ADVANCES IN THE STUDY OF BEHAVIOR, VOL. 36

Preexisting Male Traits Are Important in the Evolution of Elaborated Male Sexual Display

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I. INTRODUCTION

The evolutionary cause of elaborate male sexual display traits remains controversial despite extensive recent research. R. A. Fisher is credited with developing the most widely discussed models: the good genes hypothesis (Fisher, 1915; see also Hamilton and Zuk, 1982; Maynard Smith, 1976; Zahavi, 1975, 1977) and runaway selection (Fisher, 1930, 1954; see also Arnold, 1983; Heisler, 1985; Lande, 1981, 1987). The good genes hypothesis has gained support from models showing how male traits and good genes preferences could coevolve (Houle and Kondrashov, 2002; Iwasa and Pomiankowski, 1999; Pomiankowski, 1987, 1988) and, most importantly, by strong empirical support (Göransson *et al.*, 1990; Hasselquist *et al.*, 1996; Hill, 1991; Hoikkala *et al.*, 1998; Kempenaers *et al.*, 1992; Moore, 1994; Norris, 1993; Partridge, 1980; Petrie, 1994; Reynolds and Gross, 1992; von Schantz *et al.*, 1989; Welsh *et al.*, 1998; Wilkinson *et al.*, 1998). Similar strong empirical support is lacking for runaway selection (Ryan, 1997).

Developing on a largely separate track has been preexisting preference (Burley, 1985) and related models (Basolo and Endler, 1995; Ryan and Rand, 1990). In these models, the females commonly have preferences for male traits that are not currently expressed in males. Males that appear with novel traits suited to that preference are selected by these females. These preexisting preference models differ from all other sexual selection models because the female preference evolves as a pleiotropic side effect rather than from the benefits of mate choice (Burley, 1985) and may involve maladaptive female preferences (Ryan and Rand, 1990). Preexisting preferences are not coevolutionary and do not require genetic correlations between traits and preferences. This is seen by some (Kirkpatrick and Ryan,

0065-3454/06 $35.00
DOI: 10.1016/S0065-3454(06)36006-8

1991; Ryan, 1998) as an important advantage over competing sexual selection models.

Models of female preference and sexual display trait evolution (Iwasa *et al.*, 1991; Lande, 1981) usually assume that there are no other female preferences already present. A more realistic approach is to consider how novel preferences might fare in competition with likely alternatives (Houle and Kondrashov, 2002) that are already established in the existing repertoire of female choice behaviors. Here I take an adaptive approach which suggests that multiple female preferences function as a coadapted set weighted in importance so that the total effect of mate choice brings the highest net payoff for females. Clearly then, new preferences must not only be functional, and must outcompete alternatives, but they will be selected in relation to their importance relative to other female preferences. This adaptive view is supported by the occurrence of situation-specific female choice behavior that is dependent on the choosing female's age (Coleman *et al.*, 2004; Morris *et al.*, 2003), past experience (Hebets, 2003), threat from predators (Breden and Stoner, 1987), and social circumstance (Doutrelant and McGregor, 2000; Otter *et al.*, 1999) that appear to enhance the fitness of choosing females.

Here I propose a broadened version of a model Fisher (1930) described as "war propaganda." That model suggests that females use preexisting male aggressive traits in mate choice. We have suggested previously that these preexisting traits can indicate male genetic quality as sires and can result in females evolving preferences for using (co-opting) these male cues in mate assessment (Borgia, 1979; Borgia and Coleman, 2000; Borgia *et al.*, 1985; see also Berglund *et al.*, 1996). I suggest that a wider array of traits can be co-opted for use as indicators of male quality. Co-option of preexisting traits for mate choice should be viewed as an important model for the evolution of elaborate display because (1) it provides an explanation for how good genes preferences evolve with fewer of the limitations than other sexual selection models, and because (2) there is widespread evidence of co-option of preexisting traits for use in sexual display traits and mate choice by females.

II. ALTERNATIVE MODELS OF DISPLAY TRAIT EVOLUTION

A. WAR PROPAGANDA MODEL

Fisher considered trait borrowing (or co-option) as a third mechanism for the evolution of elaborated male sexual display traits. He argued (Fisher, 1954, p. 151) that traits exaggerated by runaway selection might sometimes require "... an initial advantage not due to sexual preference." Thus, an initial nonrunaway trait was suggested to be co-opted for use in mate choice by a female preference that evolved under runaway selection. He also raised the possibility that male display might have dual functions in aggression and courtship saying, "... a sprightly bearing with fine feathers and triumphant song are quite as well adapted for war propaganda as for courtship" (p. 115). But he then plays down the idea saying, "Male ornaments acquired in this way might be striking but could scarcely ever become extravagant" (p. 116). Beebe (1929) and Wynne-Edwards (1962) noted the similarity between aggressive and courtship displays and suggested dual use of these traits. The co-option of traits for male display has been extensively discussed in the ethological literature (Schenkel, 1956; see Bradbury and Vehrencamp, 1993, Chapter 13). These discussions suggest the widespread occurrence of co-option of display traits, but they are focused on the evolution of these traits as ritualized signals, not as indicators of mate quality in mate choice.

Borgia (1979, see also Borgia, 1995; Borgia and Coleman, 2000; Borgia and Presgraves, 1998; Borgia *et al.*, 1985; Loffredo and Borgia, 1986a) and Berglund (Berglund and Rosenqvist, 2001; Berglund *et al.*, 1996) argued in support of the war propaganda hypothesis proposing that already elaborated male aggressive signals may be co-opted for use in sexual display serving as effective indicators of good genes. The same vigorous, aggressive displays that are useful for intimidating competitors and that honestly indicate males' ability to win fights may also indicate to females high male genetic quality. Females that evolve preferences for these display traits can gain a good genes benefit. Males producing aggressive display are policed by other males, so use of these displays by inferior males is often checked (Hurd, 2004; Parker and Ligon, 2002). On leks, males are often arrayed by their relative quality with more preferred males in more central positions (Kokko *et al.*, 1998; Wiley, 1991), thereby enhancing female ability to find high-quality males. Additionally, the displays themselves may be intense, for example, vocal displays often involving broadband calls, so that only especially fit males may be able to produce them effectively (Loffredo and Borgia, 1986a). Females also appear to incite males to fight and then use this information in mate choice (Bisazza *et al.*, 1989; Borgia, 1981; Cox and LeBoeuf, 1977; Farr and Travis, 1986; Thornhill, 1988).

Berglund *et al.* (1996) reviewed more than 200 cases of traits with aggressive and nonaggressive functions across a wide variety of taxa as evidence for the co-option of aggressive traits for use in courtship display. They renamed the "war propaganda" hypothesis the "armament–ornament" hypothesis and classified it as a preexisting trait (as compared to a preexisting preference) model. Several studies have supported general predictions of the war propaganda/armament–ornament hypothesis

(Hein *et al.*, 2003; Mateos and Carranza, 1999; Parker and Ligon, 2002; Thusius *et al.*, 2001) and have used phylogenetic comparisons to show the direction of trait co-option (Borgia and Coleman, 2000).

Currently, runaway, good genes and preexisting female preference models dominate the sexual selection literature. Neither the war propaganda (armaments–ornaments) model nor the preexisting traits model is considered in any of the recent major reviews of sexual selection (Andersson, 1994; Andersson and Iwasa, 1996; Arnold, 1983, 1987; Candolin, 2003; Cuervo and Møller, 1999; Endler and Basolo, 1998; Fuller *et al.*, 2005; Jennions and Brooks, 2001; Jennions and Petrie, 1997; Jennions *et al.*, 2001; Kokko *et al.*, 2002, 2003; Mead and Arnold, 2004; Møller, 1994; Ryan, 1997; Sargent *et al.*, 1998; Zeh and Zeh, 2003). This omission is important because each of these widely discussed models has controversial aspects that may limit its application. By contrast, there are no similar limitations to the application of the war propaganda and related models. Additionally, because preexisting trait models predict adaptive female preferences that can lead to good genes without genetic correlations and can explain the evolution of costly displays, they may be most suited to explaining highly elaborated male displays. These models do not require genetic correlations between male traits and female preferences because male traits already exist, and the female preferences evolve to choose male traits that indicate male genetic quality or other benefits. These models lead only to adaptive mating preferences, in contrast to preexisting trait models, because the female preferences that are expressed are those that evolve as they increase female fitness in competition with already existing preferences. Because the male trait is already present, the problem of how initially rare female preferences are able to find initially rare male traits is avoided. New preference variants that appear can be readily tested by selection and if they increase female fitness then the preference can evolve to replace already existing preferences. This opportunity for new female preferences to be readily expressed indicates the potential for a high level of adaptive tuning of mate choice based on the frequent emergence of new preferences and competition among these preferences.

B. Preexisting Trait Model

Advocates of the war propaganda model suggest that aggressive display traits might be unique in providing information to females about the quality of males (Borgia, 1979), but what was not recognized is that there are multiple ways of indicating good genes in addition to aggressive display traits. Elaborate traits, such as the finely crafted bowers of bowerbirds, and the elaborate nests of cichlid fish, appear to have evolved initially for functions not related to a good genes indicator function. Male variation in the construction and/or development of these traits may indicate genetic differences that are important to females in mate choice. While these male traits initially did not have an indicator function, differences in male performance and morphology may allow females who attend to these traits to choose males of high genetic quality. Those traits that indicate heritable differences in brain and motor development (Nowicki and Searcy, 2004), developmental stability (Thornhill and Moller, 1998), disease resistance (Hamilton and Zuk, 1982), or other characters that positively affect the performance and success of offspring may be used by females, or co-opted, to indicate differences in male quality as sires. The relatively simple preexisting trait model offers an important alternative to existing models because (1) it needs to explain only the evolution of a female preference for an already existing male trait; (2) it explains how costly sexual displays can evolve; (3) there is no requirement for genetic correlations between male traits and female preferences or coevolution of these traits; and (4) it allows new female preferences to evolve readily and compete with alternatives leading to females with a repertoire of highly adaptive female preferences.

Given that traits that are not aggressive can be co-opted, the war propaganda or armament–ornament labels are no longer appropriate. Instead, a more suitable name for this expanded hypothesis is the "preexisting trait hypothesis." While this chapter is focused on the evolution of female preferences for male genetic quality indicators, it is noteworthy that other benefits can be indicated by preexisting traits, for example, high-quality male parental care (Soler *et al.*, 1998a,b) and lowered risk for disease transmission (Borgia and Collis, 1990).

III. Problems with Current Models of Elaborate Display Trait Evolution

A. Zahavian Handicap Models

While there is strong empirical support for the hypothesis that females choose males for good genes, the widely held view that these preferences coevolve with male traits dependent on genetic correlations leading to costly Zahavian handicaps (1977) has not been well supported. Zahavi's requirement for costly male traits has two important problems that receive little attention: costs lower the male viability (Maynard Smith, 1976) and, if the traits are not completely sex limited, there will be costs to females. Also, the requirement for costs raises the issue of how good genes are honestly indicated when these traits are in their incipient stages. Many versions of Zahavi's handicap also depend on male condition to explain variation in the expression of elaborated traits. However, condition dependence in a variable environment may obscure rather than amplify differences among males and can reduce rather than improve the likelihood that females will choose males of high genetic quality. Here I review these potential complications of the handicap hypothesis as part of a comparison with the other explanation for good genes: the preexisting traits hypothesis.

