BIOLOGY
LETTERS

royalsocietypublishing.org/journal/rsbl

Opinion piece

Cite this article: Moehring AJ, Boughman JW. 2019 Veiled preferences and cryptic female choice could underlie the origin of novel sexual traits. *Biol. Lett.* **15**: 20180878. http://dx.doi.org/10.1098/rsbl.2018.0878

Received: 10 December 2018
Accepted: 4 February 2019

Subject Areas:
behaviour, evolution

Keywords:
cryptic female choice, novel male mating trait, novel female mate preference, sexual selection

Author for correspondence:
Amanda J. Moehring
e-mail: amoehrin@uwo.ca

THE ROYAL SOCIETY
PUBLISHING

Evolutionary biology

Veiled preferences and cryptic female choice could underlie the origin of novel sexual traits

Amanda J. Moehring[1] and Janette W. Boughman[2]

[1]Department of Biology, Western University, London, ON, Canada N6A 5B7
[2]Ecology, Evolutionary Biology and Behavior Program, Michigan State University, East Lansing, MI 48824, USA

AJM, 0000-0002-8088-4007; JWB, 0000-0002-5731-7389

Males in many species have elaborated sexual traits that females strongly prefer, and these traits often conspicuously differ among species. How novel preferences and traits originate, however, is a challenging evolutionary problem because the initial appearance of only the female preference or only the male trait should reduce the ability to find a suitable mate, which could reduce fitness for individuals possessing those novel alleles. Here, we present a hypothesis for how novel preferences, as well as the novel male traits that females prefer, can originate, be favoured and spread in polyandrous species. Novel preference mutations can arise as 'veiled preferences' that are not expressed when the corresponding male trait is not present in the population, allowing preferences to be hidden from selection, and thus persist. In those cases when a male trait is present, veiled preferences provide a selective advantage, and females disproportionately produce offspring from preferred males through either mate choice or cryptic female choice. This tips the fitness advantage for novel males, allowing both preference and trait to spread, and limiting selection against them in the absence of the corresponding trait or preference.

1. Background

Obtaining reproductive success is a critical component of fitness. In most sexual species, females evaluate male traits and choose to copulate with 'better' males to gain benefits for themselves or their offspring [1–8]. Selection for female choice means that preferences often arise prior to the preferred male traits [1], and sometimes evolve because they are advantageous in a non-mating context [9,10]. However, the preference and the preferred trait often do not provide increased fitness outside of mating, making it unclear how such preferences and traits would initially arise; hence, we focus on these. Female preferences can exert profound selective forces upon male traits, sometimes manifesting as selectivity for male trait values that are more exaggerated than those produced by males in the current population, potentially driving male traits to extremes via Fisherian runaway sexual selection [10–13]. Existing theory provides powerful explanations for the exaggeration and complexity of sexually selected traits.

2. The problem

While selection on preference–trait combinations has been extensively studied, the field has focused on trait and preference exaggeration or on enhancing complexity more than their origin. Cues that evolve outside of mating, such as body size, can be co-opted for mate choice, but we do not address these situations here, instead focusing on the evolution of preferences for novel traits. How novel preference–trait combinations initially arise is still contentious, particularly for novel preference–trait combinations that incur a fitness cost via natural selection. Indeed, the origin of preference is not typically factored into the classic runaway selection models, which assume that preference and preference variation are already present (e.g. [10,14]). Preference–trait origin can be problematic because either the male trait or the female preference alone could initially be disadvantageous owing to natural selection, or owing to lack of desired mates and the associated cost of going unmated. Further, when present at low frequencies, preference would not exert a significant sexual selection force [15] hindering the spread of the preferred trait. How do novel preference–trait combinations initially arise and overcome selection against them?

