# Armaments and ornaments: An evolutionary explanation of traits of dual utility

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# Armaments and ornaments: an evolutionary explanation of traits of dual utility

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Secondary sexual characters in many species function both in male-male competition and as cues for female choice. Based on a literature compilation of existing knowledge of traits with this dual function, we propose that they commonly arise through intrasexual selection processes and serve as honest signals to other males regarding fighting ability or dominance. Faking these traits, here called armaments, (i.e. weapons and status badges) is difficult, as they are constantly put to trial in male-male contests. Females that subsequently utilize them as indicators of male phenotypic quality when selecting a partner will benefit by acquiring males of higher quality to father their offspring. Thus, evolution of armaments through male-male competition is seen as a usually initiating process, whereas female choice later may assume a role as an additional selective factor. The reverse, that males use information from traits evolved through female choice, is, however, also possible. The traditional view of independently evolved and temporarily unordered intra- and intersexual selection processes fails to explain dual trait functions. Moreover, our model may more satisfyingly than traditional ones explain how trait honesty and trait genetic variance are maintained: theoretical and empirical evidence suggests that such honesty and variation are more easily maintained under male-male competition than under female choice.

ADDITIONAL KEY WORDS:—sexual selection – mate choice – mating competition – weapon – badge.

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## INTRODUCTION

The evolution of secondary sexual traits traditionally is pictured as occurring through two processes: male-male competition, producing weapons, and female choice, producing ornaments (Darwin, 1871). However, the evolution of ornaments has spurred much more controversy than has the evolution of weapons: the function of weapons was readily understood. While wide consensus exists that many male ornaments are used as cues by mate-choosing females, the exact mechanism through which these traits can evolve is still a matter of discussion. In this field, two main bodies of theories exist: (1) the Fisher run-away models (e.g. Fisher, 1930; O'Donald, 1977; Arnold, 1983), all of which are less than adequate if mate choice is costly (e.g. Pomiankowski, 1988; Iwasa, Pomiankowski & Nee, 1991), and (2) indicator theories where ornaments are reliable signals of quality (e.g. Fisher, 1915; Williams, 1966; Zahavi, 1975; Hamilton & Zuk, 1982). If the quality in question is genetic (good genes models), the need to maintain genetic variance for the trait as well as trait reliability have been noted as potential problems. To overcome their respective problems, both the run-away and the good genes models have become increasingly complex.

After Darwin, biologists have discovered that ornamental traits, such as long tails, colourful plumage or beautiful songs, are often used in aggressive displays in competition for mates or for other resources. Many of these ornaments have been shown to convey information about the fighting ability of their bearer. Moreover, some traits classically thought to be weapons, such as the antlers of ungulates or the chelae of the fiddler crabs, may also function as signals revealing the fighting ability of the male and thus serve to settle contests without real fighting (Hyatt & Salmon, 1978; Barrette & Vandal, 1990).

In this paper we define ornaments as traits preferred by females, and armaments as weapons and signals used in male-male competition (i.e. status badges). The existence of both ornaments and armaments is abundantly documented (for a review, see Andersson, 1994), but attention has mostly been focused on the ornament function and how to explain its evolution. We here attempt to redress this imbalance, and we will briefly examine the empirical support and the current theoretical understanding of inter- and intrasexual selection, and present a novel extension of the indicator model that combines these two mechanisms.

## SECONDARY SEXUAL CHARACTERS OF DUAL FUNCTION

Biologists have recognized for a long time that exaggerated secondary sexual characters may function both in male-male combat and in female choice: indeed, much early-century biology was devoted to this duality of function (Hingston, 1933;

Noble & Bradley, 1933; Noble, 1938). The idea that many conspicuous secondary sexual traits arise through intrasexual selection was renewed by several authors in the seventies (Smith, 1972; Peek, 1972; Borgia, 1979). Around the same period others stressed that in many cases ornaments may function as status signals in the context of competition for resources other than mates, for example, to regulate access to food in bird flocks (Rohwer, 1975; West-Eberhart, 1979).

