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Widespread loss of sexually selected traits: how the peacock lost its spots

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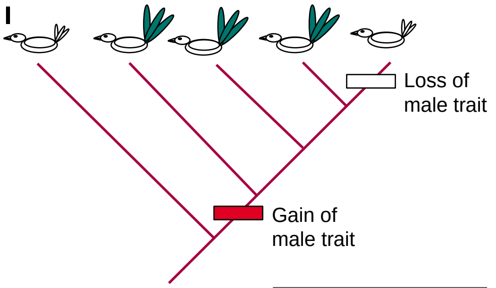
Current and traditional research on sexual selection focuses largely on explaining the evolution (gain) of elaborate male traits and of female preferences for these traits. However, recent phylogenetic studies have revealed a surprising trend: that losses of these elaborate male traits are widespread and can be much more common than are gains. Furthermore, recent studies also show that female preferences for these male traits can be reduced, lost, or even reversed. These losses of traits and preferences could have important implications for competing models of sexual selection. Integrated phylogenetic, experimental and theoretical studies are needed to explain these unexpected patterns.

PHYLOGENIES (see Glossary) are becoming widely used in studies of evolution and ecology. At their most basic level, comparative phylogenetic studies identify many of the evolutionary patterns that theoretical and experimental studies strive to explain. Thus, phylogenies are not only important in helping to provide answers to evolutionary questions, but they are also essential in identifying many of the relevant questions in the first place. An obvious example of the importance of phylogenies is determining the direction of evolutionary change. Given that some species in a group of organisms have a feature of interest and others do not, phylogenies are necessary to establish whether this characteristic has been GAINED, LOST, or both. This fundamental question has received surprisingly little attention from researchers in the field of SEXUAL SELECTION.

Darwin[1] first proposed sexual selection to explain the evolution of the elaborate ornaments and behaviors used by males that are courting or competing for females. In recent decades, sexual selection has become one of the most active and important areas of research in evolutionary biology and behavioral ecology. Most recent studies in sexual selection have used experimental and theoretical approaches to address the origin and elaboration of male TRAITS and, more specifically, why females prefer to mate with males that have these traits[2,3].

Given this traditional emphasis, recent phylogenetic studies have revealed a surprising trend. In many different groups of organisms, the male trait appears to have been lost in some species (Box 1). This trend is surprising for several reasons. First, this pattern was largely (but not entirely) unknown until very recently. For example, Andersson's thorough review[3] of the field of sexual selection does not discuss the loss of male traits. Second, this pattern seems to be extremely widespread (Fig. 1). Not only do losses occur in insects and in all major groups of vertebrates, but, in larger clades, these losses can outnumber gains by 5:1 (Ref. 4). Third, this trend is surprising because the traits that were lost were presumably being actively maintained by sexual selection. These losses imply that other forces are frequently

Box 1. Using phylogenies to reconstruct the loss of sexually selected male traits



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In this hypothetical clade of five bird species (Fig. I), the most parsimonious interpretation is that the male trait has been gained and subsequently lost (rather than being gained multiple times), given the initial assumption that gains and losses are equally probable. Gains and losses can be inferred using LIKELIHOOD (see Box Glossary) methods as well as PARSIMONY[a,b]. In general, losses can be reconstructed with the greatest confidence when character changes are infrequent, and when species that lack the trait are deeply nested among species in which the trait is present.

References

a Pagel, M. (1994) Detecting correlated character evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. London B Biol. Sci.* 255, 37–45
b Schluter, D. *et al.* (1997) Likelihood of ancestor states in adaptive radiation. *Evolution* 51, 1699–1712

Box Glossary

Likelihood: a statistical approach that can be used to estimate ancestral character states and rates of gain and loss using a phylogeny. Likelihood methods incorporate an explicit model of evolution and information on estimated amounts of change (lengths) on each branch of the phylogeny.
Parsimony: a method that can be used to reconstruct character evolution on a phylogeny, assuming a minimal amount of evolution and ignoring information on branch lengths.