The presence of novel preferences for non-existent male traits has been observed in a range of species, including in birds for males with white crests [16], and in grasshoppers for particular complexities of courtship song [17]. A previously proposed mechanism whereby novel preference–trait combinations could arise is sensory bias. This hypothesis proposes that female sensory systems evolve a heightened response to stimuli that provide non-mating fitness advantages, such as attraction to food coloration, and that males subsequently evolve mating traits that exploit this bias [9,10]. Although sensory bias is clearly a powerful mechanism [8], it cannot explain the origin of all preference–trait combinations [18,19]. In particular, preference based on sensory bias may be difficult to evolve if females pay costs for responding to exploitative male signals (e.g. dishonest signals leading to females choosing inferior males or paying costs for choice). Under sensory bias, sensory tuning evolves outside of mating, but females gain no mating benefit from responding to exploitative males. Therefore, mating costs would select females to ignore exploitative traits or evolve counter measures, thus limiting the pervasiveness of sensory drive [20]. An example of this is shown in jumping spider preference for complex seismic signals in foreign males that might have evolved to overcome exploitation by local males [21].

3. Our solution

Here we describe a mechanism by which novel female preferences arise first as 'veiled preferences' that allow them to spread throughout a population without a fitness cost. These veiled preferences exist in a population but are not expressed because the preferred trait has not yet evolved, and the preference is thus 'veiled' from the action of selection. The veiled preference mechanism may be especially likely when females exert choice after copulating (cryptic female choice), or when there is a relative choice threshold (best-of-*n*) [22] because both of these mechanisms ensure females do not go unmated.

The veiled preference hypothesis does not rely on sensory evolution or sensory bias and thus can explain the origin of novel preferences for cases where sensory evolution does not apply. Unlike sensory bias models, in this scenario, the neurological or physiological basis of preference does not have to be associated with a fitness advantage via natural selection in a non-mating context. In addition, the neutrality of novel preferences and traits is assumed in some versions of Fisherian models, and veiled preference provides a mechanism by which novel preferences and traits could be neutral. This hypothesis is therefore related to classic neutral theory and more recent ideas regarding randomly occurring mutations affecting the evolutionary divergence of mating traits [23]. Although that research has assumed neutral preference and/or male trait, rarely have studies asked why or how such preferences and traits can actually be neutral, which is a primary focus of the veiled preference hypothesis.

As a hypothetical example, imagine a mutation arises that causes preference for males with orange feathers, and males with orange feathers confer a selective advantage to females and/or their offspring. However, all males currently have blue feathers (figure 1). While a female that has the orange preference mutation views all blue males as non-preferred, she will mate and use their sperm for fertilization in the absence of preferred (novel trait) males. A mutation then occurs that produces orange feathers. Males with the orange feather mutation will have a distinct advantage with any females who possess a preference for orange coloration, and father a disproportionate number of their offspring. If the female preference allele is at high frequency, orange feathered males would have high reproductive success, causing the orange feather mutation to spread. Non-random mating will likely generate a genetic correlation between trait and preference, causing the orange preference allele to increase in frequency through indirect selection [11,24]. The preference can be for a novel phenotype, such as the orange feathers we described above, or for an entirely novel structural trait, such as the presence of a head crest.

Veiled preferences are especially likely if females accept matings with non-preferred males when no preferred males are present, particularly in instances where females exert post-copulatory selection via cryptic female choice [25–27]. In this way, they ensure reproduction while exhibiting choice. In most species, females mate multiply (are polyandrous) and selectively mate with males of higher quality [28]. But there have been many documented cases where females will mate with non-preferred males when preferred males are not present [29,30], sometimes even with males of another species [31,32]. This strategy of low selectivity in no-choice situations prevents females from producing no offspring and having zero fitness. Cryptic choice then allows females to produce offspring with preferred sperm and realize the benefits those males provide.