B. ARE GOOD GENES INDICATOR TRAITS HANDICAPS?

Zahavi (1975, 1977) was among the first to use the good genes hypothesis to explain the origins of highly elaborated male display. He has focused on the cost of display proposing that costly handicaps are necessary to allow females to reliably identify high-quality males. Zahavi (1977) proposed that males with handicaps produce displays of varying size and cost, and only the genetically best males are able to bear the high costs associated with producing the largest displays. He argued that by choosing males with these large costly displays, females are guaranteed to receive a good genes benefit. But Zahavi's view (Zahavi, 1991, 1993; Zahavi and Zahavi, 1997) on the role of costs is extreme, arguing for "inefficiency" and "waste" as critical to insuring honesty (John, 1997). He says, "... the evolution of signals differs fundamentally from the logic by which all other characters are selected. All other characters are selected for efficiency ..." (Zahavi, 1991). But the high cost of handicaps might outweigh the expected good genes benefits to offspring (Borgia, 1979; Davis and O'Donald, 1976; Maynard Smith, 1976). Despite this criticism, the handicap hypothesis has become the basis for many models that emphasize the role of costly traits in some form for producing honest advertisement of male genetic quality (Folstad and Karter, 1992; Getty, 1998; Grafen, 1990, 1991; Johnstone, 1995; Kokko *et al.*, 2002; Kotiaho, 2001a; Nur and Hasson, 1984; Zahavi, 1975, 1977, 1991). Among these models, there has been surprisingly little effort directed at separating these models from Zahavi's extreme views on the role of costs.

Zahavi's hypothesis has become so pervasive that some texts (Krebs and Davies, 1993) refer to all good genes indicator traits as handicaps. Overreliance on the handicap has caused some authors to assume that the presence of costly male display traits justifies a conclusion of good genes function (Alatalo *et al.*, 1998; Kotiaho *et al.*, 1998; Møller and Pomiankowski, 1993; van Doorn and Weissing, 2004; Verhulst *et al.*, 1999) without considering alternative explanations. Møller and Pomiankowski (1993; see also Candolin, 2003) have claimed that males with multiple display traits could only afford a single good genes trait because of the necessarily high cost of these displays. And with little other support, they have claimed that the remaining display elements must be inexpensive results of runaway or functionless vestigial traits. But there are several problems with this argument. First, male displays could be costly for a variety of reasons that are not due to selection for a wasteful Zahavian handicap. For example, male display traits could be selected for high signal value as in a passive attraction display (Parker, 1983) or as an advertisement call. Traits that are products of runaway are also predicted to be costly when there are intense female preferences (Arnold, 1983; Lande, 1981; Mead and Arnold, 2004), or expensive male displays that evolved in another context could be secondarily co-opted for use as cues for male quality (Borgia and Coleman, 2000). Second, evidence supporting the role of waste and high cost as necessary components in male sexual display is still not established. Kotiaho (2001a) reviewed evidence for costly display and found that "... the data do not provide direct general support for the assumption that sexual traits are costly in line with the indicator mechanism models of sexual selection." He concluded that there may be a problem with how costs are measured but did not consider the possibility that cost may not always be critical for honest display. Third, theoretical studies that consider the evolution of handicaps disagree about the necessity for costs to insure honest display. For example, contrary to Zahavi's arguments that male displays must be generally expensive, Getty (1998) and Johnstone and Grafen (1993) suggest that only poor-quality males must pay a cost for there to be honest displays.

The alternative hypothesis that males can reliably indicate good genes without costly displays has been given little attention. Several authors (Borgia, 1979, 1981, 1993; Maynard Smith, 1991; Maynard Smith and Harper, 1995; von Schantz *et al.*, 1989) have proposed that athletic displays indicate intrinsic differences in male genetic quality that cannot be easily cheated, for example, by the input of extra investment (see also Viljugrein, 1997; Wedekind, 1994 for other models of cheap honest sexual signaling). Lachmann *et al.* (2001) developed a model in which cost-free signals evolve, but this model relies on the unrealistic assumption that male signals greater than their true quality are lethal. However, male signals can be constrained to signal their true quality in a more realistic way. For example, if they are limited by individual physiological, neurological, or athletic abilities, then low-cost honest advertising of individual quality could occur. The existence of human and animal (e.g., horse and dog) championship performers who consistently win races and other athletic competitions with few obvious costs that lower survivorship or future reproduction suggests that inexpensive cues that honestly signal quality are common and are not difficult to choose. In satin bowerbirds, males show extreme skews in mating success and individual male display quality and success are correlated across multiple years, which suggests that these displays are not extremely costly (Borgia, 1993). Additionally, there is no evidence of higher male mortality during the mating season when bowers and male display sites are maintained than at other times. In other species, high-intensity athletic displays, for example, display rate, display intensity, strut rate or singing rate, are commonly used to indicate differences in genetic quality among displaying males but often these displays do not carry significant costs (Aparicio *et al.*, 2003; Borgia, 1993; Jennions *et al.*, 2001; Kotiaho, 2001a,b). Female preferences for costly displays in males could also raise mate searching costs for females. In satin bowerbirds, females tend to remate with successful males over successive years and appear to benefit from this remating because it lowers the cost of their mate searching. Females who lose a mate they have mated with over multiple years put the greatest effort into mate searching after that male dies. Thus, if males can indicate their quality with displays that differ only in cost, males with low cost displays will live longer and females who choose them will have lower mate searching costs.

C. Costs of Honesty in Incipient Traits

If large costly traits are necessary to reliably indicate male quality, a critical problem for the handicap hypothesis is to explain how incipient male display traits can function as honest good genes indicators when they are still small and have relatively low cost. Such traits are unlikely to stress even poor-quality males and thus reduce their ability to use these displays. Thus, in the early stages of their evolution, these traits would provide little honest information to females about good genes and they would be unlikely to be selected for their good genes indicator function. Alternatively, if already enlarged traits are co-opted for an indicator function, then the problem of how incipient traits function as honest indicators of good genes is resolved because these traits evolved initially because of another function.

Zahavi's handicap hypothesis suggests that elaborated traits are designed to be costly. Alternatively, costs of display traits may be associated with their construction. Maynard Smith and Harper (1995) argue that if females were interested in what Zahavi (1991) refers to as waste, they would prefer males with asymmetric tails that would handicap their flight. I suggested (Borgia, 1979) that in most avian species, bright and enlarged crests and other plumage elements used exclusively for sexual displays (and not as weapons) appear to have a high signal value relative to their cost, for example, light-weight feathers that are hidden or folded away when not used in courtship (Gadagkar, 2003; Gilliard, 1969). This suggestion is supported by Barbosa and Møller (1999) and Aparicio *et al.* (2003) (see also Møller in Guilford, 1995) who found that elaborated feathers are often reduced in thickness indicating a design to lower production and aerodynamic costs. So, while some cost is necessary to produce any highly visible structure or display, there is no evidence that these traits are designed to enhance cost as expected from handicap models and there is evidence for cost reduction in many displays.

Some traits like elongated male peafowl coverts appear to be costly, raising the question that if costly traits reduce benefits and are not a necessary requirement for honest display, why do they evolve? One likely answer is that already costly traits that evolved for another function have been co-opted for a secondary function as indicator traits. For example, weapons that initially evolved for combat, like large antlers, provide an important immediate benefit to their owner that requires a high-cost investment. These traits may be co-opted as good genes indicators at little or no additional cost (Borgia and Coleman, 2000). The high cost of growing antlers combined with the use of these weapons to limit the opportunity of inferior males to cheat may provide a reliable signal of male fighting ability that also functions as a reliable cue indicating good genes (Berglund and Rosenqvist, 2001; Berglund *et al.*, 1996; Borgia, 1979, 1981). The co-option of traits as male quality indicators may provide the best opportunity for cost to function in enforcing honest signaling because it avoids many of the difficulties associated with the coevolution of costly male traits and female preferences. Since the good genes indicator function evolves only after the trait is already elaborated, there is no requirement that this trait produce honest signals when they are small and not very costly. Co-option can also explain why costly indicators might evolve if there are cheaper low-cost alternatives. If the original function of the co-opted indicator trait remains important, then the costs of building that trait are tied to its original function, for example, as a weapon. Because these costs were there before the co-option occurred, the addition of the secondary indicator function may occur with little or no additional cost, yet the initial costliness of the trait can help enforce honest advertising in its indicator function. Thus, the *de novo* evolution of costly genetic quality indicators may be limited because their costs must be subtracted from their benefits, but the evolution of costly good genes indicators may be more likely to arise where the indicator function has secondarily evolved in a preexisting, already expensive trait.

D. Are Condition-Dependent Traits the Best Good Genes Indicators?

Another problem for the handicap hypothesis is that male condition-dependent traits may not reliably indicate male quality. The handicap hypothesis including most recent models (Andersson, 1994; Andersson and Iwasa, 1996; Getty, 1998; Iwasa *et al.*, 1991; Johnstone, 1995; Rowe and Houle, 1996) claims that males in better condition are able to invest more in display and that the differences in ability to invest honestly indicate differences in male genetic quality. This condition dependence of traits introduces a strong environmental component into a process that is designed to assess genetic quality (David *et al.*, 2000). Experiments designed to measure the genetic contribution of traits typically control for and reduce the effect of environmental variation (Falconer and Mackay, 1996). While females are unable to control the histories of males they are choosing among, they can choose traits less subject to environmental effects. Because male condition can be strongly influenced by the environment in ways that may not be representative of male genetic quality, for example, the quality of parental care received (Clutton-Brock *et al.*, 1982), local differences in the availability of resources, competition, past reproductive effort (Kokko, 1997), stress during development (Leitner *et al.*, 2001; Nowicki *et al.*, 2000, 2002; Polak *et al.*, 2004; Spencer *et al.*, 2003) or cheating on future reproductive investment (Candolin, 1999), and so on, females should assess male genetic quality with relatively condition-independent traits if their choices are to be reliable indicators of quality. For example, females could choose males based on the display length (to test their endurance) that may tire them after each courtship or peak call frequency (Howard and Young, 1998) which may be less costly and is a more repeatable and reliable signal because it is influenced less by the demands of previous courtships.

