

## Editorial

# New Horizons in Sexual Selection Research

Kenyon B. MOBLEY<sup>1</sup>, Kristina KARLSSON GREEN<sup>2</sup>, Guest Editors

<sup>1</sup>Max Planck Institute for Evolutionary Biology, Department of Evolutionary Ecology, August-Thienemann-Straße 2, 24306 Plön, Germany, mobley@evolbio.mpg.de

<sup>2</sup>Metapopulation Research Group, Department of Biosciences, PO Box 65 (Viikinkaari 1), FI-00014, University of Helsinki, Finland, Kristina.karlssongreen@helsinki.fi

## 1 Introduction

One of the most important decisions that a sexually reproducing organism must make in its lifetime is with whom shall it mate? From an evolutionary perspective, the importance of this decision is paramount: make the right choice and your offspring will continue your genetic legacy; make the wrong choice and your lineage will be at a disadvantage or worse, it may become extinct. It is this fundamental question that drives research in sexual selection since Darwin first proposed the idea in *The Origin of Species* (1859) and expanded on the topic in *The Descent of Man and Selection in Relation to Sex* (1871). Since Darwin's original musings on sexual selection, the field has undergone many addendums and transformations but at the heart of the theory remains two key features proposed by Darwin, namely mate competition and mate choice. Today, sexual selection is recognized as a salient evolutionary force that often trumps natural selection and understanding the causes and consequences of sexual selection remain a vibrant, and frequently controversial, area of evolutionary biology.

In this special column, we explore the current state of sexual selection research and take up several of the ongoing debates that are sure to influence the future direction studies on this topic. Contributions to this special column are inspired by a post-conference symposium entitled “Recent Developments in Sexual Selection Research: History, Trends and New Horizons” held on August 18, 2012, in Lund Sweden, following the International Society for Behavioral Ecology 2012 congress. The focus of the symposium was to take a fresh look at the state of sexual selection and discuss possible future directions of this dynamic field of research. Topics of discourse included the development and current state of sexual selection theory, the re-evaluation of the role that females play in sexual selection and broadening of sexual selection theory to include non-traditionally repre-

sented mating systems such as hermaphroditism. Contributions to this special column reflect these themes and also highlight important gaps in our knowledge as well as outlining possible future directions of research in this burgeoning field.

## 2 Contributions to this special issue

Our first contribution by Fritzsche and Booksmythe (2013) ambitiously tackles two important and current debates in sexual selection literature. The first of these topics concerns the contributions of females to the sexual selection process. The female perspective in sexual selection has traditionally been downplayed but gained a greater appreciation through recent theoretical and empirical advancements (Kirkpatrick, 1987; Clutton-Brock, 2007, 2009; Rosvall, 2011; Rosenthal, 2013) and highlighted in themed issues of *The Philosophical Transactions of the Royal Society B* ‘sexual selection, social conflict and the female perspective’ (Rubenstein, 2012) and ‘the polyandry revolution’ (Pizzari and Wedell, 2013). This re-appraisal of sexual selection in females has led several studies to focus on the potential for male mate choice and female-female competition for mates to drive the evolution of female traits and behaviors (Edward and Chapman, 2011; Rubenstein, 2012; Tobias et al., 2012). Fritzsche and Booksmythe (2013) review the current scope of females in sexual selection and conclude that studies, particularly in polyandrous, sex-role reversed species, are an important test to sexual selection theory and that our current understanding of what constitutes sexual selection is improved by our knowledge of sexual selection in females.

The second topic addressed by Fritzsche and Booksmythe (2013) concerns the current debate on which quantitative measures should be used to measure sexual selection (Klug et al., 2010; Krakauer et al., 2011; Jennions et al., 2012). Many qualitative and quantitative measures of sexual selection have been proposed over

the last few decades such as the operational sex ratio, the opportunity for selection, the opportunity for sexual selection and the Bateman gradient, just to name a few (reviewed in Shuster and Wade, 2003; Jones, 2009; Mobley, 2013). Therefore identifying the best method(s) to quantify sexual selection becomes a daunting task particularly since not all methods appear appropriate to all study organisms or research questions. Fritzsche and Booksmythe (2013) review different points of view and suggest that incorporating multifarious methods to estimate sexual selection tailored to the particular question at hand is the most amenable way forward. In addition, Fritzsche and Booksmythe (2013) outline several new lines of inquiry such as studies that simultaneously consider both pre- and post-copulatory sexual selection and studies that compare sexual selection in both males and females which should prove fertile areas for future research.