Most contemporary studies have dealt primarily with female choice mechanisms (as reviewed by Andersson, 1994), and only recently did it become evident that traits traditionally viewed as ornaments are used in aggressive displays at least as often as in courtship: examples are bright coloration in mammals (Wickler, 1967), birds (Studd & Robertson, 1985; Foster, 1987; Butcher & Rohwer, 1989; Stutchbury, 1991), reptiles (Noble & Bradley, 1933; Werner, 1978; Cooper & Vitt, 1988) and fishes (Stacey & Chiszar, 1978; Fernald, 1980); tail elongation in birds (Petrie, Halliday & Sanders, 1991; Savalli, 1994); and sexual calls in mammals (Sekulik, 1982; Mitani, 1985; Bowyer & Kitchen, 1987; Berger & Cunningham, 1991), birds (d' Agincourt & Falls, 1983; Kramer, Lemon & Morris, 1985; Searcy & Andersson, 1986), anurans (Searcy & Andersson, 1986; Schwartz, 1987; Brenowitz, 1989), fishes (Torricelli, Lugli & Gandolfi, 1986; Ladich, 1990, Ladich, Brittinger & Kratochvil, 1992) and insects (Searcy & Andersson, 1986; Wilcox & Spence, 1986).

There is good empirical evidence that ornaments are used as status badges, and that they are honest (Boake & Capranica, 1982; Järvi & Bakken, 1984; Studd & Robertson, 1985; Møller, 1987b; Jones, 1990): males with experimentally exaggerated armaments often fare ill in real contests, as in red grouse (Watson & Parr, 1981), house sparrow (Møller, 1987a, 1988) and Harris' sparrow (Rohwer, 1977; Rohwer & Rohwer, 1978), or suffer other costs, like exclusion from flocks as in white-crowned sparrows (Parsons & Babtista, 1980), or from feeding opportunities as in Harris' sparrows (Rohwer & Ewald, 1981). Status signals can also raise metabolic costs (Røskaft *et al.*, 1986; Hogstad, 1987), increase predation risk (Fugle & Rothstein, 1987; Butcher & Rohwer, 1989; Jones, 1990), or increase disease susceptibility by reducing immunocompetence as a consequence of elevated testosterone levels (Zuk *et al.*, 1990a; Owens & Hartley, 1991). In some cases, however, experimentally faked status signals have been shown to elevate dominance (Rohwer & Rohwer, 1978; Rohwer, 1985; Fugle & Rothstein, 1987), although this did not necessarily lead to increased reproductive success (Veiga, 1993). Moreover, being dominant may entail costs on its own (Røskaft *et al.*, 1986; Hogstad, 1987).

The honesty of armaments is also theoretically supported. All recent models indicate that honest status-signalling is evolutionarily stable only if signals have a cost apart from the context of signalling, and if individuals vary in their ability to sustain this cost, i.e. the signal is condition-dependent (Grafen, 1990; Owens & Hartley, 1991; Johnstone & Norris, 1993). These models have many similarities with those developed to explain honest advertisement to females. However, one aspect, namely the social control of deception, is unique to signalling in the context of aggressive interactions. In several birds, including dark-eyed junco (Balph, Balph & Romesburg, 1979), house sparrow (Møller, 1987a), great tit, greenfinch and corn bunting (Maynard Smith & Harper, 1988), fights occur most frequently between individuals of similar badge size. Similarly, in caribou, 'fidgeting' occurs only between males with similar antler size (Barrette & Vandal, 1990). Therefore, individuals bearing dishonestly large status badges will be exposed to escalated fights with opponents of higher status. Maynard Smith & Harper (1988) modelled this situation and concluded that honest communication is evolutionarily stable even if the badge is cheap, provided that a dishonest signaller pays the full cost of a contest. A dishonest mutant can invade the population only if he can escape from contests with a more aggressive opponent without fighting (but see Johnstone & Norris, 1993).

An ornamental trait may arise through male-male competition (Rohwer, 1982; Rohwer & Røskaft, 1989; Butcher & Rohwer, 1989): badges that indicate strength may initially evolve in territorial or group living species if they make good fighters recognizable and memorable to other individuals (the arbitrary identity badge mechanism). Badges are then expected to spread in the population since poor fighters benefit from mimicking good fighters. However, exceptionally good fighters are selected to diverge from the appearance of the mimics, and ultimately an honest-signalling badge system could become established given that one of the criteria for equilibrium (condition-dependent cost of signal or social control of deception) is met.

