Introduction

Sexual selection has continued to be a popular focus of research in evolutionary biology since its rise to prominence around the 1970s and 1980s (e.g., Andersson, 1994). Active debate still remains about many of the fundamental processes of sexual selection (e.g., Parker and Pizzari, 2015; Hill, 2015); despite the fact that the field originated in the time of Darwin (1859, 1871) some basic principles remain unresolved. Furthermore, the way that sexual selection interacts with, and is affected by, other processes and phenomena has also attracted a lot of attention. One research area that originated decades ago but has received an increasing amount of notice in recent years is the fact that mating cues (“traits”), preferences, and other aspects of the sexual selection process may often display phenotypic plasticity (reviewed in Price, 2006; Ingleby et al., 2010; Rodriguez et al., 2013; Ah-King and Gowaty, 2015). One of the manifestations of plasticity is the alteration of trait and preference phenotypes by learning.

When traits or preferences are passed on solely through learning or imprinting they are said to be culturally inherited. These phenotypes may not have a genetic basis, but are instead ultimately determined by others in the animal’s surroundings. Individuals, for example, may learn a trait or mating preference from their mother (maternal imprinting), father (paternal imprinting) or from adults in the population at large (oblique imprinting). Mating preferences and traits may also be formed by learning from previous experience (e.g., behavioral reinforcement) or by copying the mating preferences of others (see reviews in Freeberg, 2000; White, 2004; Galef and Laland, 2005; Verzijden et al., 2012). The effect of cultural learning or inheritance could potentially be absolute in the sense of resulting in a phenotype that is solely culturally determined, as described above, but in many cases cultural factors will instead combine with genetic ones to determine a phenotype. In either of these cases cultural (or partly-cultural) and genetic traits can affect one another, resulting in gene–culture coevolution (reviewed in Boyd and Richerson, 1985; Feldman and Laland, 1996; Aoki, 2001).

Research at the intersection of learning and sexual selection has benefitted from attention from both empirical and theoretical studies. Evidence has been accumulating from a wide variety of taxa to indicate that learning can be important in the development of mating preferences and traits (reviewed in Verzijden et al., 2012; see also e.g., Guevara-Fiore, 2012; Westerman et al., 2014; Holveck and Reibel, 2014). In such species, learning of preferences (including courtship preferences) and/or traits (such as songs or displays) can ultimately affect species recognition (e.g., in birds: Grant and Grant, 1997; Price, 1998; ten Cate and Vos, 1999; Sorenson et al., 2003; in insects: Dukas, 2004, 2008; Svensson et al., 2010, 2014; in mammals: Kendrick et al., 1998, in fish: Magurran and Ramnarine, 2004; Verzijden and ten Cate, 2007; Kozak and Boughman, 2009; Kozak et al., 2011). There has also been a rich theoretical literature on the interaction of cultural evolution with sexual selection (e.g., Aoki, 1989; Kirkpatrick and Dugatkin, 1994; Laland, 1994a, b; Servedio and Kirkpatrick, 1996; Agrawal, 2001; Aoki et al., 2001; Ihara et al., 2003; Tramm and Servedio, 2008; Dubois et al., 2012; Chaffee et al., 2013; Santos et al., 2014). The new papers in this column contribute to both our empirical (Dukas and Scott, 2015; Fowler-Finn et al., 2015; Verzijden et al., 2015) and theoretical (Invernizzi and Gilman, 2015; Morier-Genoud and Kawecki, 2015) understanding of the ways in which learning and mate choice interact, in addition to providing a review of current issues in one particularly rich area of research on learning and sexual selection – mate choice copying (Witte et al., 2015).

New Work on the Causes and Consequences of Mate Choice Learning

The papers in this column examine both imprinting and learning that occurs based on feedback (behavioral or otherwise) from prior experience with prospective mates. Mate-choice imprinting can be defined as the
determination at an early age of a mating preference for a certain trait based on an individual’s observation of adults (the acquisition of cues for mate choice, for example displays or song, can occur in an analogous way, although the word imprinting has not traditionally been used in this context). As mentioned above, imprinting can occur upon different sets of individuals (mothers, fathers, or adults of the previous generation without regard to relatedness; resulting in maternal, paternal, and oblique imprinting respectively). The evolutionary consequences of these different “imprinting sets” (sensu Tramm and Servedio, 2008) can differ because, if there is sexual selection, the trait composition in these sets can vary substantially. Successfully mated males, for example, can have a higher frequency of a sexually selected trait than would either mothers or random adults.

Paternal imprinting has been shown to be favored evolutionarily over maternal or oblique imprinting both because of these differences in imprinting sets and because of the associations that arise between imprinted phenotypes and the genes in the system (Tramm and Servedio, 2008; Chaffee et al., 2013). In this column, Invernizzi and Gilman (2015) depart from the previous assumption of polygyny that has been pervasive, to my knowledge, in previous imprinting models, and examine the evolution of imprinting in monogamous populations that have the possibility of extra-pair paternity. Specifically, they use a mathematical model both to show that, under this type of mating system, paternal imprinting can be more likely to evolve than paternal imprinting, and to study the strength of choosiness that is expected to evolve. They further demonstrate an interesting interplay of selective forces between imprinting for the choice of social partner versus for the choice of extra-pair mating partner; this leads to the counterintuitive result that a higher degree of extra-pair paternity can lead to greater choosiness for a social partner. Their models emphasize that the predictions for the evolution of imprinting are quite nuanced, but at the same time provide the basis of potentially testable hypotheses.