Condition dependence may allow cheating by genetically inferior males in several ways. In a cost-dependent handicap system in which males mate over multiple years, inferior males might cheat by saving investment across years, allowing them to build up their condition, then spend these accumulated resources to perform well in one year (Kokko, 1997; Kotiaho, 2001a); or they may invest heavily in one year at the expense of future reproduction. These life history adjustments could allow cheaters to match or even surpass the investment of high-quality males for at least one year (Kokko, 1997), improving their chance of reproducing and exposing females to unreliable signals of male quality. Female mammals adjust their reproduction based on past investment often skipping reproduction or investing in less expensive female offspring in the year after producing more expensive male offspring (Clutton-Brock *et al.*, 1982). Candolin (1999) found evidence for cheating behavior in male sticklebacks which mate repeatedly through the year. Poor-condition males cheat by developing the red color of good condition males, and she suggests that cheating males develop these displays at the expense of future reproduction. Badyaev and Duckworth (2003) found that male house finches that did not breed the previous year invested more in chest patch coloration. In these cases, there is evidence for advantageously adjusting investment between reproductive bouts. It is unclear if such adjustment occurs in species where males do not invest parentally and display across multiple years. Delayed maturation and plumage expression and lower attendance at display sites by young males are common among these species (e.g., bowerbirds, Marshall, 1954; birds of paradise, Gilliard, 1969; black grouse, Höglund and Alatalo, 1995). We found that male satin bowerbirds may take on permanent bower sites at different ages, raising the possibility that males who delay bower holding may be saving resources for this task. But males with high-quality displays maintained them across successive years, and there was no evidence that low-quality males could enhance the quality of their displays in a single year (Borgia, 1993). This may be related to the important role of experience accumulated across multiple years in allowing males to construct successful displays such that cheating is suppressed by the lack of experience rather than by the costs of display.

Good genes models differ in the extent to which they rely on costly handicaps to insure honesty. The limited evidence for cost associated with male display and evidence showing design for reduced costs imply that there has been no selection for waste. Reliable low-cost male displays should have an advantage in competition with costly condition-dependent displays because they provide the offspring of choosing females higher net benefits and allow the male display trait to be a reliable signal across a variety of environmental conditions, and make him available for mating across multiple years. Thus, cost may have a more limited role than Zahavi's handicap model suggests.

Studies differ in the role of male condition in affecting female choice; some show that females choose on the basis of male condition (Holzer *et al.*, 2003; Rantala *et al.*, 2003), whereas others do not (Gray and Eckhardt, 2001) and some show mixed results (Badyaev and Duckworth, 2003; Hunt *et al.*, 2004). Experimental studies commonly show that males reared on depleted resources are less attractive to females than males who are not (Leitner *et al.*, 2001; Nowicki *et al.*, 2000, 2002; Spencer *et al.*, 2003). The positive results of these experiments show that strong environmental effects can be sufficient to override the effects of genetic quality. They offer no clear evidence to support the hypothesis that females gain genetic benefits from choosing males in good condition. More suitable experiments would involve designs that show a connection between genotype, condition and female choice.

IV. Evaluating Genetic Correlation Models

A. Genetic Correlations and Mate Choice

The two most discussed sexual selection models, runaway and coevolutionary good genes models, both require a genetic correlation between male traits and female preferences (Andersson, 1994; Hall *et al.*, 2004; Iwasa and Pomiankowski, 1995, 1999; Iwasa *et al.*, 1991; Kokko *et al.*, 2002; Lande, 1981; Pomiankowski and Iwasa, 1998). These genetic correlations result from gametic phase disequilibrium (linkage disequilibrium not due to physical linkage; Andersson, 1994). In these models, males with attractive traits obtain a mating advantage because of female preferences for that trait. This causes an increase in frequency of both the male trait and the female preference among offspring in the next generation. The statistical association of the male trait and the female preference in offspring produces the gametic phase disequilibrium. The occurrence of these correlations has been viewed as critical in assessing the plausibility of both good genes and runaway models (Andersson, 1994; Arnold, 1983; Bakker and Pomiankowski, 1995; Kirkpatrick and Ryan, 1991; Ryan, 1998) but remains controversial. Genetic correlations may be difficult to maintain under variable selection pressures (Barton and Turelli, 1991; Breden *et al.*, 1994; Nichols and Butlin, 1989, 1992). Bakker and Pomiankowski (1995) indicate that when selection is suspended for one generation, the genetic correlation will be reduced by 50%. Sexual selection studies suggest a complicated mate choice dynamic that could limit the occurrence of genetic correlations in natural populations. Female preferences needed to maintain genetic correlations may be suppressed or altered by reductions in efficiency or increases in costs of mate searching resulting from predation threat (Breden and Stoner, 1987), parasitization (Simmons *et al.*, 1999), male–male competition (Houde, 1994), or loss of top males requiring additional searching by females (Uy *et al.*, 2000). The development of genetic correlations may also be limited by age-dependent (Coleman *et al.*, 2004) or learned (Hebets, 2003) mating preferences, mate choice copying (Gibson *et al.*, 1991; Grant and Green, 1996; Höglund *et al.*, 1995), frequency-dependent preference for male morphs (Hughes *et al.*, 1999; Qvarnström *et al.*, 2004), or other factors that reduce the association between a particular female preference genotype and the corresponding male trait genotype. Female preferences for multiple traits (Borgia, 1985a; Mays and Hill, 2004; Møller and Pomiankowski, 1993) could also complicate choice and limit the evolution of genetic correlations if different mixes of male trait values suit females, thus lowering the intensity of selection on any single male trait. Additionally, with inbreeding avoidance females may be programed to discriminate against male relatives as mates who would, if genetic correlations were present, carry their most preferred traits. Thus, many mechanisms known to affect mate choice can reduce genetic correlations, so it is not clear that correlations with sufficient strength to drive and maintain correlation-based sexual selection are present in natural populations.

Artificial selection experiments have been used to show a correlated response to selection (Bakker and Pomiankowski, 1995; Houde, 1994; Wilkinson and Reillo, 1994) that has been interpreted as evidence for genetic correlations. But Gray and Cade (1999) argue that this correlated response test overestimates the genetic correlation. Genetic correlations also have been reported in some unselected populations (Bakker, 1993; Isyengar *et al.*, 2002) but not others (Jang, 1997; Mühlhäuser and Blanckenhorn, 2004). Evaluating these results is complicated because genetic correlations could occur because of pleiotropy (Kokko *et al.*, 2002), physical linkage (Gilburn *et al.*, 1993), intrapopulational mate choice polymorphisms, or gametic phase disequilibrium, with only the latter being consistent with genetic correlation-based sexual selection models. Where genetic correlations have been found without artificial selection, the male displays are not the extreme types of highly elaborated traits that Fisher (1930) and others have sought to explain with runaway and good genes models. Bakker (1993) found a genetic correlation between the red coloration of male sticklebacks and a female preference, but the evolution of this trait could also be explained by its role in male–male territorial signaling with a secondary use as a quality indicator, perhaps for parental care (Candolin, 1999; Künzler and Bakker, 2001).

Blows (1999) followed the evolution of genetic correlations on *Drosophila* across multiple generations and found correlations between traits and preferences. Initially, the correlations increased but they eventually collapsed as predicted by Nichols and Butlin (1989). Similarly, Houde (1994) found that divergence in female preferences in high and low selected lines in the first two generations decreased or reversed in the third generation. She attributed this loss of divergence in all four of her selection experiments to a breakdown in the genetic correlation. These results do not support models requiring the ongoing maintenance of genetic correlations (Hall *et al.*, 2000; Kirkpatrick, 1982; Lande, 1981) and suggest that the importance of genetic correlations in shaping sexual display is still unresolved.

B. COMPARING GENETIC CORRELATION MODELS

Kokko *et al.* (2002) proposed that good genes and runaway models should be merged into a larger model because in both models female preferences enhance the reproduction of males with attractive traits (see also Andersson, 1986; Eshel *et al.*, 2000; Mead and Arnold, 2004). Thus, while differences among these models are usually cast as being between the male mating (sexy son) advantage of runaway models versus a viability enhancement to both sons and daughters of good genes models, a more appropriate comparison is the sexy son benefit alone from runaway models versus a sexy son *and* good genes benefits from good genes models. Females initially choosing males for good genes give males they choose, if as in many cases females choose the same males, a mating advantage as a side effect of their choices with the result that the sons of females receive both kinds of benefits. On the other hand, females choosing because of a runaway trait would not necessarily choose males that provide high viability to offspring (Lande, 1981). Although there are similarities between coevolutionary good genes and runaway models, this and other important differences suggest that these models should not be merged.

There are at least three different good genes models that differ in their dependence on genetic correlations between the male trait and the female preference and on the coevolution of male traits and female preferences. The genetic correlation models (Iwasa *et al.*, 1991) discussed earlier are the most widely discussed versions of the good genes models, but it remains unresolved if genetic correlations are critical to explaining elaborated male display. The second kind of good genes model is the simpler coevolution model that does not require a genetic correlation between male traits and female preferences. Male indicator traits increase because of the enhanced survivorship of offspring of males indicating high quality of males with these traits and because males have a mating advantage with females showing a preference for the indicator trait. Females mating with males having viability indicator traits gain an advantage because their offspring have higher fitness than females who do not attend to this male trait. This causes the female preferences for the male trait to increase. Because this kind of coevolutionary model does not depend on genetic correlations between male traits and female preferences, the inability to maintain genetic correlations is not critical for the successful coevolution of traits and preferences (although genetic correlations may occur). The simplest good genes model is the preexisting traits model. There is no genetic correlation or coevolution required because the male trait is already present and the female preference evolves because of gains in offspring quality. One potential problem for this hypothesis taken alone is that sexual selection via female preferences is not involved in trait elaboration. It may be that female choice-based sexual selection has little role in trait elaboration. Another possibility is that co-option of preexisting male traits acts as a starting point for coevolutionary models that can lead to further trait elaboration. With the male trait already present in the population, it is not difficult for females to find males that may have variable expressions of the trait correlated with their genetic quality (the problem of males with incipient traits that do not correlate with fitness is bypassed if these traits are large), and by choosing males with more developed versions of the trait, females can enhance the fitness of their offspring which in turn selects for females choosing more extreme versions of the trait. This process may lead to elaboration of the male trait beyond the size at which co-option occurred, particularly if this enlargement is not costly for top males.

The disparity in the evidence for good genes versus runaway may be explained because of two advantages for the good genes models when they are in competition with runaway. First, at least two good genes models do not rely on genetic correlations and thus can evolve with less demanding requirements. Co-option of preexisting traits does not require genetic correlations or the evolution of a novel male trait. The coevolution good genes model is more complex because it requires the evolution of the male trait; but because it does not require genetic correlations, it may allow good genes preferences to evolve under conditions when runaway cannot operate, for example, when genetic correlations cannot be maintained. Second, because good genes models provide both sexy son and good genes benefit, they should evolve more readily when in competition with pure runaway models that provide only a sexy son benefit.