Continuing with the theme of the female perspective on sexual selection, Berglund (2013) ponders why sexually-selected female weapons have evolved so infrequently in nature. Central to the evolution of elaborate sexually-selected ornaments, weapons and aggressive behaviors in females is the notion that expression of these traits suffers an additional cost to fecundity that exists in females but not males (Fitzpatrick et al., 1995; Clutton-Brock, 2007, 2009). This cost to fecundity is primarily due to the high investment in large nutrient-rich eggs as a result of anisogamy. Despite this hypothetical cost, female ornaments used in mate choice and female-female competition appear in many species (Amundsen, 2000; Tobias et al., 2012) while the evolution of female weaponry via sexual selection remains in doubt. In this special column, Berglund (2013) evaluates the current evidence for female weaponry and postulates that, as juxtaposed to male weaponry that appears frequently in the animal kingdom, the cost of producing sexually-selected weapons in females may be so high as to prohibit their expression. Moreover, in the few instances where sexually-selected weapons might exist, males also share these traits calling into question whether females may independently evolve sexually-selected weapons. Future studies in the evolution of female sexually-selected traits should focus on potential costs to fecundity such as the trade-off between gamete numbers or size and trait expression and also disentangle the role of female-female competition and male choice on the evolution of such traits.

A deeper appreciation of sexual selection in the past few decades has led to extraordinary insights into the

evolution of animal communication. One such topic is the evolution of chemical signaling systems, or pheromones, and the role they play in mediating reproductive decisions and social interactions in different species. Pheromones serve as a means of interspecific communication for a variety of purposes including to identify individuals and kin, species recognition, territory marking, to alert conspecifics to food sources or predators, and are used in discriminant mate choice and the formation of mating aggregations (Symonds and Elgar, 2008). Despite the near ubiquitous use of pheromones in organisms, the selective agents for their evolution and diversification remain a black box in many cases (Symonds and Elgar, 2008). In this special issue, Harari and Steinitz (2013) review the evidence for three types of selection to mitigate the evolution of female-specific pheromones in moths: natural, sexual and social selection. Traditionally, pheromone evolution has been thought of as a means of species recognition via natural selection to avoid hybridization, particularly since many species or populations have unique compounds or particular blends of pheromones that serve as private communication channels. However, there is a growing consensus that species recognition can be driven by sexual selection and that the avoidance of mating with the wrong species is simply the first step in the process of choosing the right mate (Ryan and Rand, 1993; Detto et al., 2006; Ritchie, 2007; Mendelson and Shaw, 2012). In this issue, Harari and Steinitz (2013) compare and contrast evidence for natural and sexual selection to act on female-specific moth pheromones. They also review the potential for social selection to affect the evolution of female-specific moth pheromones, or the idea that females may not compete directly for mates but for resources such as breeding habitats that indirectly influences the outcome of sexual selection (West-Eberhard, 1979; Lyon and Montgomerie, 2012; Rubenstein, 2012; Tobias et al., 2012; Berglund, 2013). Harari and Steinitz (2013) conclude that, while each form of selection may seem disparate in their effects on pheromone signaling, all three forms of selection may be operating simultaneously and can help to explain the maintenance of female pheromone signaling systems.