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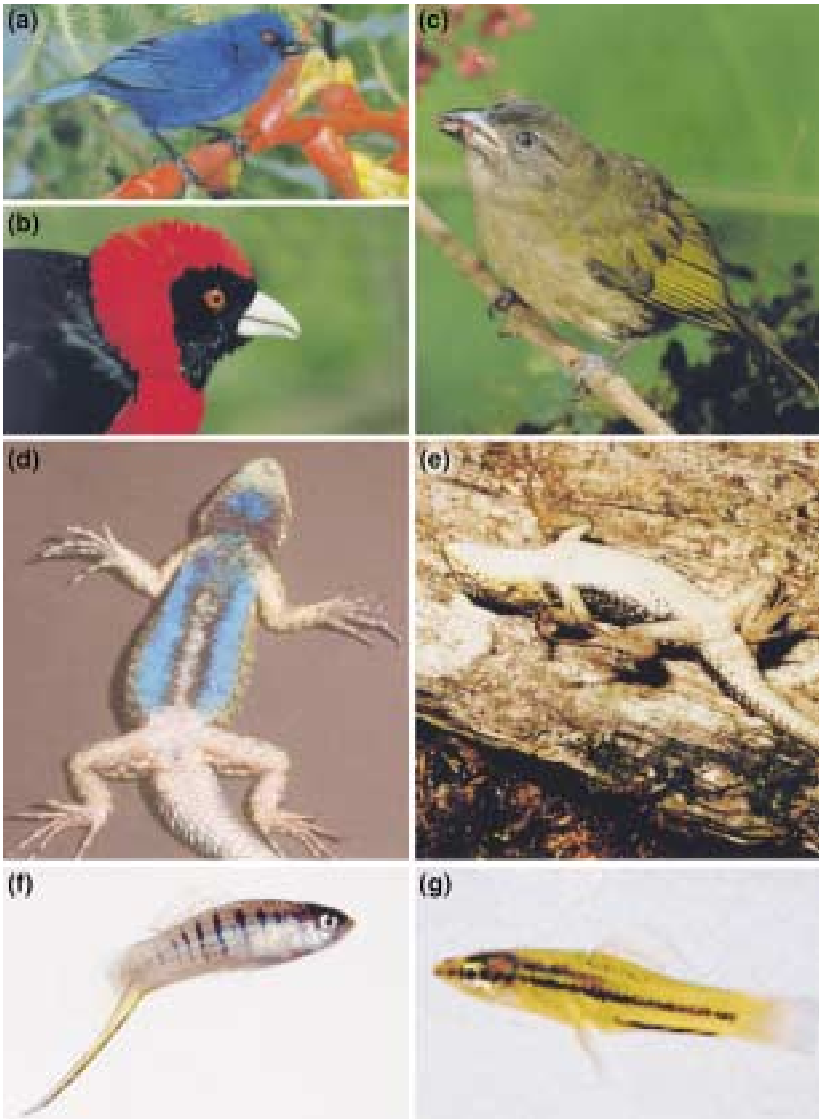


Fig. 1. Representative birds, lizards, and fish from groups showing the loss of sexually selected male traits. Conspicuous plumage coloration in tanagers (Thraupidae) is present in (a) the Indigo Flowerpiercer *Diglossa indigotica* and (b) Crimson-Collared Tanager *Ramphocelus sanguinolentus* and lost in (c) the Ochre-breasted Tanager *Chlorothraupis stolzmanni*. Display patches on the throat and belly in phrynosomatid lizards are present in (d) *Sceloporus taeniocnemis* and lost in (e) *S. siniferus*. Elongate sword and vertical pigment bars in swordtails *Xiphophorus* spp. are present in (f) *X. nezahualcoyotl* and lost in (g) *X. pygmaeus*. Reproduced, with permission, from J. Dunning/VIREO (a), P. Freed/Carnegie Museum of Natural History (b), D. Wechsler/VIREO (c), E. Smith (d,e), and K. de Queiroz (f,g).

able to overcome the power of sexual selection or that sexual selection might become weaker or reverse direction over time, or both. The discovery of this widespread but largely unexplored pattern suggests a new area for comparative, experimental and theoretical investigations within the field of sexual selection.

Here, I summarize the phylogenetic studies that have identified losses of sexually selected traits. I review processes that might account for these losses and discuss the potential significance of reductions in male traits and FEMALE PREFERENCES for competing models of sexual selection. Finally, I outline areas for future research.