Consistent with the more difficult requirements for evolving runaway traits, there is scant evidence clearly supporting Fisher's runaway hypothesis. For example, it is suggested that highly variable male display among sister groups at the tips of phylogenies provides evidence of runaway (Candolin, 2003; Omland, 1996a,b; Prum, 1997). But, there are many reasons for lability in male display among sister taxa including adaptation to different local sensory environments (Boughman, 2001; Endler *et al.*, 2005; McKinnon and Rundle, 2002; Seehausen, 2000; Uy and Borgia, 2000); different levels of sexual competition regulated by the mating site (Panhuis and Wilkinson, 1999); or sexual isolation (Danley and Kocher, 2001) that does not depend on runaway selection. Alternatively, the existence of genetic correlations between traits and preferences is cited as evidence for runaway (Arnold, 1983), but this could occur for different reasons as discussed earlier.

V. Evaluating the Preexisting Preference Model

A. General Issues

Preexisting preference models, sometimes called sensory exploitation, are attractive because, like preexisting traits models, they are relatively simple and do not require genetic correlations to explain the evolution of female preferences for male display traits. Sherman and Reeve (1999) discuss limitations in the operation of preexisting preference models arguing that because these preferences start as unselected side effects, it is unlikely that they provide genetic or other benefits and may, as Ryan and Rand (1990) suggest, produce maladaptive consequences for choosing females (see also Fuller *et al.*, 2005). Such traits should be less likely to evolve and resist invasion if they were to become established than alternative positive benefit-providing (e.g., good genes) traits (Houle and Kondrashov, 2002). Unfortunately, preexisting preferences are commonly considered as part of a larger model also involving sensory bias and sensory drive (Endler and Basolo, 1998), but this includes a range of different models that differ in their likely importance in shaping sexual selection. Sensory bias used in its original sense (Endler, 1992) to indicate that the environment affects the transmission characteristics of light and sound and therefore affects the form of signals is well supported (Boughman, 2001; Endler *et al.*, 2005; McKinnon and Rundle, 2002; Seehausen, 2000; Uy and Borgia, 2000), but this is different from the question of whether there are preexisting preferences that are important in sexual selection (Fuller *et al.*, 2005). Here I review three cases often cited as providing the best support for preexisting preferences and point out significant problems with each of these examples.

B. Reconsidering Preexisting Preferences

Preexisting preferences are suggested to be simple by-products of the sensory system (Autumn *et al.*, 2002; Basolo and Endler, 1995; Ryan, 1998). But in order for these preferences to operate, they may require much more complex and sophisticated mechanisms than are typically suggested. For example, in the Túngara frog, Ryan *et al.* (1990) propose that male ancestors produced whine calls in mate sexual advertisement and that in a descendent species they evolved an additional and acoustically distinct chuck element in response to a preexisting female preference for a chuck call. Two different auditory structures are used to detect these call components. The whine component is perceived by the amphibian papilla, and the basilar papilla is used to detect the chuck elements. They argue that the basilar papilla of the female is tuned to respond to the frequency range of the chuck and is more responsive to slightly lower than average frequency chucks in the population that are associated with larger males. Females thus choose larger males and gain a reproductive advantage (Autumn *et al.*, 2002; Ryan *et al.*, 1990).

One significant problem for this hypothesis is how the proposed preexisting preference for chucks involving an auditory structure (the basilar papilla) can be fully functional in mate choice if it has not been previously used in that capacity. In Ryan and Rand's experiments, they play chuck calls to females from species in which males do not give chucks and females show evidence of a preference for these calls. Their hypothesis requires a complex of interaction among functional traits that seems unlikely to be present in a basilar papilla that had not been previously used to detect chucks. For such a system to operate (1) there must be already existing neural circuits that detect the chuck as distinct from environmental noise; (2) these particular chuck-sensitive neuronal elements must be linked to brain centers affecting mate choice; (3) but not other centers where stimulation would cause inappropriate or harmful effects; (4) the centers stimulated by the chuck call must cause females to be more inclined to mate with chuck-producing males; (5) in contrast to being indifferent to or less inclined to mate; and (6) females are tuned to respond to a lower than average frequency of chucks that allow them to choose larger than average males. While there is little doubt that natural selection can shape an auditory system to achieve these tasks, it is unlikely that such a complex set of integrated capabilities tuned to function in an adaptive way (tuned so that females would choose large males) could arise, as these authors propose, without selection. Shaw (1995) suggested an alternative hypothesis consistent with the possibility that selection has directly shaped the functioning of the basilar papillae for mate choice. She hypothesized that ancestral calls in this lineage contained both the chuck and whine elements but that chuck elements were lost in some species while females retained their ancestral (now atavistic) preference for these call elements. Because these atavistic preferences for lost male traits had been shaped by selection, this hypothesis provides a more plausible explanation for how a female from a species in which males do not produce chucks can immediately and apparently adaptively respond to experimentally provided chucks in a way that indicates a preference for these calls. Ryan's discovery (1985) that predatory bats use chucks to locate male frogs as prey is also consistent with this second hypothesis. Ryan and associates (Ryan, 1990, 1997; Ryan and Rand, 1993, 1995; Ryan *et al.*, 1990) justified their preexisting preference hypothesis with a parsimony argument based on the mapping of chuck calls onto the phylogeny of this frog genus. Shaw's hypothesis (1995) leads to an equally parsimonious mapping of these vocal displays as compared with the preexisting preference hypothesis calling into question the validity of that hypothesis as applied to the evolution of chuck calls and their perception by females. This analysis suggests an even stronger argument against the hypothesis that preexisting preferences favored the evolution of chuck calls. It is extremely unlikely that the Tungara frog's auditory system would have, without selection for hearing and responding to chuck calls, basilar papillae in females capable of detecting these calls and then causing them to respond by identifying and mating with high-quality males, all without the benefit of selection for these functions.

Another frequently cited example is the suggested preexisting preference for swordtails in the platyfish genus *Xiphophorus* and its close relatives. Basolo (1990) found that females from *Xiphophorus* species with unsworded males associate more with males from other species with swords and with conspecific males with artificially appended swords (Basolo, 1990, 1995a,b). This and a mapping of traits onto the *Xiphophorus* phylogeny led her to suggest a preexisting preference for swords in females of these unsworded species (but see Borowsky *et al.*, 1995; Meyer *et al.*, 1994). As with the Tungara frogs, an alternative hypothesis is that the preference for the elaborated male trait (swords) evolved in an ancestor and that they were lost in the lineages that do not have them. Suggesting why swords might be lost, Rosenthal *et al.* (2001) found that sworded males were more subject to predation than unsworded males. Additionally, Rosenthal and Evans (1998) found that female *Xiphophorus* prefer video images of males with large male body size and that this replaced the female preference for swords. They suggested an alternative interpretation for the behavior of females in nonsworded species (see also Sherman and Reeve, 1999) that females prefer to associate and perhaps mate with males with a large body size and that swords make males appear larger than similar sized counterparts. Basolo (2002) found an association preference in three of four unsworded species for experimentally sworded members of the opposite sex. She suggested that males share the latent preference shown by females, but this result also supports the hypothesis that this is a general preference for association with individuals with large body size (Gabor, 1999) not necessarily associated with mating preferences.

Preexisting female mating preferences are also suggested to be important in mate choice in unionicolid water mites (Autumn *et al.*, 2002; Proctor, 1991, 1992; Ryan, 1998). Proctor (1992) argues that this may be one of the clearest cases of preexisting preferences because of strong supporting behavioral and cladistic evidence, but close examination of this evidence suggests a less convincing case. Proctor (1991, 1992) hypothesized that male water mites produce water surface vibrations during courtship that mimic copepod swimming motions that attract the predatory females of their species. Thus, males are able to exploit the female "preference" for copepod vibrations to gain matings. As support for her hypothesis, Proctor (1991) argues that (1) the frequency of male trembling matches that of copepod water surface vibrations; (2) females grasp males using the same motions they use to grasp prey suggesting that females are deceived to initially identify males as prey; and (3) hungry females appear more sexually receptive than well-fed females, supporting her contention that females are mistaking males for prey.

The most significant problem for Proctor's hypothesis (1991) is that the behavior she reports is not consistent with the claim (see also Autumn *et al.*, 2002) that male vibrations are used to mimic copepods and attract females from a distance. She says (Proctor, 1992), "Males search for mates by walking or swimming until they contact a female, whereupon they vibrate their first and second legs near the female ('male courtship trembling')" (p. 745). Thus, males touch females first and then vibrate; they are not attracting females from a distance. This is critical because by touching her first, the male water mite alerts her to his presence, making it unlikely that she would be fooled (sensorially exploited) by male mimicry of copepod vibrational signals. If vibrational signals are not used in mimicry, why are they present? Such signals are common in water mites in species for which copepod mimicry has not been suggested and are used in positioning the female, directing her to spermatophores and in postcopulatory mate assessment (Proctor and Smith, 1994). Also, the frequencies of copepod and male water mite vibrations are not so similar to provide unambiguous evidence of convergence necessary to support a claim for mimicry: trembling male water mites produce vibrations at 10–23 cycles/sec and copepods produce vibrations at 8–45 cycles/sec (Proctor, 1991). Overlap could occur because the mechanics of leg movements may constrain the possible frequency range of these vibrations. Proctor (1991) argues that hungry females show a greater response to courtship vibrations than well-fed females as an explanation for why females grasp males. But, as suggested earlier, because males tremble after they touch females, hungry females should not be deceived into reacting to male vibrations as if they were indicators of prey. An alternative hypothesis is that hungry females may gain a nutritional contribution from male spermatophores and are thus more likely to seek matings. Proctor also suggests that similarity in how females mount males and attack prey indicates that females are being deceived by male mimicry of copepods. Female water mites commonly mount males for courtship even in species in which mimicry is not suggested to occur (Proctor and Smith, 1994), and it is common for individuals in predatory species to use predatory movements to gain access to potential mates. For example, in the yellow dung fly *Scatophaga*, males capture females for copulation in the same way they capture prey (Borgia, 1982; Parker, 1970), and there is no suggestion that male dung flies are deceived into reacting to females as prey as has been suggested for female water mite's reaction to males.

Proctor's cladistic analysis (1992) also does not convincingly prove the case for mimicry and sensory exploitation. She argues that net stance (the position males and females use in waiting to capture prey) occurs before or simultaneous with male courtship trembling that she associates with male mimicry of copepods. Her cladogram of 13 species shows branching into two major clades with no net stance and no trembling in one, and in the other 7 of 8 species show both of these behaviors and one does not show trembling. This results in two equally parsimonious maps requiring three transitions: net stance and male trembling evolving simultaneously and then one loss of male trembling which supports her hypothesis, or net stance evolving first and then male trembling evolving later in two separate events which fails to support her hypothesis. She concludes from this analysis that "... when taken together with previous behavioral evidence, this cladistic study strongly supports sensory exploitation as an explanation for male trembling in Unioncoidal mites" (1992, p. 745). But the cladogram at best suggests that these two alternatives are equally likely and that sensory exploitation may be less likely if losses are considered more likely than gains. Thus, the behavioral or cladistic data offered to support Proctor's predation hypothesis are not clear-cut, and there are alternatives that are at least equally plausible that do not support sensory exploitation.