Darwin originally drew predominantly from his knowledge of the animal kingdom when he postulated his theory of sexual selection. However, he was befuddled by the problem of hermaphroditism and thought that the evolution of bright coloration in hermaphroditic organisms was a product of natural selection as opposed to sexual selection (Darwin, 1871). Today we recognize

that sexual selection can operate in a diversity of hermaphroditic organisms ranging from plants and fungi, to animals (Charnov, 1979; Willson, 1979; Leonard, 2006; Anthes et al., 2010; Avise, 2011; Moore and Pannell, 2011; Nieuwenhuis and Aanen, 2012). Not only can classical sexual selection drive the evolution of complex sexual behaviors in hermaphrodites, but a range of unique adaptations have evolved as a response to sexual conflict and postcopulatory selection (Abbott, 2011; Schärer and Pen, 2013). Still, applying sexual selection theory to hermaphroditic organisms provides an interesting challenge to theorists. For example, how can we reconcile the diversity of sexually selected traits in simultaneous hermaphrodites with the theoretical reduced potential for sexual selection to operate in these organisms (Greeff and Michiels, 1999)? In this issue, Leonard (2013) explores the current evidence of sexual selection in hermaphroditic organisms with special reference to the predictions of mating system, operational sex ratio and sex allocation theories and suggests that theory based on Bateman principles is not adequate to explain sexual selection in hermaphrodites. Leonard (2013) emphasizes that quality, rather than quantity, of mates may be more informative to help understand mate choice in hermaphroditic organisms. Also, since sexual selection in hermaphrodites may be associated with a preferred sexual role, hermaphrodites can act as their own control for tests of hypotheses about the relative importance of sexual selection on male versus female function. In sum, hermaphroditic organisms present a golden opportunity to test theories of sexual selection yet many aspects of mate choice are still unknown and warrant further investigation.

We conclude the special column with a comment concerning the use of the word sexual selection by Zahavi (2013). Previously Zahavi (1981) proposed that signaling systems evolve uniquely compared to other traits that are not used in social signaling and therefore represent a separate selection mechanism. He argues that traits that advertise honest signaling via the handicap hypothesis should form the basis of mate choice and discrimination in mating decisions (Zahavi, 1975, 1977). While the premise is intriguing and certainly animal communication is one very important aspect of sexual selection, time will tell if researchers will abandon the term sexual selection or modify theory. First and foremost signal selection incorporates many aspects of social communication that fall outside the realm of Darwin's original concept of mating competition. For example, social signaling includes, but is not limited to,

locating prey or avoiding predators, aposematic coloration and batesian mimicry, alarm calling, species, family and individual recognition, and parental-offspring conflict (Searcy and Nowicki, 2005; Hare, 2012). Therefore viewing signaling systems as a selective mechanism may be useful to answer the proximate cause for the evolution of the transmission of information from the signal producer to the receiver but addressing the underlying ultimate cause of traits used specifically in mating and reproduction will require further refinement of signal selection theory.

To sum up, now more than ever sexual selection plays a vital role in deciphering the diversity of mating behaviors and traits found in nature. The question is, how do we now move forward? First, the theoretical underpinnings of sexual selection are constantly being questioned and healthy debate promotes new ideas and the re-assessment of past findings. For instance, the current discussions on the evolution of sex roles may help improve our understanding of how our past views of gender have influenced the development of sexual selection theory (Schärer et al., 2012; Ah-King, 2013; Kokko et al., 2013). Likewise, recent breakthroughs in methodology, particularly relating to genomic techniques open new lines of inquiry on the evolution of mate choice and sexual antagonism (Cummings, 2012; Parsch and Ellegren, 2013), the genetic link between traits and preferences (McNiven and Moehring, *in press*), and the influence of sexual selection in the speciation process (Servedio, 2013). Finally, building stronger dialogue between theory and empirical studies is not only necessary to help provide the right context for sexual selection but should reveal new insights and lines of inquiry into the causes and consequences of sexual selection for generations to come.

**Acknowledgements** We would like to thank all of the contributors and especially Zhi-Yun Jia for his kind invitation and dedication to publish this special column. We would also like to thank our co-organisers Malin Ah-King, Anders Berglund, Åsa Lankinen, Josefin Madjidian and Gunilla Rosenqvist, the invited speakers Jessica Abbott, Malin Ah-King, Anders Berglund, Tim Clutton-Brock, Hans Ellegren, Hanna Kokko, Nina Wedell and Marlene Zuk as well as the participants of the "Recent Developments in Sexual Selection Research: History, Trends and New Horizons" postconference symposium at the International Society for Behavioral Ecology 2012 congress, in Lund, Sweden.