Loss of sexually selected male traits

Recent phylogenetic studies show the loss of sexually selected male traits to be taxonomically widespread (Table 1). Furthermore, losses can be considerably more common than are gains in phylogenetic comparisons encompassing large numbers of taxa. For example, in a phylogenetic study of 47 genera of tanagers (Thraupidae), Burns[4] found that transitions involving changes from colorful males to drab males are approximately five times as common as changes from drab to colorful males. There is abundant evidence that conspicuous plumages in birds are important in sexual selection[3]. Among 130 taxa of phrynosomatid lizards, colorful male ventral patches are lost about four times as often as they are gained[5]. Males display these patches during their courtship and aggressive encounters. Water striders (Hemiptera: Gerridae) show a nearly equal gain:loss ratio in the evolution of clasping genitalia on a phylogeny for 141 taxa, but this is largely because the clasping structures seem to be secondarily regained after having been lost – otherwise, there is a single gain and at least eight losses of this trait[6]. In all of these studies, gains and losses were reconstructed using parsimony with the assumption that gains and losses were equally likely to occur. Note that I distinguish between loss of male traits and loss of sexual dimorphism[7,8], because very different processes can be involved in each (Box 2).

The studies of tanagers and lizards, along with a study of plumage evolution in blackbirds (Emberizidae: Icterinae)[9], show another surprising phylogenetic pattern: the same conspicuous traits seen in males are actually gained more frequently in females than in males. Typically, the females gain these ornaments in species in which the male trait is already present so that the species becomes monomorphic for trait presence or degree of elaboration (Box 2). This pattern also appears to be widespread, poorly studied and counter to the current research focus on the gain of male traits and female preferences. These repeated gains of traits in females seem to be related to MALE MATE CHOICE and FEMALE–FEMALE COMPETITION[10].

Why male traits are lost

Why are male traits lost if they are important in sexual selection? Several explanations have been proposed, which are not mutually exclusive, and there seems to be at least circumstantial evidence for all of them. They can be grouped into three types: environmental, social and random.

Environmental factors

Several studies have shown that differences in habitat between populations and species are important in shaping differences in sexually selected traits. There are three obvious ways in which the environment can have its effects: predation risk, signal transmission and nutrient availability. Sexually selected

Table 1. Phylogenetic studies demonstrating loss or reduction of sexually selected male traits

Clade	Male trait lost	Refs
Insects		
Water striders (Hemiptera: Gerridae)	Clasping structures on legs and genitals	6
Stalk-eyed flies (Diptera: Diopsidae)	Exaggerated eye span (reduced)	44
Horned beetles (Coleoptera: Scarabaeidae: Onthophaginae)	Horns	[a]
Fish (teleosts)		
Swordtails and platyfish *Xiphophorus* spp.	Sword (elongate, colored, caudal extension) and vertical pigment bars	18,45
Sticklebacks (Gasterosteidae)	Red nuptial coloration on pelvic spines	46
Amphibians		
Southeast Asian frogs *Rana* spp.	Calling behavior	24
Reptiles (non-avian)		
Lizards (Phrynosomatidae)	Display coloration and display behavior	5,26
Mammals		
Peccaries (Tayassuidae)	Canine size and zygomata width (reduced)	47
Birds		
House finch *Carpodacus mexicanus*	Plumage coloration	15
Birds (43 families, 158 species)	Plumage coloration	27
Flycatchers *Ficedula* spp.	Plumage coloration	22
Tanagers (Thraupidae)	Plumage coloration	4
Peacock pheasants *Polyplectron* spp.	Plumage coloration (eye spots)	48

[a] D. Emlen, pers. commun.

characters can have a significant cost in terms of natural selection, especially because of increased conspicuousness to predators. For example, coloration of male guppies *Poecilia reticulata* varies between streams in relation to predation intensity, and conspicuous coloration is greatly reduced in populations experiencing high predation risks[11]. High predation pressure can also act on females as they are selecting mates, leading to a high cost for choosiness and reduced female preference for male traits[12].