C. THEORETICAL ISSUES

The argument for preexisting preferences becomes less convincing when set in the context of a new mate preference evolving in competition with other already existing adaptive mating preferences. While most models consider the evolution of new preferences in species where there are no other mating preferences, the widespread occurrence of mate choice among animal species suggests that this may be rare. In many species, male displays involve multiple traits that females use in mate choice (Borgia, 1985a; Candolin, 2003; Møller and Pomiankowski, 1993; Schluter and Price, 1993). The incorporation of a new unselected preference into the existing repertoire of female preferences should lessen the importance of other preferences. If these already existing preferences are advantageous to females, then replacement or lessening of importance of these preferences by a new unselected preexisting preference should reduce female fitness and lead to selection against these less advantageous preferences. Thus, the expression of a novel preexisting preference may be selected against both because it is unlikely to be beneficial and its use reduces the benefits provided by other previously established preferences.

There may also be selection against latent preexisting preferences as they await the evolution and expression of a suitable male trait. First, latent (not used in mate choice) preexisting preferences have costs necessary to make them operational so that females can choose appropriate male traits as they appear. These costs include the costs of structures and energy needed to allow females to identify appropriate novel male traits preferred by the latent preference and the cost of attending to nonexistent male signals at times during courtship when this attention may be more profitably directed toward assessing existing male display elements or threats such as predation. Although these costs maybe small, in the absence of a suitable male trait, there is no compensating benefit, so there should be selection for the elimination of these traits while they are still latent and before compatible male traits appear. This problem may be lessened if the latent preferences are adjuncts to existing preferences. For example, Burley and Symanski (1995) found in estrildine finches that both sexes have a preference for natural plumage colors in the opposite sex and when these are applied to artificial head crests. They interpret this as a preexisting preference, but it may also be viewed as an extension of an existing preference to other areas of the bird. Such "latent" preferences that use the same underlying mechanisms for mate choice as operational preferences seem more plausible given that there may be fewer added costs to expressing these preferences.

Arguments supporting preexisting traits have relied heavily on mapping of male display traits and female preferences onto phylogenies. However, the mapping of male display traits onto well-established phylogenies in a variety of other species shows a high level of rapid evolution at the tips including frequent reversals and convergences (Baker and Wilkinson, 2001; Ellsworth *et al.*, 1995; Johnson, 1999; Kusmierski *et al.*, 1997; Omland, 1997; Omland and Lanyon, 2000; Prum, 1997; Sturmbauer *et al.*, 1996; Wiens, 2001). This suggests that parsimony use in trait mapping may neither be reliable for interpreting the evolutionary history of these traits (Cunningham *et al.*, 1998; Losos, 1999; Reeve and Sherman, 1993; Shaw, 1995) nor useful for evaluating competing hypothesis, particularly when a small difference in the number of character state changes affects which hypothesis is supported. Wiens (2001) has suggested that the high level of turnover of male display traits and female preferences would rapidly deplete the store of latent female preferences. Thus, it is unlikely that preexisting preferences give rise to the rapid evolution of diverse traits seen in many species with highly elaborate display. Also, because these preferences are not selected for their mate choice function, they are unlikely to explain the evolution of complex adaptive mate choice behaviors such as conditional preferences that change as females age (Coleman *et al.*, 2004) or with female social circumstances (Doutrelant and McGregor, 2000; Otter *et al.*, 1999) or that involve complex courtship communication (Patricelli *et al.*, 2002). Preexisting biases that affect mate choice may be important in some contexts. For example, in satin bowerbirds, females are threatened by high-intensity male courtship display (Coleman *et al.*, 2004; Patricelli *et al.*, 2002). Females are often chased at feeding sites by the larger and more dominant males so it is not surprising that they would be sensitive to threat when courted with high-intensity displays that have aggressive elements by these same males (Patricelli *et al.*, 2002, 2003). Female signaling of their level of comfort in courtship and males modulating in reaction to signals of discomfort provide a means by which males and females can overcome the threat associated with attractive high-intensity displays. In this case, not all females are threatened to the same degree with older females showing less discomfort from high-intensity displays than younger females (Patricelli *et al.*, 2004; Coleman and Borgia, submitted for publication). Also, this preexisting trait is adaptive in providing protection to females in what they perceive to be dangerous circumstances and this causes females to avoid rather than prefer particular males. It may be relatively more common for biases that are generally protective to influence mate choice by limiting danger to females rather than compelling them to mate based on traits not related to adaptively evolved preferences. (For a comparison of sexual selection models see Table I.)

TABLE I
COMPARISON OF MODELS OF SEXUAL SELECTION

Model	Genetic correlation required	Coevolution required	Early costly trait problem	Evidence	Adaptive preferences
Runaway	Yes	Yes	No	No	No
Coevolutionary good genes	Yes	Yes	Yes	Maybe[a]	Yes
Preexisting preference	No	No	No	Maybe[b]	No
Preexisting trait good genes	No	No	No	Maybe[a]	Yes

[a] Good genes have been related to particular phenotypic traits females choose in males in a variety of species, but it has not been resolved if these traits evolve by coevolution or from preexisting preferences. There is independent evidence of many male display traits having a preexisting function.

[b] While there are several studies that claim to show a preexisting preference evolution, most subject to alternative interpretation. One likely case is discussed by Burley and Symanski (1995), but it may have limited application, see text.

VI. EVIDENCE FOR THE CO-OPTION OF PREEXISTING TRAITS

A. INTRODUCTION

The preceding review suggests an important role for the preexisting traits version of the good genes model. This model is particularly attractive because of its relative simplicity and because it makes clear testable predictions. Since the model assumes that male indicator traits are co-opted from traits that have previous function, a useful test is to determine if the existing indicator display shows evidence of a previous function. For this, detailed phylogenies which allow the order of trait evolution to be resolved can be valuable, particularly if there is evidence of multiple co-options. But even then, assessing the order in which trait functions evolve can be difficult if there has been rapid evolution of display functions (Kusmierski *et al.*, 1997), or if, as is often true, it has not been determined whether a trait has an indicator function across a group of species. Without phylogenies we can identify traits that have dual functions as being likely candidates in which one was co-opted but we cannot resolve the order in which they evolved. Sometimes traits are widespread and have obviously long histories, for example, bird nests, so that a secondary use in a small set of species can be inferred even without detailed phylogenetic information. Despite these limitations, there is growing evidence that co-option has been important in the evolution of indicator displays, and with more reliable phylogenies and information on trait functions as indicators, we can better assess the importance of the preexisting trait model.

B. ICONIC NONMORPHOLOGICAL DISPLAY

Many cases of iconic (exemplar), highly elaborated sexual display traits show evidence of co-option and suggest that co-option may be generally important in the evolution of elaborated displays. Display trait co-option is likely affected by the preexisting conditions associated with courtship. The kinds of traits that may be most readily co-opted are especially large or difficult to build structures or other traits expressed near courtship sites that are effective in showing differences among males (e.g., neurological function, parasite resistance, developmental stability, or resistance to interference by other males) that correlate with and can indicate good genes. For some traits, there may be post-co-option evolution such that those traits shown only briefly during display may be selected to be exposed longer or presented where they can be more easily viewed by females.

The nests of birds, sticklebacks, and mouth-breeding cichlids that have long histories with a clearly defined initial function as a repository for eggs now show evidence of a secondary function as indicators of male quality. Barber *et al.* (2001) suggest that stickleback nests secondarily function as male quality indicators. Males differ in their ability to produce Spiggin, a glycoprotein glue used to hold nest-building materials together, and this results in nests that differ in quality. They suggest that variation in ability to produce costly Spiggin and its use in building high-quality nests has secondarily become a condition-dependent indicator that females assess as part of mate choice.

Bird nests have been discussed as having a secondary function in advertising male quality (Collias and Victoria, 1978). Soler *et al.* (1998a,b) suggest that females discriminate among male nests to assess the quality of male parental care. Several studies have shown that males of some species build multiple nests and those males with more nests are more likely to attract a mate (Verner and Englesen, 1970). The ability of males to build multiple nests may be attractive to females because they indicate male quality, or because freshly built nests may be better nests that attract females because eggs are better protected. The first case would be consistent with a co-opted indicator function, while the second would suggest a proximate benefit for females. Quader (2005) found that in baya weavers (*Ploceus philippinus*), females chose nests based on location (e.g., over water and height) and architecture (neatness of weave). It is possible that neatness may indicate differences in male quality.

Mouth-breeding African cichlids build large volcano-shaped sand display structures that originated as nests (McKaye *et al.*, 1993; Tweddle *et al.*, 1998) and currently function both as a site where eggs are briefly deposited before being picked up by the mouth-breeding females and as a trait used in mate selection. Outgroup comparisons suggest that ancestral nests were small, and it remains unclear when and how these sand structures became enlarged. McKaye *et al.* (2001) suggest that these sand structures function to protect eggs from sneaker males who might eat them during transfer, and enlargement may have occurred for this function. Their hypothesis suggests that there were two co-option events in the evolution of mouth-breeding cichlid sand structures, the first involving the co-option and modification (enlargement) of the sand structure for use as a site for protected egg transfer and a secondary co-option of these structures as display elements that females use in assessing males (Taylor *et al.*, 1998).

Bowerbird bowers were initially thought to be modified nests (Sodderberg, 1929), but the absence of evidence for egg laying in bowers and differences between nests and bowers in shape, location (tree vs ground) and builder (male vs female) indicate a separate origin (Borgia *et al.*, 1985). Across different bower types, bowers show a design most consistent with

protecting females from forced copulation by courting males. Two species that have lost bower-building show alternative adaptations that allow female choice (Borgia, 1995), and generally females not protected by the bower during courtship are susceptible to forced copulation. Bowers may serve to calm females and increase female visitation which, for high-quality males, likely outweighs the reduced opportunity for forced copulations (Borgia, 1995; Borgia *et al.*, 1985). Bowers are also used in mate choice in at least one of the two clades of bower-building bowerbirds (Borgia, 1985a; Borgia and Mueller, 1992), and I proposed that they have been co-opted for this mate choice function secondarily after they evolved initially as barriers that, for males, increase female visitation and, for females, protect them from forced copulation (Borgia, 1995). Under this hypothesis, bowers were present on the display court and available for inspection by females while serving their initial protective function and then females evolved to use already existing differences in the quality of bower construction to assess males. In satin bowerbirds, various characteristics of the bower, including its symmetry, neatness in construction, and the fineness and density of sticks, are strongly correlated with male mating success (Borgia, 1985a), and these traits may indicate to females heritable differences in male motor skills and resistance to destruction by competing males (Borgia, 1985b).

Among structure-building species, there are also cases where the preexisting traits hypothesis is not supported. Several species of fiddler crabs build sand hoods and pillars near their burrows. Christy *et al.* (2003) propose that these structures are built from sand leftover from burrow construction and that they now function as markers allowing males to quickly relocate their burrows when threatened by a predator. They suggest that females also use these structures in finding burrow entrances when threatened by predators. Males benefit from this behavior because females tend to mate with males once in burrows, although females do not show a preference for males with pillars. It may be that sand pillars do not reflect owner's quality with sufficient accuracy for females to use them in mate choice or that the relatively simple visual system of these crabs may not allow such discrimination.