The preferential production of orange-coloured offspring (figure 1) could act in several ways before or during copulation, such as via a female's overt preference for the trait, using a choice rule such as best-of-*n*, or by increasing latency until subsequent mating. However, in these cases, the preferred male's fertilization success could still be limited by the presence of sperm from other males. Thus, the most potent selective force would be through post-copulatory sexual selection, whereby a female exerts cryptic choice and disproportionately uses the sperm from the preferred male [32–34]. Females achieve cryptic choice through a variety of mechanisms, including by altering copulation duration and sperm transfer, ejecting sperm of non-preferred males and selective use of sperm of the preferred male to fertilize eggs [32,34,35]. Cryptic female choice would cause a preferred male to obtain a disproportionate share of offspring, further enhancing the spread of the male trait even after females have mated with non-preferred males.

4. Conditions that facilitate the evolution of novel mating traits by veiled preference

While the majority of veiled preference alleles that arise may be lost or remain unmatched by male traits, those rare cases where

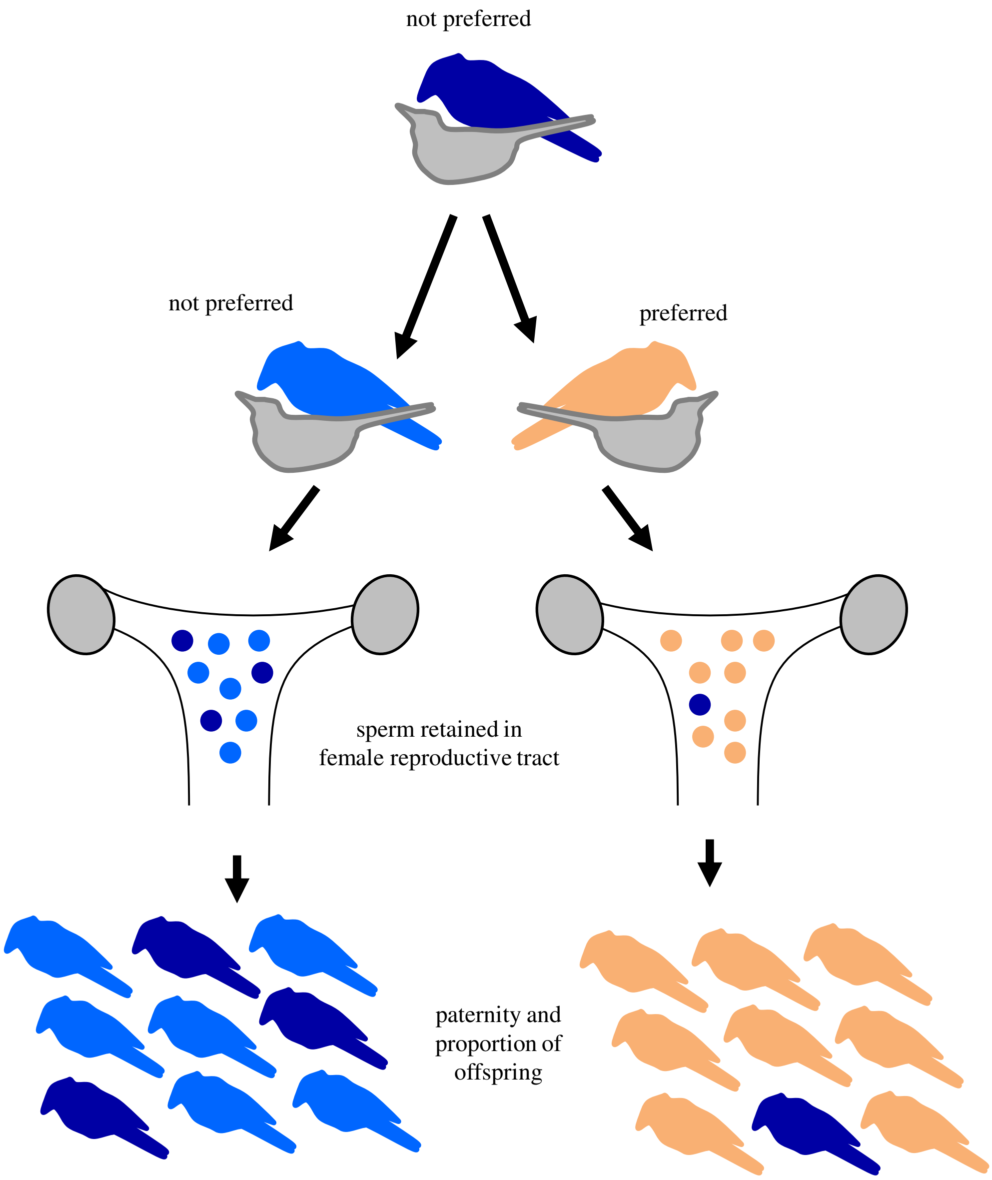

Figure 1. Illustrative example of how veiled preferences can persist in a population, and later lead to selection for novel male traits. When females mate multiply, cryptic choice favours sperm from orange mates (right side of figure), leading to a disproportionate frequency of orange alleles in offspring. This does not occur when mating with multiple non-preferred mates (left). (Online version in colour.)

a novel preference–trait combination is formed are those likely to be observed in nature. Veiled preferences are most likely to evolve for traits that are correlated with genetic or direct benefits. Because the first males to display the novel preferred trait only benefit from enhanced fertilization success with females possessing novel preference alleles, the preference alleles either need to be at a high enough frequency to offset the cost of trait production or the cost for producing the trait must be negligible for males. Additionally, when first expressed, the novel preference cannot be so strong as to prevent mating with non-preferred males; otherwise, females with this preference will forgo matings because males with the novel, newly preferred trait are rare. Avoiding the cost of going unmated is a key reason why we invoke best-of-*n* rules and/or cryptic choice. Costs of trait production are likely to trade off with veiled preference frequency, and for our mechanism to work, these must offset one another. Moreover, the magnitude of the benefit that females gain from choosing novel males will impact how rapidly the preference–trait combination spreads after both arise, as it affects offspring fitness and thus allele prevalence [23].