Regarding the maintenance of genetic variance for armaments, mechanisms proposed to maintain variability under mate choice, such as mutation or spatial and temporal heterogeneity (Hamilton & Zuk, 1982; Kondrashov, 1988), may work just as well to maintain armament variation. For instance, Howard & Minchella (1990) suggested that coevolutionary cycles between hosts and parasites are more important in male-male competition than in mate choice. There is also empirical evidence to suggest that this variation is substantial: in *Drosophila* success in male-male competition for territories showed a considerable genetic variation (Hoffmann, 1988), in female honeybee workers dominance had a high heritability (Moritz & Hillesheim, 1985), in three-spined stickleback aggressiveness and dominance were both variable and heritable in wild populations (Bakker, 1986), and in the cockroach *Naupeta cinerea* social dominance showed moderate to high levels of additive genetic variance (Moore, 1990a).

## FEMALE PREFERENCE FOR MALES SIGNALLING HIGH STATUS

The assumption common to all indicator models of the evolution of female mating preferences is that ornamental traits honestly reflect differences in quality among males. Some conspicuous sexual traits may allow females a direct assessment of male quality. For example, some characteristics of calls, such as pitch, may correlate directly with other phenotypic traits, such as size or age (Davies & Halliday, 1978); call duration may reflect the energy reserves of the male and thus indicate his ability to acquire food (Halliday, 1987); the ability of a male to find food may be revealed through dietary pigments (Endler, 1983); ornaments such as bright plumage or skin coloration may help the female to recognize the degree of parasite infection (Borgia & Collins, 1989).

A second possibility is suggested by a theoretical development of the original Zahavi's handicap principle (Zahavi, 1975, 1977); a trait may provide the female with reliable information if it is costly to produce and if the cost is related to male quality (Grafen, 1990; Michod & Hasson, 1990; Iwasa *et al.*, 1991). Several possible costs for producing and maintaining ornaments have been suggested (Folstad & Karter, 1992; Andersson, 1994).

A third possibility is that signals directed to females are honest because they are also used to communicate in another context, where they cannot be faked. Several authors have suggested that conspicuous traits used by females are also used by males to indicate fighting ability or dominance in contests over mates and other resources such as food. Fisher (1915, 1930) was probably the first to recognize that the same ornamental trait may often be used to both threat males and attract females. Zahavi (1975) also noted that some signals were used in more than one context. He suggested that because showiness reveals superior quality of males (such as ability to escape predators), males should use their ornaments both to attract females and to intimidate their opponents. Borgia (1979) proposed the "war propaganda model": in species with leks, and to some extent in species with territorial males, females should favour male displays that were conspicuous to other males. This would ensure that a courting male is the real owner and not a short-term intruder. Because males willing to advertise their presence have won previous combats, the function of many extravagant characters may be to signal dominance both to males and to females. A similar idea has also been proposed by Kodric-Brown & Brown (1984; see also Kodric-Brown, 1990).

Yet, none of the above authors provided a satisfactory model of how this mechanism could evolve and be maintained. Empirical evidence accumulated in the last decade, showing that ornamental traits used in male-male contests are honest, and the recent theoretical development of status-signalling, now allow us to present a more detailed model of the evolution of ornaments with a dual function.

## THE ARMAMENT-ORNAMENT MODEL

We propose that secondary sexual characters usually do not evolve primarily through female choice, but originate through male-male competition. The underlying assumptions are that male ornaments evolve to signal fighting ability to conspecifics at least as often as to signal male quality to females. In species where males contribute only sperm to the progeny, traits with the former function are more likely to be maintained through time, because armaments do not require genetic variance to be maintained in a population (e.g. Andersson, 1994). Signals used in contests are honest because they are more costly to produce for low quality males and because they are constantly tested in combat with other males. Females benefit by subsequently using the information about male quality contained in these male-male signals to select high-quality males.