Weakly electric fish (order Gymnotiformes) generate multifunctional electric organ discharges (EODs) for electrolocation (e.g., finding prey) and social communication. Hagedorn and Zelick (1989) suggest that the strength of the EODs provide information about the internal state of the animal, including their state of health, which may be useful to females in assessing males as mates. Phylogenetic analysis suggests that EODs have been selected for greater signal complexity resulting in lower detectability by key predators. For extant species in the families Gymnotidae, Hypopomidae, Rhamphichthyidae, and Apteronotidae, an additional wave phase was added to the ancestral monophasic signal that shifts its spectrum above the most sensitive frequencies of electroreceptive predators (Stoddard, 1999). Signals in the family Hypopomidae are sexually dimorphic, and males have extended the duration and amplified electric signal pulses of these secondary EODs for use in sexual display. Curtis and Stoddard (2003) found that female *Brachyhypopomus pinnicaudatus* preferred males with longer duration and higher amplitude EODs in mate choice. These traits correlate with male body size and success in encounters with other males. They suggest that these secondary EOD elements that evolved to enhance crypsis to predators have been co-opted by females for assessment of male quality.

Many moths have independently evolved ears on various parts of their body to respond to ultrasonic pulses of predatory bats. In many groups, this is associated with the evolution of ultrasonic clicks and other calls by both sexes. These calls may have initially functioned to jam bat signals (Fullard *et al.*, 1994) or warn bats about the distastefulness of the signaling moth (Hristov and Conner, 2005). Quite remarkably, a wide variety of sound production mechanisms have independently evolved in different groups of moths (Connor, 1999), and in many cases these have resulted in a series of co-options resulting in the use of male ultrasonic signals in mate choice.

Wax moth, *Achroia grisella* (Pyralidae), males call continuously near the wax combs of honeybees (Greenfield and Colfelt, 1983; Snedden *et al.*, 1994). Although males simultaneously release a sex pheromone (Dahm *et al.*, 1971), the ultrasonic acoustic signal alone appears critical for the female approach to the male (Jia and Greenfield, 1997; Spangler, 1984; Spangler *et al.*, 1984). Jang and Greenfield (1996) found that females more often approach synthetic calls with high pulse amplitude, pulse duration, pulse repetition rate, and pulse asynchrony, providing strong evidence that these ultrasonic calls are important in mate choice. In the rice moth *Corcoran cephalonica*, these ultrasonic calls attract virgin females. Jang (1997) showed that females prefer males who produce calls with high levels of acoustic energy and/or asynchrony.

Noctuid moth *Hecatesia exultans* males perch in vegetation producing high rates of chirp calls. Male–male agonistic interactions involve ultrasonic calls and calling males increase chirp duration in response to conspecifics (Alcock and Bailey, 1995). These calls function in mate attraction as females approach calling males on their lek and solicit copulations. Alcock and Bailey (1995) suggest that females may be choosing among the lekking males who have proven their quality through aggressive interactions with other males. It remains unclear to what extent females use differences in male chirps in mate choice (Alcock *et al.*, 1989; Surlykke and Fullard, 1989). The noctuid *Amyna natalis* also displays on well-exposed vegetation and makes a buzzing call by twisting its vertically held wings at a high frequency which activates a thinly scaled forewing "tymbal." Sound production in this species may be associated with the release of a pheromone from putative scent-disseminating structures on the underside of the forewing tymbal (Heller and Achmann, 1993). These studies suggest that ultrasonic calls that have evolved to confuse, or signal distaste fitness to bats have gained a secondary function in mate choice.

C. Co-option of Morphological Traits

Many morphological traits appear to be co-opted for mate choice. Often these traits are co-opted from aggressive display (Beebe, 1929; Berglund *et al.*, 1996). Deer antlers and similar weapons of antelope clearly evolved for aggressive functions (Clutton-Brock *et al.*, 1982; Darwin, 1871), and several authors suggest an additional role in mate choice (Barrette and Vandal, 1986, 1990; Geist, 1971; Lincoln, 1994; Markusson and Folstad, 1997). Ditchkoff *et al.* (2001) have related enhanced antler size to the expression of a particular major histocompatability (MHC) genotype and resistance against parasites, indicating that females may use antler size as a good genes indicator.

Sivinski (1997) in his review of dipteran ornamentation says, "Ornaments that appear to be used in aggressive interactions with members of the same sex seem to be concentrated on the head. Since the head is often used in the pushing style of confrontation and combat typical of Diptera, such elaborations are probably embellishments of weapons or advertisements of size and the ability to use weapons. They may then take on a presumably secondary function by advertising sexual competitiveness to potential mates (e.g., stalk-eyes)." Male Diopsid flies have eyes on the end of long stalks sometimes with eyespans wider than their body length. These structures are sexually dimorphic and function in male–male aggression (Panhuis and Wilkinson, 1999) and allow males to assess size directly and the fighting ability of rivals. In highly dimorphic species, females use male eyespan in mate selection (Panhuis and Wilkinson, 1999). In root aggregating Malaysian flies, those that defend large groups of females have larger eyestalks (Wilkinson and Dodson, 1997). This suggests that male–male aggression associated with female control has had a key role in driving eyestalk elaboration and that female use of male eyespan in mate choice may be secondarily evolved in these species.

Male fiddler crabs have an asymmetrically enlarged claw that may account for half of their mass. Co-option has clearly reshaped the use of these claws from an initial feeding function (still retained by the males' minor and females' claws) to an enlarged and robust design for male–male combat associated with burrow acquisition and defense (Hyatt and Salmon, 1978; Jennions and Backwell, 1996). Studies show that male major claw waving rates increase sharply when females are present (Pope, 2000), suggesting that waving functions primarily in mate attraction. Females do not discriminate in favor of males with more robust nonregenerated claws but these males win fights against males with narrower regenerated claws (Backwell *et al.*, 2000), suggesting that the robustness of claws is primarily associated with their fighting function. It remains to be resolved whether the initial cause of claw enlargement was for fighting ability or for mate attracting through waving, but what is clear is that there have been successive co-options of the major claw for its ultimate use in sexual combat and sexual display.

Combs in male junglefowl are used as signals of dominance status and are also used by females in mate choice (Ligon and Zwartjes, 1995; Zuk *et al.*, 1990). Parker and Ligon (2002) showed that the comb size in male junglefowl is a dominance indicator that is suppressed when subordinate males are in the presence of more dominant males. Female fowl generally prefer dominant males (Leonard and Zanette, 1998). A likely hypothesis consistent with the occurrence of small combs in females is that comb size originally functioned as a signal of dominance that was co-opted for use in mate choice.

D. Co-option of Visual and Chemical Traits

Similar kinds of bioluminescent signals are used in fireflies and ostracode crustaceans (Herring, 2000) and appear to have been co-opted for use in sexual display. Branham and Wenzel (2000) argue that bioluminescence in the beetle family Lampyridae and close relatives originally functioned as an aposematic warning in larvae and was later co-opted for this same function in adults (see also Sivinski, 1981). Only larvae are bioluminescent in the basal-most luminous taxon, and they have only laterally located light organs that are used for signaling their unpalatability to predators. Adults in more derived species have lateral and ventral organs and use the latter for sexual signals and have also developed the capability of pulsing these signals (Ghiradella, 1998). The relatively late use of this historically old trait in sexual display suggests that it was co-opted for that function. Flash patterns differ among firefly species, and sexually ready females respond to conspecifics suggesting that flashes function in species recognition (Lloyd, 1971). Also, female *Photinus* fireflies discriminate among conspecific males (Branham and Greenfield, 1996) based on flash intensity (Vencl and Carlson, 1998) and duration (Cratsley and Lewis, 2003; Lewis *et al.*, 2004a). Flash characteristics are good predictors of spermatophore mass (Lewis *et al.*, 2004b), suggesting that females may benefit from using these signals in assessing males. Although different aspects of ventral male flashes are associated with species recognition and courtship, the dual use of the ventral light organ suggests that one function was co-opted from the other. Fireflies present a particularly interesting but not unique case in which there appears to have been multiple successive co-options, first the co-option of bioluminescence from larval predator defense displays, then use in predator defense in later life-history stages, and then use of this trait for producing ventral light organs for sexual display, and then possibly co-option of this species recognition signal for use in mate assessment.

Like the fireflies, the Caribbean ostracode *Vargulae* uses bioluminescence both in defense and sexual signaling (Morin, 1986). When attacked, the ostracode squirts a pulse of luminescent fluid from its upper lip into the water as antipredatory behavior. The same pulsing system is used by males signaling to sexually receptive females. A phylogenetic analysis of the ostracodes (Cohen and Morin, 2003) suggests that, like fireflies, the evolution of bioluminescence as a defensive signal preceded its use in sexual display function. This is consistent with the hypothesis that bioluminescence which was used first as an antipredator adaptation has been co-opted for sexual display. It is unresolved whether these sexual signals are used by females to assess male quality.

Co-option is extremely common at the molecular level and is increasingly important in understanding the evolution of new genes and gene families (Holland *et al.*, 1994). Like sexual signaling, the evolution of the unique firefly bioluminescence enzyme luciferase appears to be the product of co-option. Day *et al.* (2004) report that this is a bifunctional enzyme catalyzing light emission and functioning as a fatty acid CoA ligase. They suggest that the light-emitting function was initially a side effect that was co-opted for display. Other unrelated nonbioluminescent beetles have the ability to support luciferin-dependent bioluminescence, indicating that this capability is not unique to the Lampyridae and preceded the evolution of bioluminescent organs, which appear to be co-opted from fat storage organs.

Volatile olfactory signals are used in many aspects of animal communication such as scent marking and mate assessment (Blaustein *et al.*, 1993; Zala *et al.*, 2004). Sweat, urine, and dung commonly contain many biochemical by-products that can potentially reveal the condition and other aspects of the physiological state (Gosling and Roberts, 2001; Zala *et al.*, 2004) and genetic characteristics of individuals. These may be viewed as preexisting traits that have been co-opted as indicators of male condition or health by male opponents and are used by females for assessing male quality (Isvaran, 2004). Where these odorants have taken on important functions in social interactions and their production has positive benefits for at least some individuals producing them, there may be selection for increased production to better advertise these traits. Specialized structures, such as scent glands, probably evolved to enhance and control the production of particular components of sweat apart from the normal physiological functions associated with sweating. It is possible that scent glands may have first functioned as part of a territory marking system used to communicate with other males and females, and were then co-opted for assessment by females, although the reverse pattern of co-option could have also occurred.