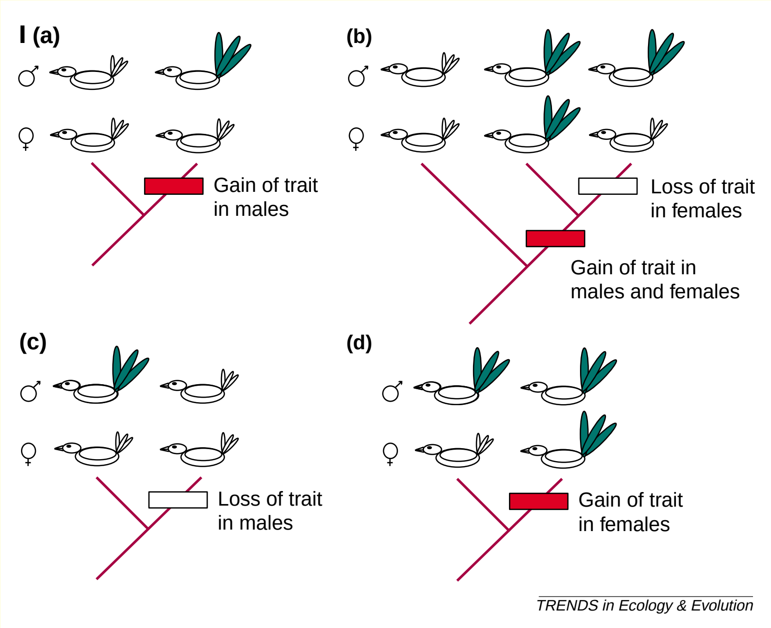
Signal transmission in some habitats might be either so difficult or so easy that display traits become obsolete. For example, red nuptial coloration is lost in some populations of threespine sticklebacks *Gasterosteus aculeatus* seemingly because the dark-stained water in the lakes inhabited by these fish renders the coloration inconspicuous[13]. Similarly, many conspicuous male plumage traits are maintained in some warbler species *Phylloscopus* spp. inhabiting a dark environment, but are lost in warbler species living in brighter environments[14].

Limited availability of nutrients in some environments can also lead to loss of sexually selected traits. For example, conspicuous male ventral coloration seems to be reduced in some populations of house finch *Carpodacus mexicanus*, because of the lower availability of the carotenoid pigments needed to develop this trait[15]. In some environments, developing individuals might simply be unable to afford the added physiological cost of producing display ornaments. For example, dung beetles *Onthophagus acuminatus* will fail to make the typically elongate male horn if reared in an environment with limited food[16].

Social factors

Sexually selected male traits can be involved in FEMALE CHOICE or MALE–MALE COMPETITION. A single trait can serve both functions, and male and female responses to the same trait can be gained and lost independently[17]. Many sexually selected characters are thought to arise and be maintained through female choice[2,3]. For traits to be lost, the strength of female choice must be overcome by random or environmental effects; alternatively, female preferences must be reduced, lost, or reversed (such that female preference favors absence of the male trait), or a combination must occur (i.e. preferences lost and then the trait is lost because of natural selection or drift). Studies of female preference in species (or populations) in which the male trait has been lost show conflicting evidence as to the role of changes in female choice in trait loss. For example, a study involving two closely related species of swordtail fish (*Xiphophorus nigrensis* and *X. pygmaeus*), in which a male trait (vertical pigment bars) had been lost, showed that female preference favored the trait in one species and discriminated against the trait in the other[18].

Box 2. Gains and losses of sexual dimorphism



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Sexual dimorphism (Fig. I) occurs when males and females differ in a given trait. Dimorphism in sexually selected traits usually involves the presence of elaborate traits in males, with the trait poorly developed or absent in females (although the reverse can occur in polyandrous social systems[a]). This type of sexual dimorphism is thought to come about through gain of the trait in males alone (a), or else through gain of the trait in both sexes (because of genetic correlations) with subsequent reduction or loss of the trait in females[b,c] (b). Remarkably few studies have attempted to assess the generality of these hypotheses, and results have so far been mixed[d,e]. Sexual dimorphism is typically lost through either loss of the male trait (c; such that the trait is absent in both sexes) or through gain of the trait in females (d; such that the trait is present in both sexes).

References

a Andersson, M. (1994) *Sexual Selection*, Princeton University Press
b Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon Press
c Lande, R. (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34, 292–307
d Wright, D.B. (1993) Evolution of sexually dimorphic characters in peccaries (Mammalia, Tayassuidae). *Paleobiology* 19, 52–70
e Emerson, S.B. (1994) Testing pattern predictions of sexual selection: a frog example. *Am. Nat.* 143, 848–869

The reduction or loss of female preferences for male traits appears to be widespread, and female preferences seem to be reduced in some groups in which male traits are lost (e.g. swordtails[18,19] and ducks *Anas* spp.[8,20]). There is, however, insufficient data to show that loss of the female preference leads directly to the loss of the male trait in these groups. Correlation between female choice and male trait development has been shown among populations of the guppy, but, in this case, strong predation pressure on conspicuous males might drive the loss of female preference causing a reduction in conspicuous coloration[21].