Our model makes several assumptions that must be justified:

*(1) Females benefit from mating with high status males*. There is a general consensus that, other things being equal, females should choose high status individuals as mates. As pointed out by Borgia (1979), male success in fights summarizes lifetime success in collecting food, resisting disease, and avoiding predators and injury. In addition, if the trait is heritable, females selecting mates for their fighting ability will have progeny that on average reproduces more successfully (Alexander, 1975). Indeed, in many species females are known to choose winners in contests (as in pronghorn: Byers, Moodie & Hall, 1994, cock of the rock: Trail, 1985, domestic fowl: Graves, Hable & Jenkins, 1985, the fish *Gambusia holbrooki*: Bisazza & Marin, 1991, and the fly *Physiophora demandata*: Alcock & Pyle, 1979), or even incite such contests (as in elephant seals: Cox & LeBoeuf, 1977, jungle fowl: Thornhill, 1988, the fish species *Poecilia latipinna*: Farr & Travis, 1986; *Padogobius martensi*: Bisazza, Marconato &

Marin, 1989a and *Gambusia holbrooki*: Bisazza, Marconato & Marin, 1989b, the fly *Scatophaga stercoraria*: Borgia, 1981, and the spider *Linyphia litigiosa*: Watson, 1990). However, in most species a direct assessment of male fighting ability should prove time-consuming or even risky for the female, and therefore we expect that this way of assessing male quality is rare.

*(2) Ornaments frequently evolve primarily as status signals*. Evidence that ornamental traits often function to settle contests for both food and breeding opportunities is provided in the survey below. Unfortunately it is unknown how frequent the aggressive function is relative to the mate choice function. However, the high proportion of an armament function relative to an ornament function among cases with a single function (see below) suggests that signalling in an aggressive context may be a more frequent reason for the evolution of secondary sexual traits than female choice of mates.

*(3) Ornaments with a dual function do not lose their utility due to exhaustion of variance in male quality*. As already stated the genetic variance of an armament is not easily lost, and is also unnecessary for the stability of honest status-signalling. Several models also suggest that the genetic variance in male quality can be maintained under selection generated by female choice (see Andersson, 1994). However, what happens to genetic variance under the combined effects of male-male competition and female choice is a task for future modelling.

*(4) Traits used in contests may be more honest than traits purely used for choice*. The rationale for this is that males should be better able to recognize cheaters than should females since they can instantly test the rival's quality in combat. In addition, it should be more costly to fake the trait in male-male contests (i.e. by losing a fight) than in courtship (i.e. if discovered, by a loss of a mating opportunity). At the present, experimental research using artificially increased signals supports this in one species: male brown-headed cowbirds, experimentally induced to emit a potent song, attracted more females but also received more attacks from other males, and were sometimes even killed (West & King, 1980, West, King & Eastzer, 1981).

*(5) The stability of the honest status-signalling is maintained if the status badge acquires a functional role outside the context of fighting assessment*. In an ESS model Johnstone & Norris (1993) analysed the maintenance of honest signalling of aggressiveness. Provided that the aggressive individuals suffer a contest-independent cost (for instance, a reduction in immunocompetence due to a raise in androgens), and that this cost differs from one individual to another, selection can maintain both variation for aggressiveness and honesty. In a further analysis, they showed that the predictions of the model are qualitatively unchanged even if there is a benefit to badge size outside the context of fighting, i.e. if badge size serves as an advertisement cue to females.

## A SURVEY OF ARMAMENTS AND ORNAMENTS

We have compiled studies that have examined the function of visual, acoustic, chemical and electric signals in both intra- and intersexual communication (Table 1), excluding body size as this particular trait may be under confounding intense natural selection. If sexually selected traits can evolve through either of the two processes, contest or choice, we would not expect that a particular trait commonly functions in both male-male competition and female choice. A dual function would be either sheer coincidence or a deliberate economic use of trait numbers by the males, and

TABLE 1. Signals that visually, acoustically, chemically, or otherwise serve a dual function in both intra-sexual (armament) or inter-sexual (ornament) sexual selection. Ambiguous cases as when dynamic signals are used differently in the two contexts are omitted, as are cases when different parts of the signals are used by males and females