Chemical cues associated with the MHC loci in sticklebacks are used in mate choice (Reusch *et al.*, 2000). MHC odorants may have been released as by-products across permeable membranes into the water, and females began to use these odorants as effective cues in mate choice (Haberli and Aeschlimann, 2004), preferring more genetically diverse males. Singer *et al.* (1997) claim that co-option may be common in the evolution of chemical signals used in mate choice, "Organisms as diverse as marine invertebrates and mice and humans may have seized these serendipitously available volatile signals of individual identity [MHC] to identify appropriate mates, thereby avoiding inbreeding, or to recognize siblings, parents, or offspring." Extending Singer *et al.*'s argument, MHC by-products may have started as a mechanism for inbreeding avoidance and then generalized to allow selection of mates that contribute toward more disease-resistant MHC genotypes (see Penn and Potts, 1999). In less viscous populations, selection for discrimination among male MHC by-products may have been more direct without first involving inbreeding avoidance.

E. Co-option of Vocal Displays and Display Mechanisms

Searcy and Andersson (1986) point out that the songs of birds, frogs, and insects, although acoustically very different, have important functional similarities. The origins of these songs represent independent evolutionary events in each of these groups with multiple independent origins occurring among the insects, for example, *Drosophila*, Caribbean fruit flies, Orthoptera, cicadas, moths, and beetles. In many cases, these signals have dual uses in female choice and male contests (see also Brenowitz and Beecher, 2005; Nowicki and Searcy, 2004) and use the same anatomical and neurological mechanisms. The commonness of these dual use vocal displays suggests widespread co-option, but it is unclear which function occurred first. In birds, Beecher and Brenowitz (2005) claim that small repertoires are associated with male territorial contests and large song repertoires are more often associated with female choice. The more widespread occurrence of small repertoires in birds suggests a possible origin for song learning associated with territoriality and then a later co-option of the song mechanism for use in sexual display, but this is far from conclusive. What may be overlooked in these discussions is that females may use male calls for locating males and for assessing male quality. Female use of male calls to locate males seems a less demanding task than assessing male quality. So the initial function of these calls may have been advertisement in which females already recognized males and then, secondarily, females used differences in this preexisting male trait for mate assessment.

The use of learned song by passerine birds provides a mechanism particularly susceptible to co-option. The vocal systems of passerine birds are built for young birds to learn songs from tutors on the same or nearby territory, which they will use for their lifetime (Marler and Peters, 1981, 1982, 1987, 1988; Nelson, 1992; O'Loghlen and Beecher, 1997). Some species have a more open-ended ability to learn songs (Nottebohm and Nottebohm, 1978) which may be particularly suited for the co-option of calls from other species through mimicry. Males of many species mimic song elements from other species (Baylis, 1982; Dobkin, 1979; Harcus, 1977; Hindmarsh, 1986; Robinson and Curtis, 1996) or sounds used in other contexts (Bostwick, 2000). Several experimental studies provide direct evidence that avian vocal mimicry is learned (Payne *et al.*, 1998; Pepperberg *et al.*, 1998) and mimicry is commonly used in mate attraction.

There is strong evidence for co-option for the "skraa" calls of bowerbirds (Borgia and Coleman, 2000), which are used in aggressive displays across the bowerbirds and are also used in the courtship displays of some species. The high level of similarity of skraa calls used in courtship and aggressive display suggests that one was co-opted from the other. Mapping of these calls onto a molecular phylogeny of the bowerbirds shows the more limited distribution of skraa calls used in courtship which first occurred in the lineage leading to the *Chlamydera* bowerbirds in which all five species are the only bowerbirds to use these calls in courtship. This more restricted distribution as a courtship display element suggests that skraa calls were first used in aggressive display and that there was a later co-option event before the diversification of the *Chlamydera* bowerbirds. This scenario is consistent with predictions of the war propaganda version of the preexisting traits model.

Sexual selection models differ in their suitability in explaining learned mimicry. Because runaway (Lande, 1981; Mead and Arnold, 2004) and some versions of good genes (Eshel *et al.*, 2000; Iwasa *et al.*, 1991; Kokko *et al.*, 2002) depend on genetic correlations between male traits and female preferences, they are not well suited to explain learned displays where the particular form of the display is important in mate choice. Preexisting female preferences (Burley, 1985) and related models (e.g., sensory exploitation, Ryan and Rand, 1990; or sensory drive, Endler and Basolo, 1998) assume genetically determined female preferences that are side effects of selection for other traits. Searcy (1992) suggested that the evolution of starling calls was driven by preexisting female preferences for complex calls, but this was not supported in a phylogenetic analysis (Gray and Hagelin, 1996). Several studies show that mimicry enhances repertoire size that is used in mate selection by females (Catchpole, 1987; Hasselquist *et al.*, 1996; Howard, 1974; Yasukawa, 1981; but see Forstmeier and Leisler, 2004; Hamao and Eda-Fujiwara, 2004). Females might have preexisting preferences for variable and/or prolonged male song output that would cause them to favor males who enlarge their repertoire by mimicking songs of other species. Alternatively, females might have preexisting preferences that coincidentally favor songs from another species and the males of their species mimic these calls. In either case, females may be able to select for imprecise mimetic songs seen in some species (Dobkin, 1979; Searcy, 1992). Because there is no selection on preexisting preferences to allow preferences to precisely match male calls, they are unlikely to discriminate high-frequency allospecific songs of multiple species mimicked by male bowerbirds (Loffredo and Borgia, 1986b; Coleman *et al.*, submitted for publication), lyrebirds (Robinson and Curtis, 1996), and manakins (Trainer *et al.*, 2002).

Female preferences for precise mimetic songs could evolve for preexisting traits. In satin bowerbirds, Patricelli *et al.* (2002, 2004, 2005) found that the intense and threatening broadband "mechanical" portion of the male courtship song startles females causing rapid movements upward out of a crouching position that may lead to the courted female leaving the bower without copulation. Male satin bowerbirds may have interspersed calming melodic mimetic songs between intense mechanical elements to lower the threat to females during male courtship. The inclusion of this threat reducing mimicry should result in more complete courtships and in more copulations for the displaying male. Mate choice based on mimetic quality may have evolved later as females observing male courtship displays that incorporated mimicry began discriminating in favor of higher quality mimicry because it indicated male quality. Thus, females may have started to use these threat-reducing mimetic display elements for a secondary function as indicators of male quality. Male mimetic abilities, although learned, may indicate heritable differences in neural circuitry that can affect individual survival and serve as an important good genes indicator (Leitner *et al.*, 2001; Nowicki *et al.*, 2000, 2002; Spencer *et al.*, 2003).

F. Preexisting Traits Explain General Indicator Mechanisms

Several modes of display trait evolution that have attracted wide attention in the literature may have evolved as preexisting traits. Developmental stability, measured by fluctuating asymmetry, is suggested to be used by females to assay male genetic quality (Møller, 1988, 1989; Thornhill and Moller, 1998) and has become a controversial topic in sexual selection (Bjorksten *et al.*, 2000; Lens *et al.*, 2002; Markow, 1995; Simmons *et al.*, 1999). Traits measured for symmetry, such as tail feathers, wings, and so on, typically have clear designs for other functions. Swaddle (1999) points out that in initial stages of trait evolution small symmetry differences may be undetectable, lending support to the hypothesis that differences in symmetry are best detected in already large preexisting traits that have been secondarily used (co-opted) by females for assessment of male symmetry. Male barn swallow tail streamers that have been at the center of many discussions of fluctuating asymmetry are known to have an aerodynamic function (Norberg, 1994), and both length and symmetry are used in mate choice (Møller, 1988). Natural tail streamers increase aerodynamic function in barn swallows, and the addition of artificial streamers in the streamerless sand martins also increases their maneuverability. These and later experiments by Evans *et al.* (2004) on barn swallows led them to state "... variation in pre-existing naturally selected traits may provide a starting point for the evolution of ornamental traits." This is probably true for most other traits that are used for symmetry assessment (Møller, 1990) in that it is unlikely that any traits have evolved specifically to exhibit symmetry differences. Among the many traits mentioned including wings, tails, facial structure, breasts, and so on, all have already established functions before they were used for symmetry assessment. As such, symmetry indicating traits used in mate choice are preexisting traits co-opted for a secondary function.

Hamilton and Zuk (1982) suggested that bright plumage or integument color functions as an indicator of parasite resistance with only high-fitness individuals able to make the brightest colors. This hypothesis has received mixed support (Borgia *et al.*, 2004; Hamilton and Poulin, 1997). Plumage and integument color are unlikely to evolve *de novo* as an indicator because incipient colorful male displays are not likely to be sufficiently bright to allow females to effectively identify males with low levels of infection. This may be particularly true if large expensive displays are necessary for indicating differences in male quality (Folstad and Karter, 1992). Alternatively, co-option of these preexisting colorful displays for a secondary indicator function may occur if differences in already existing colorful male plumage or integument displays are coincidentally inversely correlated with parasite infection resistance, as might occur if sickly individuals are unable to make these displays. Bright plumage and integument color are used across a wide variety of species for many different functions, for example, status signaling (Rohwer and Rohwer, 1978), territorial display (Wolfenbarger, 1999), species identification signals (Alatalo *et al.*, 1994), and so on. Females may then evolve to use these already existing traits as indicators of heritable male parasite resistance.

G. Preexisting Traits and Multiple Display Elements

There is growing evidence that multiple display elements are used in mate choice. Most focus on multiple display elements has focused on distinctly different traits used in display such as plumage and behavioral displays. However, studies suggest that multiple components of a single male signal are used in mate choice. For example, Scheuber *et al.* (2004) found that male chirp rate and carrier frequency are important in mate choice by females (Holzer *et al.*, 2003). It seems unlikely that these preferences would evolve simultaneously. A more likely possibility is that females selected for one of these traits, and, while being exposed to males who varied in the other attribute, females who chose on that trait could increase their fitness further. Thus, the complexity of female choice can increase as females utilize (co-opt) additional information from the signals they are already using in mate choice.

H. Timing of Display and Co-option

It is not always clear when in the history of trait elaboration co-option has occurred. A critical issue is to what extent co-opted traits are elaborated before or after co-option. In cases where nests are co-opted for a secondary function, comparisons with related species that do not show evidence of co-option may indicate if the co-opted nest is or is not more elaborate than others. However, as has been suggested for African mouth-breeding cichlids or sticklebacks, there may be enlargement before co-option. If elaboration occurs after co-option (Box I, Model 1), then other mechanisms may be needed to explain elaboration, and it suggests that even less than fully elaborated traits may be effective indicator traits and that co-option may function as a starting point of a coevolutionary process leading to enhancement for an even better indicator function. But if commonly co-opted displays are already in a fully elaborated state (Box I, Model 2), then full elaboration is available for the indicator function and the need for other

BOX I

The Preexisting Trait Model of Sexual Selection: Different Modes of Operation

The co-option of male display traits can occur in many different patterns with respect to when traits are elaborated. Evolution is opportunistic so there are many different ways that co-option can occur. Co-option could occur before or after elaboration and involve nonsexually selected traits or male–male aggressive traits that become preferred by females. It can also allow for selection for good genes or other male attributes.