Recent studies have demonstrated that female choice can actively favor loss or reduction of male traits. For example, Saetre *et al.*[22] showed that when the pied flycatcher *Ficedula hypoleuca* and collared flycatcher *F. albicollis* do not overlap geographically (i.e. are allopatric), females of each species prefer conspecific males with conspicuous black and white coloration. However, where the two species do overlap (i.e. are sympatric), *F. hypoleuca* females prefer males with inconspicuous coloration. This reversal of preference in *F. hypoleuca* females reduces the frequency of heterospecific matings. Similarly, a study of swordtails suggests that female preference for absence of male bars in *X. pygmaeus* evolves because of sympatry with another species, *X. cortezi*, which has the bars[18]. In an island population of the house sparrow *Passer domesticus*, females prefer males with a small ornamental patch[23]. In other populations, females either prefer large patches or have no preference for patch size. Differences in female preference and patch size between populations might reflect differences in male hormone levels and in different female priorities for different male services (i.e. high testosterone leads to a large patch, good nest site and bad parental care, whereas low testosterone leads to a small patch, bad nest site and good parental care). The loss of male calling behavior in Asian frogs *Rana* spp. also seems to be associated with evolution of male parental care and a reduction in testosterone level[24].

Although male–male competition has not been as widely discussed as female choice, it might also be very important in the gain and loss of sexually selected traits. Males of some bird species (e.g. the long-tailed finch *Poephila acuticauda*) seem to lose their conspicuous coloration to mimic females and reduce aggressive interactions with other males[25]. The loss of many male display behaviors in horned lizards *Phrynosoma* spp. might be associated with a reduction in male territoriality[26].

Random factors

Genetic drift is often cited as a possible cause for the loss of male traits, and some support for this comes from the observation that losses of conspicuous plumage coloration in birds occur frequently in small populations on islands (but see review by Peterson[27]). In general, the effects of genetic drift will depend heavily on the effective population size and the countering strength of sexual selection. Under some models, drift might also have random effects on the direction of female choice, possibly causing a change in female preference that favors the loss of the male trait[28].

From a stochastic, macroevolutionary perspective, the many losses of male traits relative to the few gains is not entirely surprising. Given a character that evolves early in a large clade, a higher frequency of losses than of gains of that character should be expected[29]. However, this expectation rests on the assumption that the evolution of the trait is entirely stochastic. If sexual selection is responsible for the origin and maintenance of these traits, then traits should only be lost when other forces (i.e. drift or natural selection) are strong enough to override sexual selection, or when sexual selection is weak.

Implications for models of sexual selection

Much research in sexual selection is concentrated on testing competing models for the origin of female preferences for male traits[2,3]. The surprising patterns of change in traits and preferences revealed by recent studies could have important ramifications for these models. Female preferences appear to have become reduced, lost, or reversed in several different groups, based on phylogenetic studies comparing preferences between species[18,19,22,30] and (more tenuously) studies of single species in which females show no significant preference for the male trait within the range of natural variation[20,31,32]. In all the studies cited, reduction in female preference occurs while the male trait is still present, which suggests that selection against the male trait is unlikely to explain the loss of female preference.

I discuss four models of sexual selection and whether they are consistent with reductions or reversals in female preference and loss of male traits. Note, however, that several factors mentioned previously might cause changes in female preference regardless of how those preferences arose, including high predation pressure on choosy females, effects of habitat on signal transmission, presence of sympatric species, and selection for characters inversely correlated with male trait expression (e.g. parental care).

Runaway model

Under Fisher's runaway model[33], a correlation develops between the expression of the male trait and female preference for that trait. Greater expression leads to greater preference, and the trait exaggerates until it is constrained by natural selection. This model predicts that the male trait and female preference will be tightly co-distributed among species. Thus, a reduction in female preference in species in which the male trait is present (and vice versa) is inconsistent with this model[15]. However, some modifications of the runaway model predict a cyclic gain and loss of female preferences (which could lead to loss of male traits), without changes in environmental selective pressures[34].

Good genes model

Under this model, male traits are reliable indicators of male quality (i.e. healthier males can produce better ornaments), and females that choose to mate with males that have these traits pass these 'good genes' on to their offspring (e.g. genes for parasite resistance[35]). As with the runaway model, the good genes model has generally been used unidirectionally (explaining origin and elaboration only) and predicts tight correlation between the distribution of the trait and preference. However, theoretical studies suggest that if multiple male traits are present, female preferences might switch from traits that are unreliable signals of male quality to traits that are more reliable[36]. Thus, female preferences for unreliable male traits might be lost, followed by a loss of the traits themselves. There is some support for this hypothesis from studies in mallard ducks *Anas platyrhynchos*[20]. Regardless of the specific model of sexual selection, the general idea of switching the focus of female preference from one male trait to another could be very important in explaining the loss of male traits and of female preferences for those traits (Box 3).