| Species | Signal | Support armament | Support ornament |
|---|---|---|---|
| A. Visual signals | | | |
| Mountain sheep, *Ovis canadensis* | horns | Y*[1] | Y*[1] |
| Red deer, *Cervus elaphus* | antlers | Y*[2] | N[2] |
| Puku antelope, *Kobus vardoni* | neck patch | Y*[3] | Y*[4] |
| Great tit, *Parus major* | breast stripe | Y*, H[5] | Y*[6] |
| Peacock, *Pavo cristatus* | train | Y*[7] | Y*[7] |
| Long-tailed widowbird, *Euplectes progne* | tail | N[8] | Y*[8] |
| Yellow-shouldered widowbird, *Euplectes macrourus* | head coloration | Y*, H[9] | N[9] |
| Purple martin, *Progne subis* | blue plumage | Y*[10] | N[10] |
| Swallow-tailed manakin, *Chiroxiphia linearis* | definitive plumage | Y*[11] | N[11] |
| Yellow-headed blackbird, *Xanthocephalus xanthocephalus* | head coloration | Y*[12] | N[13] |
| Red-winged blackbird, *Agelaius phoeniceus* | epaulettes | Y*[14,15] | Y[16] |
| House sparrow, *Passer domesticus* | badge | Y*, H[17] | Y*[18] |
| Grey partridge, *Perdix perdix* | brown breast patch | Y*[19] | Y*[19] |
| Red jungle fowl, *Gallus gallus* | comb | Y*[20,21] | Y*[20,22] |
| Great snipe, *Gallinago media* | white tail | N[23] | Y*[23] |
| Pheasant, *Phasianus colchicus* | spurs | Y[24,25] | Y*[24,25] |
| Rock ptarmigan, *Lagopus mutus* | comb | Y*[26] | Y*[26] |
| The lizard *Anolis carolinensis* | dewlap | Y[27] | Y*[28] |
| Pecos pupfish, *Cyprinodon pecosensis* | blue coloration | Y*[29,30] | Y*[29,30] |
| Three-spined stickleback, *Gasterosteus aculeatus* | red belly | Y*[31,32] | Y*[33] |
| The damselfish *Chrysiptera cyanea* | orange caudal fin | Y*[34] | Y*[34] |
| Green swordtail, *Xiphophorus helleri* | sword in caudal fin | Y[35,36] | Y*[37] |
| Sailfin molly, *Poecilia velifera* | dorsal fin | Y[38] | Y[39] |
| Guppy, *Poecilia reticulata* | colour spots | Y*, H[40] | Y*[40,41] |
| The pipefish *Nerophis ophidion* | skin fold, colour | Y[42] | Y*[42,43] |
| Common earwig *Forficula auricularia* | forceps | Y*[44] | N[44] |
| The dragonfly *Libellula luctuosa* | white wing patches | Y*[45] | Y*[45] |
| Stalk-eyed fly, *Cyrtodiopsis whitei* | eye span | Y[46] | Y*[47] |
| Fiddler crab, *Uca pugilator* | major chela | Y*[48] | Y[49] |
| B. Acoustic signals | | | |
| Gibbon, *Hylobates agilis* | song | Y*[50] | N[50] |
| Bison, *Bison bison* | bellow | Y*[51] | N[51] |
| Red deer, *Cervus elaphus* | roar | Y*, H[52] | Y*[53] |
| Red-winged blackbird, *Agelaius phoeniceus* | song | Y*, H[54,55] | Y*[55] |
| Brown-headed cowbird, *Molothrus ater* | song | Y[56,57] | Y*[56,57] |
| Great reed warbler, *Acrocephalus arundinaceus* | long song | Y*[58] | Y*[58] |
| Bobolink, *Dolichonyx oryzivorus* | α nd β songs | Y*[59] | Y*[59] |
| Scott's seaside sparrow, *Ammodramus maritimus* | song | Y*[60] | Y*[60] |
| Great tit, *Parus major* | song | Y*[61] | Y*[62] |
| The Australian frog *Uperoleia rugosa* | advertisement call | Y*, H[63] | Y*[64] |
| Natterjack toad, *Bufo calamita* | advertisement call | Y*, H[65] | Y*[65] |
| Croaking gurami, *Trichopsis vittatus* | vocalisations | Y*[66] | N[66] |
| The gregarious cricket *Ampiacusta maya* | audible "chirps" | Y*,H[67] | Y*[67] |
| Whistling moth, *Hecatesia thyridion* | song | Y*[68] | Y[68] |
| The wandering spider *Cupiennius getazi* | vibration | Y*[69] | Y*[69] |
| The social spider *Achearanea wau* | A-wing (vibration) | Y[70] | Y[70] |