Mate-choice copying occurs later in life than imprinting; it is the alteration of preference to favor an individual that is observed to be preferred by others. Mate choice copying was long proposed to be occurring based on field observations, but was demonstrated more conclusively by experiments in the 1990s (for review see e.g., Gibson and Hoglund, 1992; Pruett-Jones, 1992; Galef and Laland, 2005; Vakirtzis, 2011). In this column, Fowler-Finn et al. (2015) present evidence that females tend to copy the mate choice of other females that they observe mating with either ornamented or non-ornamented male *Schiozocosa* wolf spiders. This mate choice copying, however, is only part of a complex interplay of a number of factors that determine mate choice in this system. Specifically, Fowler-Finn et al. were able to demonstrate that both ornament status in males and preference in females are at least partly genetically determined, but that the latter can be influenced by age and copying as well. These complex interactions have unfolded on the background of a population structure in which some populations are polymorphic for the ornament while others are not. It is possible that mate choice, and copying, may ultimately affect these polymorphism patterns. In addition to this study of copying in wolf spiders, in this column Witte et al. (2015) present a review of current research directions on mate choice copying. This targeted review first discusses the fact that while copying has been studied more commonly in females, it is found in both sexes. It points out that copying may differ to some degree between the sexes, and has the potential to lead to sperm competition when it occurs in males. It additionally covers the impacts that copying can have on the evolution of novel ornaments and reviews the audience effect (whereby behavior is changed when an observer is present, McGregor, 2005). By focusing on these active research areas within the broader topic of mate choice copying this review both highlights the issues surrounding this form of learning and provides directions for future research.

Animals can also learn by the feedback that they receive when they attempt an action. Two studies in this column use *Drosophila* to explore the potential for alteration in male mate choice by this type of learning. Verzijden et al. (2015) designed an elegant experiment to test whether *D. melanogaster* males can learn to associate eye color with female mating receptivity. Specifically, by training males with unreceptive immature females vs. receptive mature females which differ based on an eye-color marker, Verzijden et al. found that males could alter their preferences to favor females with the eye color that previously indicated receptivity. They further demonstrated that this acquired preference disappeared under dark conditions in which eye color was not perceptible, thus providing tantalizing evidence that male *D. melanogaster* can learn to associate a novel and arbitrary visual cue with receptivity. Dukas and Scott (2015) also explored the potential for males to learn about females during the courtship process, by asking whether females respond to male courtship in a way that could transmit information about their level of sexual
maturity. They found that in *D. melanogaster*, immature females responded to courtship in different ways than did mature females, thus providing a potential signal that males could use to assess maturity status and modulate their future courtship behavior. Furthermore, *D. simulans* females also responded in different ways to the courtship of conspecific versus heterospecific (*D. melanogaster*) males; learning based on this information would thus have the potential to affect premating isolation (e.g., Servedio and Dukas, 2013).

Males could also learn about the types of courtship behaviors that are preferred by females (e.g. in cowbirds, West and King, 1988; Dohme et al., 2015). In this column Morier-Genoud and Kawecki (2015) use a simulation study to follow-up on a previous verbal argument that learning could facilitate the evolution of a novel courtship trait (Kawecki, 2013). They show that if females prefer, for example, a high level of a certain courtship display, and males can learn what females prefer via the fact that they gain increased attention from females when they perform more of these courtship actions, learning can then increase the selective benefit of courtship amounts that are closer to those that will elicit a response from a female. This manifestation of the Baldwin effect (Baldwin, 1896) could lead to the evolution of a new courtship behavior in a population, thereby potentially leading to the evolution of diversity in courtship behaviors among populations.

The papers in this column, although various, just scratch the surface of the diversity of ways in which learning and sexual selection can interact. They demonstrate, as has been found time and again, that when looked for, learning is often found to have an effect on mate choice (Fowler-Finn et al., 2015; Verzijden et al., 2015; review in Witte et al., 2015), and explore the ways in which different cues (Verzijden et al., 2015), tutors (Invernizzi and Gilman, 2015) and feedback (Dukas and Scott, 2015; Morier-Genoud and Kawecki, 2015) can form the basis for learning. The papers also touch on the ways in which learning involved in sexual selection may ultimately impact population differentiation and, perhaps, eventually speciation (Dukas and Scott, 2015; Fowler-Finn et al., 2015; Morier-Genoud and Kawecki, 2015). I am sure that I speak for the authors when I say that we hope that this collection serves to inspire further research into these areas (e.g., Witte et al., 2015).

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References