Direct selection model and sensory bias

Under this model, the evolution of female preference for the male trait is associated with direct fitness advantages to the female (unlike the runaway and good genes models), for example, when the male trait helps reduce matings with heterospecific or diseased males. Sensory bias has become a prominent

Box 3. Trait switching and loss of female preference

The idea of female preference switching from one male trait to another might be a very important and general explanation for the loss of female preference for male traits. If males have evolved two or more signals, females can theoretically switch their preferences to emphasize one trait over another. Once a trait is no longer preferred by the female, it can be easily lost through natural selection or drift. Switching could occur between two morphological traits, a morphological trait and a behavioral trait, or between visual (morphological, behavioral), acoustic, or chemosensory signals. Why should switching happen? Female choice might favor one signal over another because one signal is a more reliable indicator of male quality or is more appropriate (e.g. conspicuous) for a given habitat[a]. Furthermore, there might be selection on both males (directly) and females (indirectly) to switch to traits that are more energetically efficient (short term), more metabolically efficient (long term, in terms of developmental allocation[b]), and more private (e.g. can be seen by conspecifics but not by predators, such as coloration characters that are only visible when they are actively displayed).

References

a Schluter, D. and Price, T. (1993) Honesty, perception, and population divergence in sexually selected traits. *Proc. R. Soc. London B Biol. Sci.* 253, 117–122

b Basolo, A.L. (1998) Shift in investment between sexually-selected traits: tarnishing of the silver spoon. *Anim. Behav.* 55, 665–671

hypothesis for direct selection on female preferences[2,37]. Under the sensory bias model, the female prefers the male trait because it exploits pre-existing biases in her sensory system (e.g. associated with foraging or predator avoidance) that are under direct selection. The model predicts widespread biases in female sensory systems that drive male traits in a consistent direction – towards greater exaggeration and sensory stimulation[38]. Although many of the predictions of the sensory bias model have been supported by an increasing number of studies (e.g. female preferences evolve before the origin of the male trait[37]), the widespread loss of female preferences and male traits seems inconsistent with this model, unless one postulates that female sensory biases are highly plastic. A reduction or loss of female preferences has been documented in at least two groups, swordtails *Xiphophorus* spp. and wolf spiders *Schizocosa* spp., in which sensory bias is thought to be involved in the origin of the trait and preference.

Chase-away model

The chase-away model was motivated (in part) by studies showing evidence for both sensory bias and loss of female preference for male traits[39]. Under this model, sensory biases of females initially drive males to evolve a trait that increases their attractiveness. This trait not only induces females to mate, but also motivates them to mate in a suboptimal manner (e.g. too early or too often) that decreases their fitness. Females therefore evolve 'resistance' to the male trait, and males exaggerate the trait to overcome this resistance. In some cases, males will be constrained in the exaggeration of their traits, and so females can 'win' this coevolutionary arms race, and will show no response to the male trait. Thus, the chase-away model is consistent with both the initial gain and subsequent loss of female preferences for male traits. However, the model appears to be inconsistent with the frequent loss of male traits, because the authors predict that males must retain even ineffectual traits to reach a minimum threshold of female response[5]. Furthermore, it is unclear what precisely these authors[39] mean by resistance and if the lack of preference shown by females for male traits is actually consistent with this model[40].

Areas for future research

The loss of sexually selected male traits appears to be a widespread evolutionary trend. A variety of environmental, social and random factors can be involved in trait loss, and a combination of factors might be important in any given case. Future studies face the challenge of determining which factors are most important and what general principles govern their action. Answering these questions will require a combination of phylogenetic, experimental and theoretical approaches.

Phylogenetic comparative methods[41–43] can be used to identify correlates of trait loss, and thus infer potential mechanisms. Based on previous studies, losses can be associated with habitat changes (when habitats differ in predation risk, signal transmission properties, or nutrient availability), small population size (genetic drift), presence of male parental care, absence of male territoriality, presence of sympatric species with similar male traits, or exaggeration of other sexually selected male traits (suggesting trait switching).