TABLE 1. (Continued)

| Species | Signal | Support armament | Support ornament |
|---|---|---|---|
| C. Chemical signals | | | |
| House mouse, *Mus musculus* | urinary pheromone | Y*[71] | Y*[71] |
| Cockroach, *Nauphoeta cinerea* | pheromone | Y*, H[72,73] | Y*[73,74] |
| D. Electric signals | | | |
| Electric knife fish, *Eigenmannia virescens* | electric discharge | Y*[75] | Y*[75] |

Y: function supported, N: function not supported, H: armament honest with $P<0.05$.
*function statistically supported at $P<0.05$.
References: 1, Geist, 1971; 2, Clutton-Brock, Guiness & Albon, 1982; 3, Rosser, 1990; 4, Balmford, Rosser & Albon, 1992; 5, Järvi & Bakken, 1984; 6, Norris, 1990; 7, Petrie *et al.*, 1991; 8, Andersson,1982; 9, Savalli, 1994; 10, Stutchbury, 1991; 11, Foster, 1987; 12, Rohwer & Røskaft, 1989; 13, Lightbody & Weatherhead, 1987; 14, Peek, 1972; 15, Hansen & Rohwer, 1986; 16, Smith, 1972; 17, Møller, 1987b; 18, Møller, 1988; 19, Beani & Dessí-Fulgheri, 1995; 20, Graves *et al.*, 1985; 21, Ligon *et al.*, 1990; 22, Zuk *et al.*, 1990b; 23, Hölund, Eriksson & Lindell, 1990; 24, von Schantz *et al.*, 1989; 25, von Schantz, Grahn & Göransson, 1994; 26, Holder & Montgomerie, 1993; 27, Noble & Bradley, 1933; 28, Crews, 1975; 29, Kodric-Brown, 1977; 30, Kodric-Brown, 1983; 31, Pelwijk & Tinbergen, 1937; 32, Rowland, 1982; 33, Milinski & Bakker, 1990; 34, Gronell, 1989; 35, Hemens, 1966; 36, Frank & Hendricks, 1973; 37, Basolo, 1990; 38, Bildsoe, 1988; 39, Parzefall, 1969; 40, Kodric-Brown, 1993; 41, Kodric-Brown, 1985; 42, Rosenqvist, 1990; 43, Berglund, Rosenqvist & Svensson, 1986; 44, Radesäter & Halldórsdóttir, 1993; 45, Moore, 1990b; 46, Burkhardt & De la Motte, 1987; 47, Burkhardt & De la Motte, 1988; 48, Hyatt & Salmon, 1978; 49, Salmon *et al.*, 1978; 50, Mitani, 1988; 51, Berger & Cunningham, 1991; 52, Clutton-Brock & Albon, 1979; 53, McComb, 1991; 54, Yasukawa, 1981; 55, Searcy, 1988; 56, West & King,1980; 57, West *et al.*, 1981; 58, Catchpole *et al.*, 1986; 59, Capp & Searcy, 1991; 60, McDonald, 1989; 61, Falls, Krebs & McGregor, 1982; 62, Krebs, Avery & Cowie, 1981; 63, Robertson, 1986b; 64, Robertson, 1986a; 65, Arak, 1983; 66, Ladich *et al.*, 1992; 67, Boake & Capranica, 1982; 68, Alcock, Gwynne & Dadour, 1989; 69, Schmitt, Schuster & Barth, 1992; 70, Lubin, 1986; 71, Jones & Nowell, 1974; 72, Smith & Breed,1982; 73, Moore, 1988; 74, Breed, Smith & Gall, 1980; 75, Hopkins, 1974.

both explanations are difficult to imagine. Table 1 shows that in the majority of cases traits serve a dual function as both armament and ornament. Thirty-seven out of 48 (77%, $\chi^2 = 14.1$ $P < 0.001$) secondary sex traits studied have a dual function. The proportion of duality is very similar if we consider only studies with good statistical evidence (26/37; 70%, $\chi^2 = 6.08$, $P = 0.014$). Although these data may be biased (duality frequency is probably underestimated as most studies focus on only one or the other of the two processes), it is evident that, in spite of a research effort heavily biased towards female choice mechanisms, the traits serving a dual function are frequent enough to call for an explanation.

The frequency of a single function is skewed in favour of the armament function. Of these, nine are used only as armaments and two only as ornaments (one-tailed Binomial $P = 0.033$). We should be very cautious with these data, however: the finding that a signal is not used in a given context may simply be because the wrong experiment was performed, or because one function was easier to demonstrate than the other.