In addition, there are facilitating genetic conditions. The effects of genetic drift can be appreciable because the novel preference is likely to be effectively neutral in the absence of the preferred trait. Drift could facilitate the increase of novel preferences, especially in small or isolated populations, founder events, population bottlenecks, peripatric populations and the edges of species ranges [36]. Although ideas from neutral theory have permeated much of evolutionary biology, and classic Fisherian sexual selection theory allows for neutral traits before trait elaboration ensues, to our knowledge, the biological mechanisms that make such preferences and male traits neutral and thus allow their further elaboration have been rarely explored [23]. This is central to the veiled preference hypothesis. Linkage between the novel veiled preference and an adaptive trait would also facilitate the process, allowing the preference allele to hitchhike with the adaptive trait and thus increase in frequency. Pleiotropy between the novel preference and an adaptive trait could be especially effective because pleiotropy circumvents the problem of recombination faced with mere linkage [37,38]. By our conceptual model, increased prevalence of the veiled preference would permit a greater range of corresponding male traits, including those that have a relatively high fitness cost, and the resulting coevolution would likely increase the frequency of the preference–trait combination.

5. Conclusion

Here, we present a hypothetical model by which novel female preferences may first arise and spread as veiled preferences. This is facilitated by a female's willingness to mate with non-preferred males in the absence of preferred males. The veiled preferences will have the greatest effect when exerted as a cryptic female choice, by reducing fitness costs when mated to non-preferred males. Skewed production of preferred male offspring when mated to a preferred male can allow both veiled preferences and preferred male traits to spread through a population. There are shockingly few papers that explore both novel preferences and male traits along with cryptic female choice. Thus, there are too little data currently available for us to evaluate whether this mechanism could be prevalent or rare. We encourage more attention to these questions.

Data accessibility. This article has no additional data.

Authors' contributions. A.J.M. had the inspiration for this idea and drafted the manuscript. J.W.B. contributed to ideas and writing.