There is also need for more experimental behavioral studies to be carried out in a phylogenetic context. Studies that document female (and male) responses to male traits across many species, in groups in which the trait is both gained and lost, are particularly needed. Future studies must determine whether a reduction in preference phylogenetically precedes losses of male traits or whether these changes are independent. Preference studies for multiple traits are also needed to determine whether trait switching is involved in the loss of male traits and female preferences.

New theoretical studies of trait and preference loss are also needed. An important problem is explaining the reduction or loss of female preferences in species in which the male trait is still present. The loss of female preferences seems particularly inconsistent with the sensory bias model, and the chase-away model is unique (so far) in that it attempts to reconcile the origin of female preferences by sensory bias with their subsequent loss. However, the chase-away model is controversial, has not been described in explicit mathematical terms, and seems inconsistent with the loss of male traits.

Glossary

Female choice: (or female mate choice) a type of sexual selection in which females mate non-randomly due to female preferences for male traits.
Female–female competition: a type of sexual selection in which females strive against each other for greater reproductive success.
Female preferences: the tendency of females to favor (or disfavor) mating with males that have a given trait.
Gain: the evolutionary origin of a feature (character state), as detected on a phylogenetic tree.
Loss: an evolutionary transformation in which a feature (character state) becomes secondarily absent, as detected on a phylogenetic tree.
Male mate choice: a type of sexual selection in which males mate nonrandomly with females as a result of male preferences for female traits.
Male–male competition: a type of sexual selection in which males strive against each other for greater reproductive success, typically by increasing their access to females.
Phylogeny: a tree indicating the evolutionary relationships among organisms (e.g. species)
Sexual selection: selection for traits that increase the reproductive success of an individual.
Trait: for the purposes of this paper, a feature (e.g. morphological, behavioral, chemical) that evolves (or has evolved) in response to sexual selection.

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Sexual selection has traditionally been a unidirectional field, focusing largely on explaining the origin of male traits and female preferences. Recent studies, summarized here, suggest that losses of male traits are common and that female preferences for these traits can be highly changeable over time. The problem of loss has probably been neglected because losses can only be reliably identified in the context of a phylogeny. This issue demonstrates the potential value of phylogenetic approaches in ecology, behavior and evolutionary biology not only as a tool for answering long-standing questions, but also as a way to identify novel patterns to be explained by process-oriented research.

References

1 Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*, John Murray

2 Kirkpatrick, M. and Ryan, M.J. (1991) The evolution of mating preferences and the paradox of the lek. *Nature* 350, 33–38

3 Andersson, M. (1994) *Sexual Selection*, Princeton University Press

4 Burns, K.J. (1998) A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus male plumage. *Evolution* 52, 1219–1224

5 Wiens, J.J. (1999) Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. *Proc. R. Soc. London B Biol. Sci.* 266, 1529–1535

6 Andersen, N.M. (1997) A phylogenetic analysis of the evolution of sexual dimorphism and mating systems in water striders (Hemiptera: Gerridae). *Biol. J. Linn. Soc.* 61, 345–368

7 Price, T.D. and Birch, G.L. (1996) Repeated evolution of sexual color dimorphism in birds. *Auk* 113, 842–848

8 Omland, K.E. (1997) Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabbling ducks (Anatini). *Evolution* 5, 1636–1646

9 Irwin, R.E. (1994) The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness. *Am. Nat.* 144, 890–907

10 Amundsen, T. (2000) Why are female birds ornamented? *Trends Ecol. Evol.* 151, 149–155

11 Endler, J.A. (1983) Natural selection and sexual selection on color patterns in poeciliid fishes. *Environ. Biol. Fishes* 9, 173–190

12 Forsgren, E. (1992) Predation risk affects mate choice in a gobiid fish. *Am. Nat.* 140, 1041–1049

13 Reimchen, T.E. (1989) Loss of nuptial coloration in threespine sticklebacks (*Gasterosteus aculeatus*). *Evolution* 43, 450–460

14 Marchetti, K. (1993) Dark habitat and bright birds illustrate the role of the environment in species divergence. *Nature* 362, 149–152

15 Hill, G.E. (1994) Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. *Behav. Ecol.* 47, 1515–1525

16 Emlen, D.J. (1994) Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proc. R. Soc. London B Biol. Sci.* 256, 131–136

17 Morris, M.R. and Ryan, M.J. (1996) Sexual differences in signal–receiver coevolution. *Anim. Behav.* 52, 1017–1024

18 Morris, M.R. (1998) Further examination of female preference for vertical bars in swordtails: preference for ‘no bars’ in a species without bars. *J. Fish Biol.* 53, 56–63