Model 1: Fisher's Initiator Hypothesis

Naturally selected and relatively unelaborated traits are co-opted by sexual selection and then elaborated. This process was first suggested by Fisher as a possible initiator for the start of the runaway sexual selection model. Because trait elaboration occurs after co-option, it may be mostly coevolutionary. It remains unclear how common this kind of co-option is. Evidence for this kind of evolution might include traits shared among a set of related species that show evidence of co-option but which show different degrees of elaboration resulting from different strengths of female preferences. A possible example is sex combs of *Drosophila* studied by Polak *et al.* (2004) in which they show that in a Queensland, Australia population there is a female preference for enlargement of the second comb; since these combs are widely distributed in *Drosophila*, it appears that this role in mate choice is a secondary function and has driven the enlargement of these combs. Post-co-option enlargement may not be great. For example, Rowe *et al.* (2001) estimate that 9–20% of barn swallow tail streamer length occurs as a result of sexual selection which likely occurred after streamers had evolved for aerodynamic function.

Model 2: Preexisting Trait

Naturally selected and already elaborated traits are co-opted by sexual selection. Traits are already present and indicate differences in male quality. Co-option occurs when females evolve a preference for males showing versions of the trait which indicate that they are a high-quality mate. This should work most easily for traits present where females are being courted, such as at nests or bowers, and where parts of the male phenotype, such as colored plumage, are brought with him to the courtship site.

Model 2a: Aggressive Preexisting Traits

Fully elaborated traits used in male–male competition (or more generally for aggression) are co-opted for female choice. This is the best-described model for the evolution of display, and evidence to support it comes from the very common occurrence of traits of dual function. For example, males on leks may fight for position and females evolve to use aggressive displays in mate choice that occur in conjunction with these fights (Alexander, 1975). What remains unclear is the proportion of cases in which aggressive display was co-opted for courtship display and vice versa. The good genes traits from courtship displays could also be co-opted for signaling in aggressive displays; however, there are several reasons to suspect that the direction of most of these co-options has involved aggressive displays co-opted for courtship. First, the costs of large and otherwise expensive display would be less likely to evolve under female choice because the costs to sons have to be subtracted from the benefits to them of good genes, whereas the benefits from aggression are immediate and can justify a higher cost for aggressive displays. Second, co-opted traits functioning as courtship traits often have the appearance of aggressive displays, for example, broadband vocalizations (Loffredo and Borgia, 1986a), which are not typical of courtship traits that show no evidence of co-option. Third, in one study in which the direction of trait evolution has been tested for the aggressive trait function appears to have occurred first (Borgia and Coleman, 2000). So while the direction of evolution remains to be resolved in most cases, there is suggestive evidence that aggressive traits will more often be co-opted for use in courtship than vice versa.

Model 2b: Nonaggressive Preexisting Traits

Some co-opted traits that indicate male quality did not evolve in the context of aggression. These include morphological, electrical, chemical, or behavioral traits that evolve for a variety of functions such as nests, aerodynamic tail streamers, protective bowers, antipredator signals, or chemical by-products that are co-opted by females to assess male genetic quality. Indicators of male symmetry may commonly evolve from preexisting morphological traits.

sexual selection models to explain elaboration is reduced. While it is clear that co-option contributes importantly toward the use of already enlarged traits as indicators, it remains to be determined what proportion of all elaborated displays involve co-option and what proportion of these are already fully elaborated or have required further elaboration to reach current levels of exaggeration.

VII. Implications and Conclusions

The occurrence of co-option of already elaborated traits for use in sexual display offers to radically change our view of sexual display trait evolution. It raises the possibility that relatively simple co-option models may be sufficient to explain elaborated display traits in many cases rather than more controversial coevolutionary models.

A. Co-option Is a Common Source of Sexual Display Traits

This survey suggests that sexual display traits from a large number of taxa are the products of co-option. Many traits have dual functions commonly with one but not the other involved in mate choice. In some cases, it is clear that the sexual display function is derived, as suggested by the preexisting traits hypothesis, but in others the order of origin of traits is unclear. Phylogenetic mapping can help resolve some of these cases. Also, where co-opted traits are used for sexual display, it is sometimes unclear if these sexual displays function as good genes indicators or for some other function. This will require more detailed studies of how these traits are used in sexual selection. Even with this limited information, the numerous cases of co-option of traits for use as indicators suggest that this is an important mechanism for the evolution of elaborate male traits in sexual display. Development of the preexisting traits model should lead to more detailed studies directed at understanding the role of co-option in shaping good genes indicator displays, indicators of other aspects of male quality, and sexual displays generally.

B. Co-option of Indicator Traits Need Not Be Restricted to Aggressive Displays

The war propaganda/armament–ornament model has been the focus of previous discussions of preexisting traits being co-opted for use as indicator traits. This survey of male display traits indicates that co-option is common and is not restricted to, but certainly includes, aggressive displays. Any trait that shows differences in male performance correlated with male quality that is accessible to females choosing mates can be co-opted to function as a male quality indicator. Thus, differences in preexisting male traits like nests, male acoustic calls, electrical organ discharges, light flashes, plumage colors, symmetry differences can be used by females as indicators of male quality.

C. At What Stage in Male Trait Elaboration Does Co-option Occur?

Co-option can occur early or late in the process of elaboration of traits that evolve indicator functions. An important role for pre-co-option elaboration suggests a dramatic change in how we view sexual selection and provides an interesting solution to some difficult aspects of sexual display trait evolution. If most elaboration occurs pre-co-option, then the processes that build traits before co-option are critical for explaining elaboration. A prominent role for co-option of elaborated naturally selected traits for use in sexual display breaks down the separation of natural and sexual selection as causes of elaborated male displays. With co-option, natural selection is no longer just the brake on display trait evolution as suggested by Lande (1981) but may have a central role in trait evolution. Traits evolved by natural selection (and by male–male sexual competition) may be co-opted because of the evolution of a female preference. Sexual selection can then transform these naturally selected male traits to function as an indicator of male quality. Initial elaboration of male traits could also occur as a result of male–male competition which may also be co-opted to function as indicator traits (Borgia, 1979), suggesting that it will be useful to determine the relative importance of sexual and natural selection in this pre-co-option phase of trait evolution.

Alternatively, if elaboration occurs post-co-option, then other sexual selection processes are needed to explain this additional elaboration. Nonetheless, co-option can account for initiation of these display traits and to the degree that elaboration occurs may help bypass the difficult initial stages of trait evolution associated with other models. Collecting information to resolve the question of when co-option occurs as traits are elaborated is critical to understanding the role of co-option in evolution of elaborated displays.

D. Co-option of Preexisting Traits May Solve the Problem of How Costly Display Traits Evolve

Costly displays are suggested to evolve because they are more resistant to cheating, but in incipient stages in the evolution of these traits, costs are expected to be small and thus ineffective in preventing cheating. Thus, if honesty is dependent on near full elaboration of traits, then costliness of display traits cannot explain why they initially evolve. I argued earlier that cost may not be necessary to insure honest advertising, although under some conditions it may be important as one mechanism for insuring honest advertising. The co-option of already elaborated expensive traits for use as indicators of male quality in sexual display may explain the existence of costly indicator traits. Because their costs are associated with the initial trait function, indicator functions that evolve secondarily may bring no added cost and are thus not limited by this constraint but may benefit from the existing trait cost to limit the ability of other inferior males to cheat. Thus, when traits are already enlarged when co-opted, that trait can take on an indicator function without taking on additional costs and the honesty of the indicator insured by the costs needed to originally develop the trait.

E. How Important Are Currently Popular Mate Choice Models in Display Trait Evolution?

Current reviews assume that genetic correlation-based models are the only means of explaining good genes preferences. As a result, the growing evidence that females choose males for good genes has been taken as support for these genetic correlation-based models. Preexisting traits offer an alternative explanation for the occurrence of good genes selection. Evidence in this review indicating the widespread occurrence of co-option in the evolution of sexual display traits suggests that mating preferences based on genetic correlations may be of limited significance. Preexisting female preferences have been offered as an alternative to genetic correlation-based models. These preferences are suggested to evolve as side effects and are not specifically shaped by selection to enhance the selection of quality mates by females and should only infrequently produce a successful preference. The chances of a preexisting preference becoming successful are greatest for those similar to already functioning preferences. Thus, preexisting preferences at best may cause the evolution of successful mate selection patterns that are not much different from current patterns. They are unlikely to contribute to rapid divergence characteristic of sexual selection because of the limited supply of hidden female preferences established in populations and the likelihood that most present will fail when placed in competition with already selected alternatives. Burley and Symanski's claim (1995) that preexisting preferences may give rise to coevolutionary good genes traits seems improbable because there is no reason to expect that preexisting preferences would be biased toward selecting good genes in males. Preexisting preferences are most consistent with very simple patterns of mate selection and are not suited for explaining complex and highly integrated sets of mating preferences that are now being found.

VIII. Summary

The evolution of highly elaborated male sexual display traits remains an important and controversial issue in evolutionary and behavioral biology. Nearly all discussion of the evolution of these traits has focused on runaway, preexisting preference and coevolutionary good genes models. Here I evaluate each of these models, considering growing empirical support for good genes traits, and analyze the difficulties of currently popular versions of these models that limit their suitability as explanations for the evolution of elaborated male sexual displays. Co-option of preexisting traits provides an important alternative that can explain the evolution of good genes indicator traits with fewer limiting requirements, such as genetic correlations, between male traits and female preferences. The current preexisting trait model focuses on the co-option of aggressive traits for use as good genes indicators. I present a broadened version of this model which considers that females may evolve to use a wide array of preexisting male traits as indicators of differences in male genetic quality. This approach fits with the current trend in evolutionary biology to view co-option as critical in the evolution of many complex traits.

Co-option of preexisting traits emphasizes contributions from both natural and sexual selection in shaping traits used in elaborated male sexual display. This review of elaborated male display traits suggests that co-option of preexisting male traits for mate assessment is very common and has been important in mate choice and the evolution of elaborated male sexual display. The preexisting traits models must be included in any comprehensive discussion of the evolution of elaborated male display traits.

Acknowledgments

Thanks to Leo Borgia, Jane Brockmann, Seth Coleman, Brian Coyle, Jason Keagy, Jan Lauridsen, Carrie Long, Marc Naguib, Todd Oakley, Sheila Reynolds, Peter Slater, Kerry Shaw, and Claus Wedekind for helpful discussions and comments on this chapter. The NSF, Animal Behavior and Systematics Programs (USA), The National Geographic Society, and Universities of Wollongong, Melbourne, and Maryland, and James Cook University have supported this work. The federal and state governments of Australia, Papua New Guinea, and Indonesia have granted me permits and together with local landowners have allowed me access to their lands for which I am grateful. Numerous graduate students, volunteers, collaborators, and other kind individuals have made substantial contributions to this work. My desire to understand why bowerbirds build and decorate bowers inspired this work.

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