Competing interests. The authors declare they have no competing interests.

Funding. This work was supported by a Canada Research Chair to A.J.M. and an NSF Dimensions grant to J.W.B.

Acknowledgements. The ideas for this paper were developed at a Gordon Research Conference on Speciation in 2015.

References

1. Andersson M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
2. Fisher RA. 1930 *The genetical theory of natural selection*. Oxford, UK: Clarendon Press.
3. Zahavi A. 1975 Mate selection—a selection for a handicap. *J. Theor. Biol.* **53**, 205–214. (doi:10.1016/0022-5193(75)90111-3)
4. Hamilton WD, Zuk M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387. (doi:10.1126/science.7123238)
5. Price T, Schluter D, Heckman N. 1993 Sexual selection when the female directly benefits. *Biol. J. Linn. Soc.* **48**, 187–211. (doi:10.1111/j.1095-8312.1993.tb00887.x)
6. Welch AM, Semlitsch RD, Gerhardt HC. 1998 Call duration as an indicator of genetic quality in male gray tree frogs. *Science* **280**, 1928–1930. (doi:10.1126/science.280.5371.1928)
7. Houle D, Kondrashov AS. 2002 Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. R. Soc. Lond. B* **269**, 97–104. (doi:10.1098/rspb.2001.1823)
8. Neff BD, Pitcher TE. 2005 Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. *Mol. Ecol.* **14**, 19–38. (doi:10.1111/j.1365-294X.2004.02395.x)
9. Rodd FH, Hughes KA, Grether GF, Baril CT. 2002 A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proc. R. Soc. Lond. B* **7**, 475–481. (doi:10.1098/rspb.2001.1891)
10. Ryan MJ, Fox JH, Wilczynski W, Rand AS. 1990 Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* **343**, 66–67. (doi:10.1038/343066a0)
11. Lande R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725. (doi:10.1073/pnas.78.6.3721)
12. Andersson M. 1982 Female choice selects for extreme tail length in a widowbird. *Nature* **299**, 818–820. (doi:10.1038/299818a0)
13. Weary DM, Guilford TC, Weisman RG. 1993 A product of discrimination learning may lead to female preferences for elaborate males. *Evolution* **47**, 333–336. (doi:10.1111/j.1558-5646.1993.tb01225.x)
14. Lande R, Arnold SJ. 1985 Evolution of mating preferences and sexual dimorphism. *J. Theor. Biol.* **117**, 651–664. (doi:10.1016/S0022-5193(85)80245-9)
15. Arnold SJ. 1987 The consequences: sexual selection. In *The evolution of sex and its consequences* (ed. SC Stearns). Basel, Switzerland: Springer.
16. Burley NT, Symanski R. 1998 A taste for the beautiful: latent aesthetic mate preferences for white crests in two species of Australian grassfinches. *Am. Nat.* **152**, 792–802. (doi:10.1086/286209)
17. Reichert MS, Finck J, Ronacher B. 2017 Exploring the hidden landscape of female preferences for complex signals. *Evolution* **71**, 1009–1024. (doi:10.1111/evo.13202)
18. Fuller RC. 2009 A test of the critical assumption of the sensory bias model for the evolution of female mating preference using neural networks. *Evolution* **63**, 1697–1711. (doi:10.1111/j.1558-5646.2009.00659.x)
19. Frame AM, Servedio MR. 2012 The evolution of preference strength under sensory bias: a role for indirect selection? *Ecol. Evol.* **2**, 1572–1583. (doi:10.1002/ece3.273)
20. Fuller RC, Houle D, Travis J. 2005 Sensory bias as an explanation for the evolution of mate preferences. *Am. Nat.* **166**, 437–446. (doi:10.1086/444443)