19 Basolo, A.L. (1998) Evolutionary change in a receiver bias: a comparison of female preference functions. *Proc. R. Soc. London B Biol. Sci.* 265, 2223–2228

20 Omland, K.E. (1996) Female mallard preferences for multiple male ornaments. I. Natural variation. *Behav. Ecol. Sociobiol.* 39, 353–360

21 Houde, A.E. and Endler, J.A. (1990) Correlated evolution of female mating preferences and male color patterns in the guppy *Poecilia reticulata*. *Science* 248, 1405–1408

22 Saetre, G-P. *et al.* (1997) A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* 387, 589–592

23 Griffith, S.C. *et al.* (1999) Female choice and annual reproductive success favours less–ornamented male house sparrows. *Proc. R. Soc. London B Biol. Sci.* 266, 765–770

24 Emerson, S.B. (1996) Phylogenies and physiological processes – the evolution of sexual dimorphism in southeast Asian frogs. *Syst. Biol.* 45, 278–289

25 Langmore, N.E. and Bennett, A.T.D. (1999) Strategic concealment of sexual identity in an estrildid finch. *Proc. R. Soc. London B Biol. Sci.* 266, 543–550

26 Wiens, J.J. (2000) Decoupled evolution of display morphology and display behaviour in phrynosomatid lizards. *Biol. J. Linn. Soc.* 70, 597–612

27 Peterson, A.T. (1996) Geographic variation in sexual dichromatism in birds. *Bull. Br. Ornithol. Club* 116, 156–172

28 Lande, R. (1981) Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. U. S. A.* 78, 3721–3725

29 Sanderson, M.J. (1993) Reversibility in evolution: a maximum likelihood approach to character gain/loss bias in phylogenies. *Evolution* 47, 236–252

30 McClintock, W.J. and Uetz, G.W. (1996) Female choice and pre-existing bias: visual cues during courtship in two *Schizocosa* wolf spiders (Araneae: Lycosidae). *Anim. Behav.* 52, 167–181

31 Andersson, M. (1982) Female mate choice selects for extreme tail length in a widowbird. *Nature* 299, 818–820

32 Ligon, J.D. and Zwartjes, P.W. (1995) Ornate plumage of male red junglefowl does not influence mate choice by females. *Anim. Behav.* 49, 117–125

33 Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon Press

34 Iwasa, Y. and Pomiankowski, A. (1995) Continual change in mate preferences. *Nature* 377, 420–422

35 Hamilton, W.D. and Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218, 384–387

36 Schluter, D. and Price, T. (1993) Honesty, perception, and population divergence in sexually selected traits. *Proc. R. Soc. London B Biol. Sci.* 253, 117–122

37 Ryan, M.J. (1998) Sexual selection, receiver biases, and the evolution of sex differences. *Science* 281, 1999–2003

38 Ryan, M.J. and Keddy-Hector, A. (1992) Directional patterns of female mate choices and the role of sensory biases. *Am. Nat.* 139, S4–S35

39 Holland, B. and Rice, W.R. (1998) Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* 52, 1–7

40 Rosenthal, G.G. and Servedio, M.R. (1999) Chase-away sexual selection: resistance to ‘resistance’. *Evolution* 53, 296–299

41 Felsenstein, J. (1985) Phylogenies and the comparative method. *Am. Nat.* 125, 1–15

42 Maddison, W.P. (1990) A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* 44, 539–557

43 Pagel, M. (1994) Detecting correlated character evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. London B Biol. Sci.* 255, 37–45

44 Baker, R.H. and Wilkinson, G.S. Phylogenetic analysis of sexual dimorphism and eye stalk allometry in stalk–eyed flies. *Evolution* (in press)

45 Basolo, A.L. (1996) The phylogenetic distribution of a female preference. *Syst. Biol.* 45, 290–307

46 McLennan, D.A. (1996) Integrating phylogenetic and experimental analyses: the evolution of male and female nuptial coloration in the stickleback fishes (Gasterosteidae). *Syst. Biol.* 45, 261–277

47 Wright, D.B. (1993) Evolution of sexually dimorphic characters in peccaries (Mammalia, Tayassuidae). *Paleobiology* 19, 52–70

48 Kimball, R.E. *et al.* A molecular phylogeny of the peacock–pheasants (Galliformes: *Polyplectron* sp.) indicates loss and reduction of ornamental traits and display behaviors. *Biol. J. Linn. Soc.* (in press)