection could explain the evolutionary origin of female preferences, but it seems incapable of explaining the elaboration and diversity that characterize sexually selected male signals. This problem is especially clear in relation to "arbitrary" genitalic stimuli, as, for instance, in the fly *Dryomyza anilis*. The male fly taps on the external surface of the female's abdomen with species-specific genitalic structures, thereby inducing the female to discard sperm from previous males and increasing his own chances of fathering her offspring (Otronen and Siva-Jothy 1991). The apparently arbitrary nature of many other sexual signals is well-known (Fisher 1958).

A more likely version of the sensory exploitation hypothesis is that males exploit biases in female responsiveness that have resulted from both sexual selection and from selection acting on the female in other contexts (Ryan 1990). In effect, each time a female's nervous system becomes reorganized (for whatever reason), it becomes a new substrate with new properties, which can be exploited in new ways. This pattern can give rise to the classic runaway process of Fisher (1958).

Direct tests of the runaway model are notoriously difficult. Predictions include genetic correlations between male traits and female preferences for the traits and an imbalance between natural and sexual selection that could cause directional evolution of the male trait (Kirkpatrick and Ryan 1991). There is apparently no direct evidence one way or the other for genitalia on these points. It is clear,

however, that in genitalia an imbalance between natural and sexual selection would be especially easy to achieve. This is because those genitalic characteristics showing species differences (those that are evolving particularly rapidly) commonly involve relatively small details (e.g., the presence or absence of a brush of hairs, a patch of spines, or the shapes of hooks) and are often hidden except during copulation. The costs of signaling by males, in reduced survival, are often included in evaluations of models of female choice (Fisher 1958; Lande 1981; Kirkpatrick 1985; Zahavi 1987; Balmford and Read 1991; Kirkpatrick and Ryan 1991). This cost may usually be relatively small for male genitalic morphology in comparison with other secondary sexual traits.

It is also possible that genitalic structures are relatively independent of nongenetic environmental influences. Such independence would decrease the possibility that female preferences for a given phenotype would fail to pay off in male genes for this phenotype. For example, an especially oily diet rather than genes for increased glossiness might make a particular male bird's plumage more shiny. The relative intraspecific consistency of male genitalic morphology suggests that genitalic characters are generally less subject to such environmentally induced variation (see Shapiro and Porter 1989).

It is also possible that a proposed cost of female preferences—the chance that female offspring may be inferior because of partial expression of extreme male characters (Trivers 1988)—is especially low for genitalia (D. Windsor, personal communication). This is because many male genitalic characters may be especially unlikely to be expressed, in even vestigial form, in females. On the other hand, another type of cost for female preferences may be increased in genitalic characters. Usually a female can assess a male's genitalic characters only by copulating with him. Copulation is probably often more dangerous (Daly 1978) than, say, listening to different songs in a chorus and then choosing one male over another.

Genitalic characters also tend to conform to more general predictions of the runaway model: they are often quite elaborate, the elaborations seem arbitrary with respect to the apparently simple function of gamete transfer, and, at least in some cases in which genitalia have been studied in action during copulation, the elaborations have designs appropriate to produce stimulation of the female (Byers 1961; Eberhard 1985, 1993, in press; von Helversen and von Helversen 1991).

In sum, models of the runaway process via sensory exploitation of female biases that have arisen by both sexual and natural selection accord reasonably well with data on genitalic evolution.

C. SPECIES MATE RECOGNITION SYSTEMS

The SMRS model of Paterson supposes that the environments of different organisms determine which species-specific signals will be sent by males to females: "The characters of the fertilization system are adapted to the circumstances impinging on the organism in its natural habitat." Divergence is thought

to result from change in habitat: "A new constellation of adaptive characters can evolve . . . [when a population] becomes displaced into, and restricted to a new habitat" (Paterson 1985, pp. 25, 26). This type of reasoning seems incapable of explaining rapid divergent genitalic evolution. Environmental variations between different related species would seem to generally have little if any relation to the usefulness of different genitalic forms. In addition, the predicted close association between male and female genitalic morphology (see, e.g., Robertson and Paterson 1982 on nongenitalic characters; Zunino 1988 and Zunino and Palestini 1988 on genitalia) does not occur in many groups (summaries in Eberhard 1985 and Shapiro and Porter 1989). In sum, this hypothesis does not easily explain genitalic evolution.

D. AVOIDANCE OF INTERSPECIFIC MATING

Avoidance of cross-specific mating could be brought about by genitalic differentiation in two ways: mechanical incompatibility that impedes transfer of sperm to the female, and species-specific genitalic signals from the male that enable the female to determine his species identity and exercise cryptic choice in favor of gametes from conspecific partners. Both versions generate predictions about genitalia that appear not to be fulfilled.

Character displacement is expected in zones of overlap between closely related species, where the danger of cross-pairings is greater. Although many taxonomic studies include both geographical variation and genitalic morphology and the prediction of character displacement is old (Brown and Wilson 1956) and well-known (Mayr 1963), the expected pattern is virtually unknown in genitalia (Eberhard 1985; Shapiro and Porter 1989). The strength of this evidence, however, is weakened by the possibility that geographical patterns have been altered by frequent displacements of species' ranges resulting from climate changes (Eberhard 1985; Shapiro and Porter 1989). A recent study (Ware and Opell 1989) carefully documented geographical patterns of genitalic variation in a pair of spider species in which partial overlap may be relatively recent. The case was carefully chosen to maximize the chances of finding character displacement. Although genitalic structure varied geographically, neither the predicted displacement pattern nor reduced genitalic variance in zones of overlap where isolating selection would presumably be acting more strongly were found.

A second prediction concerns those species that are not confronted in nature with the problem of avoiding cross-specific pairings because close relatives are never present in their immediate environment. Genitalic evolution should fail to show the typical pattern of rapid diversification into species-specific forms. Data from species endemic to islands in oceanic archipelagoes, and from parasitic species that never share hosts with close relatives, do not conform to these predictions (Eberhard 1985).

CONCLUSION

The hypothesis for female preference best able to accommodate data on genitalic evolution is classic runaway choice involving a generalized version of sensory

exploitation. Relegation of the runaway model to the status of an idea that is interesting mostly for "its historical importance as the first modern hypothesis for preference evolution" (Kirkpatrick and Ryan 1991, p. 34) is thus premature. Good gene models seem unable to explain genitalic evolution, and the impression that "cases in which females are directly detecting components of fitness are probably much commoner" (Maynard Smith 1991, p. 151) is called into question. The temptation to suppose that, in those species in which males contribute resources, female preference should focus exclusively on these resources (Kirkpatrick 1985; Maynard Smith 1988) is also called into question, as in many groups of this sort (e.g., odonates, scorpionflies, pisaurid spiders) male genitalia are often species specific in form.

Conclusions from data on genitalia obviously cannot be automatically extended to other characters. Selected examples can in fact be used to support many different models of sexual selection (Kodric-Brown and Brown 1984). Rapid divergent genitalic evolution is nevertheless extremely common and is such a widespread phenomenon that it should be taken into account in any discussion of sexual selection that aims at generality.

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