21. Elias DO, Hebets EA, Hey RR. 2006 Female preference for complex/novel signals in a spider. *Behav. Ecol.* **17**, 765–771. (doi:10.1093/beheco/arl005)
22. Janetos AC. 1980 Strategies of female mate choice: a theoretical analysis. *Behav. Ecol. Sociobiol.* **7**, 107. (doi:10.1007/BF00299515)
23. Mendelson TC, Martin MD, Flaxman SM. 2014 Mutation-order sexual selection: diversification of sexual signals in similar environments as a first step in speciation. *Ecol. Lett.* **17**, 1053–1066. (doi:10.1111/ele.12313)
24. Kirkpatrick M, Barton NH. 1997 The strength of indirect selection on female mating preferences. *Proc. Natl Acad. Sci. USA* **94**, 1282–1286. (doi:10.1073/pnas.94.4.1282)
25. Parker GA. 1970 Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* **45**, 525–567. (doi:10.1111/j.1469-185X.1970.tb01176.x)
26. Eberhard WG. 1996 *Female control: sexual selection by cryptic female choice*. Princeton, NJ: Princeton University Press.
27. Firman RC, Gasparini C, Manier MK, Pizzari T. 2017 Postmating female control: 20 years of cryptic female choice. *Trends Ecol. Evol.* **32**, 368–382. (doi:10.1016/j.tree.2017.02.010)
28. Slatyer RA, Mautz BS, Backwell PRY, Jennions MD. 2011 Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biol. Rev.* **87**, 1–33. (doi:10.1111/j.1469-185X.2011.00182.x)
29. Bakker TCM, Milinski M. 1991 Sequential female choice and the previous male effect in bushcrickets. *Behav. Ecol. Sociobiol.* **29**, 205–210. (doi:10.1007/BF00166402)
30. Tinghitella RM, Weigel EG, Head M, Boughman JW. 2013 Flexible mate choice when mates are rare and time is short. *Ecol. Evol.* **3**, 2820–2831. (doi:10.1002/ece3.666)
31. Cramer ERA, Ålund M, McFarlane SE, Johnsen A, Qvarnström A. 2016 Females discriminate against heterospecific sperm in a natural hybrid zone. *Evolution* **70**, 1844–1855. (doi:10.1111/evo.12986)
32. Manier MK, Lüpold S, Belote JM, Starmer WT, Berben KS, Ala-Honkola O, Collins WF, Pitnick S. 2013 Postcopulatory sexual selection generates speciation phenotypes in *Drosophila*. *Curr. Biol.* **23**, 1853–1862. (doi:10.1016/j.cub.2013.07.086)
33. Sakaluk SK, Eggert A-K. 1996 Female control of sperm transfer and intraspecific variation in sperm precedence: antecedents to the evolution of a courtship food gift. *Evolution* **50**, 694–703. (doi:10.1111/j.1558-5646.1996.tb03879.x)

34. Dean R, Nakagawa S, Pizzari T. 2011 The risk and intensity of sperm ejection in female birds. *Am. Nat.* **178**, 343–354. (doi:10.1086/661244)
35. Simmons LW, Parker GA, Stockley P. 1999 Sperm displacement in the yellow dung fly, *Scatophaga stercoraria*: an investigation of male and female processes. *Am. Nat.* **153**, 302–314. (doi:10.1086/303171)
36. Kaneshiro KY. 1980 Sexual isolation, speciation and the direction of evolution. *Evolution* **34**, 437–444. (doi:10.1111/j.1558-5646.1980.tb04833.x)
37. Noor MAF. 2001 Chromosomal inversions and the reproductive isolation of species. *Proc. Natl Acad. Sci. USA* **98**, 12 084–12 088. (doi:10.1073/pnas.221274498)
38. Bousquet F, Nojima T, Houot B, Chauvel I, Chaudy S, Dupas S, Yamamoto D, Ferveur J-F. 2012 Expression of a desaturase gene, *desat1*, in neural and nonneural tissues separately affects perception and emission of sex pheromones in *Drosophila*. *Proc. Natl Acad. Sci. USA* **109**, 249–254. (doi:10.1073/pnas.1109166108)