## References

Abbott JK, 2011. Intra-locus sexual conflict and sexually

- antagonistic genetic variation in hermaphroditic animals. *Proceedings of the Royal Society B*. 278: 161–169.
- Ah-King M, 2013. On anisogamy and the evolution of ‘sex roles’. *Trends in Ecology & Evolution*. 28: 1–2.
- Amundsen T, 2000. Female ornaments: Genetically correlated or sexually selected? In: Espmark Y, Amundsen T, Rosenqvist G ed. *Animal signals: Signalling and signal design in animal communication*. Trondheim: Tapir Academic Press.
- Anthes N, Patrice D, Auld JR, Hoffer JNA, Jarne P et al., 2010. Bateman gradients in hermaphrodites: An extended approach to quantify sexual selection. *American Naturalist*. 176: 249–263.
- Avisé JC, 2011. *Hermaphroditism: A primer on the biology, ecology, and evolution of dual sexuality*. New York: Columbia University Press.
- Berglund A, 2013. Why are sexually selected weapons almost absent in females? *Current Zoology* 59: 564–568.
- Charnov EL, 1979. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences of the U.S.A.* 76: 2480–2484.
- Clutton-Brock TH, 2009. Sexual selection in females. *Animal Behaviour* 77: 3–11.
- Clutton-Brock TH, 2007. Sexual selection in males and females. *Science* 318: 1882–1885.
- Cummings ME, 2012. Looking for sexual selection in the female brain. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367: 2348–2356.
- Darwin C, 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- Darwin C, 1859. *The Origin of Species*. New York: Random House.
- Detto T, Backwell PRY, Hemmi JM, Zeil J, 2006. Visually mediated species and neighbour recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricornis*). *Proceedings of the Royal Society B*. 273: 1661–1666.
- Edward DA, Chapman T, 2011. The evolution and significance of male mate choice. *Trends in Ecology & Evolution*. 26: 647–654.
- Fitzpatrick S, Berglund A, Rosenqvist G, 1995. Ornaments or offspring: cost to reproductive success restrict sexual selection processes. *Biological Journal of the Linnean Society* 55: 251–260.
- Fritzsche K, Booksmythe I, 2013. The measurement of sexual selection on females and males. *Current Zoology* 59: 558–563.
- Greeff JM, Michiels NK, 1999. Sperm digestion and reciprocal sperm transfer can drive hermaphrodite sex allocation to equality. *American Naturalist* 153: 421–430.
- Harari A, Steinitz H, 2013. The evolution of female sex pheromones in moths. *Current Zoology* 59: 569–578.
- Hare JF, 2012. Vertebrate social communication: Ecological and evolutionary insights from social signals. *Current Zoology* 58: 677–679.
- Jennions MD, Kokko H, Klug H, 2012. The opportunity to be misled in studies of sexual selection. *Journal of Evolutionary Biology* 25: 591–598.
- Jones AG, 2009. On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution* 63: 1673–1684.
- Kirkpatrick M, 1987. Sexual selection by female choice in polygynous animals. *Annual Review of Ecology and Systematics* 18: 43–70.
- Klug H, Heuschele J, Jennions MD, Kokko H, 2010. The mismeasurement of sexual selection. *Journal of Evolutionary Biology* 23: 447–462.
- Kokko H, Booksmythe I, Jennions MD, 2013. Causality and sex roles: prejudice against patterns? A reply to Ah-King. *Trends in Ecology & Evolution*. 28: 2–4.
- Krakauer AH, Webster MS, Duvall EH, Jones AG, Shuster SM, 2011. The opportunity for sexual selection: Not mismeasured, just misunderstood. *Journal of Evolutionary Biology* 24: 2064–2071.
- Leonard JL, 2013. Sexual selection and hermaphroditic organisms: Testing theory. *Current Zoology* 59: 579–588.