## DISCUSSION

General consensus regarding intra- and intersexual selection seems to be that “the two processes are not exclusive, that they can affect traits either in the same or in different directions, and that their magnitudes may vary quite independently" (cited from Bradbury & Davies, 1987). In contrast, we propose that the two processes most often are dependent, and that intrasexual selection typically is ancestral to intersexual selection, although the latter may further promote the evolution of the trait. Given that males already possess conspicuous, honest, quality-signalling traits used in male-male competition, what would prevent females from exploiting this existing source of information, rather than selecting arbitrary or other traits? Parsimonious females that directly utilize a reliable source of information are bound to benefit compared to females that use other or no cues in their choice process: they will obtain geno- or phenotypically superior males, thereby securing good genes or direct benefits for their offspring. Such females will therefore be at a selective advantage, and the armament in question may evolve further through female choice. Moreover, signals used in male-male competition are bound to be conspicuous to males, and therefore presumably also to females. Note that this is a reversal of the sensory exploitation hypothesis (Ryan & Ryan, 1990; Ryan & Keddy-Hector, 1992): in our view, it is not the males that exploit pre-existing female sensory biases, but females who exploit pre-existing male-male signals. These signals of course must accommodate existing sensory capacities in the species or genus in question, explaining Ryan and Ryan's (1990) results. In other words, if females are preferring traits that males use in combat, and if these traits have any signal value for males, then the female preference may be 'pre-existing' (*sensu* Ryan) simply because the ability to perceive them is expressed in both sexes. A simple genetic correlation between the sexes ensures this.

An armament may eventually lose its function if, for example, the intensity of male-male competition is reduced. If it cannot be faked, because it is truly costly and cannot be produced by inferior males, females may still continue to use it as a cue to identify valuable mates, and the trait may therefore continue to be under sexual selection.

The evidence provided here suggests that the armament — ornament process really operates and that the future research should focus on demonstrating that armaments usually anticipate ornaments in the course of evolution. This can probably be tested by phylogenetic tree-building in some suitable taxon. Admittedly, a process that is the reversal of the one pictured here may also explain dual functions in a trait: males may parasitize the information content about rival quality contained in traits evolved through female choice. Because the evolution of traits used in contest seems easier to understand than the evolution of traits purely used for choice, our original model may apply more often than the reverse process.

Three specific predictions can be made from our model:

(1) Because the expression of a secondary sexual character is a compromise between attracting females and being 'punished' by other males, a male may try to display more of the signal when other males are absent, and reduce signal conspicuousness in the presence of other males. This has been described, for instance, in the red-winged blackbird *Agelaius phoeniceus* (epaulettes: Hansen & Rohwer, 1986, singing: Searcy & Yasukawa, 1990), and in the singing of the great reed warbler *Acrocephalus arundinaceus* (Catchpole, Leisler & Dittami, 1986), bobolink *Dolichonyx oryzivorus* (Capp & Searcy, 1991), and grasshopper sparrow *Ammodramus svannarum* (Smith, 1959).

(2) In order to avoid males with faked ornaments, females should evolve the habit of exerting their choice in aggregations of males, where the trait is likely to be put to trial in real male-male contests. This may explain the evolution of at least some of the lek systems (Trail, 1990; Wiley, 1991).

(3) Traits actually used as weapons cannot be elaborated via female choice so as to become inadequate as weapons (Moore, 1990b).

Throughout this paper we have discussed male traits, male-male competition, and female choice. In sex-role reversed species (e.g. Vincent *et al*., 1992), such as the pipefish *Nerophis ophidion* (Table 1), this of course translates into female traits, female-female competition, and male choice.

In conclusion, our model offers the most parsimonious explanation of the evolution of secondary sexual traits with a dual function, and perhaps also to the evolution of sexual ornaments in general. That so much effort has been devoted to study female choice, at the expense of the interplay between contest and choice, is probably a result of anthropomorphism: we cannot easily escape perceiving many secondary sexual traits as ornamental, and therefore interpret them as primarily subjected to choice, simply because they do not look like weapons to us. However, beauty lies in the eye of the beholder, and the arguments put forth here provide a simple explanation to why females find weapons 'beautiful'. We suggest modelling and direct tests of the armament explanation of the evolution of ornaments to be an extraordinarily important research challenge.

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