- Leonard JL, 2006. Sexual selection: Lessons from hermaphrodite mating systems. *Integrative and Comparative Biology* 46: 349–367.
- Lyon BE, Montgomerie R, 2012. Sexual selection is a form of social selection. *Philosophical Transactions of the Royal Society of London Series B*. 367: 2266–2273.
- McNiven VTK, Moehring AJ, *in press*. Identification of genetically linked female preference and male trait. *Evolution*.
- Mendelson TC, Shaw KL, 2012. The (mis)concept of species recognition. *Trends in Ecology & Evolution*. 27: 421–427.
- Mobley KB, 2013. Mating systems and the measurement of sexual selection. In: Yasukawa K ed. *Animal Behavior: Vol. 2. Function and Evolution of Behavior*. Westport, CT: Praeger.
- Moore JC, Pannell JR, 2011. Sexual selection in plants. *Current Biology*. 21: R176–R182.
- Nieuwenhuis BPS, Aanen DK, 2012. Sexual selection in fungi. *Journal of Evolutionary Biology*. 25: 2397–2411.
- Parsch J, Ellegren H, 2013. The evolutionary causes and consequences of sex-biased gene expression. *Nature Reviews Genetics* 14: 83–87.
- Pizzari T, Wedell N, 2013. The polyandry revolution. *Philosophical transactions of the Royal Society of London. Ser. B*. 368: 20120041.
- Ritchie MG, 2007. Sexual selection and speciation. *Annual Review of Ecology Evolution and Systematics*. Palo Alto: Annual Reviews 79–102.
- Rosenthal GG, 2013. What is it like to be a peahen? *Current Zoology*. 59: 180–183.
- Rosvall KA, 2011. Intrasexual competition in females: evidence for sexual selection? *Behavioral Ecology* 22: 1131–1140.
- Rubenstein DR, 2012. Sexual and social competition: broadening perspectives by defining female roles. *Royal Society Philosophical Transactions Biological Sciences* 367: 2248–2252.
- Ryan MJ, Rand AS, 1993. Species recognition and sexual selection as a unitary problem in animal communication. *Evolution* 47: 647–657.
- Schärer L, Pen I, 2013. Sex allocation and investment into pre- and post-copulatory traits in simultaneous hermaphrodites: The role of polyandry and local sperm competition. *Philosophical Transactions of the Royal Society Ser. B*. 368.
- Schärer L, Rowe L, Arnqvist G, 2012. Anisogamy, chance and the evolution of sex roles. *Trends in Ecology & Evolution* 27: 260–264.
- Searcy WA, Nowicki S, 2005. *The Evolution of Animal Communication*. New Jersey: Princeton University Press.

- Servedio MR, 2013. Sexual selection and speciation. *Current Zoology* 58: 413–415.
- Shuster SM, Wade MJ, 2003. *Mating Systems and Strategies*. Princeton, NJ: Princeton University Press.
- Symonds MRE, Elgar MA, 2008. The evolution of pheromone diversity. *Trends in Ecology & Evolution* 23: 220–228.
- Tobias JA, Montgomerie R, Lyon BE, 2012. The evolution of female ornaments and weaponry: Social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society of London Ser. B* 367: 2274–2293.
- West-Eberhard MJ, 1979. Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society* 123: 222–234.
- Willson MF, 1979. Sexual selection in plants. *American Naturalist* 113: 777–790.
- Zahavi A, 2013. A comment on the term sexual selection. *Current Zoology* 59: 589.
- Zahavi A, 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* 67: 603–605.
- Zahavi A, 1975. Mate selection: Selection for a handicap. *Journal of Theoretical Biology* 53: 205–214.
- Zahavi A, 1981. Natural selection, sexual selection and the selection of signals. In: Scudder GGE, Reveal JL ed. *In Evolution Today*. Pittsburg: Carengie-Mellon University Press, 133–138.