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Editorial

(Under)water love—linking mate choice and cognition in fish and frogs

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Aims and Objectives

This Special Column aims at complementing our knowledge and deepening our understanding of the complex processes involved in learning and neurobiological mechanisms in the context of sexual selection.

So far, there are a number of studies dealing with specific aspects in neurobiology OR sexual selection, however, there is no comprehensive account of studies linking neurobiological aspects with mate choice to this date. For instance, various studies investigate sex differences in a wide range of cognitive and behavioral processes in a variety of vertebrate and invertebrate groups. But investigations of sex differences in (social) learning and, for example, memory AND the underlying neurobiological substrates in the context of sexual selection and their importance in mate choice behavior have been largely neglected. Thus, studies combining learning and cognitive abilities with neurobiological substrates in the context of mate choice are still rare. Critical questions that remain to be answered include why and how does learning and cognition influence mate choice? How do environmental conditions affect the evolution of the underlying neurobiological substrates? Which neural circuits are shared or distinct between sexes within species and/or between species of the same and/or different taxonomic groups?

Sexual Selection

In the 1970s and 1980s, sexual selection became a popular focus of research in evolutionary biology and various related aspects are still being investigated today. Even though many of the fundamental processes, mechanisms, and phenomena of sexual selection (Parker and Pizzari 2015; Hill 2015; Rosenthal 2017) remain the subject of intense discussions, a number of basic questions continue being unaddressed; despite the fact that these questions date back to Darwin's time (1871). Darwin (1871) described 2 "modes" of sexual selection: intrasexual selection acts via competition "between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners" which is intersexual selection. These forces ("male competition", "female choice") mirror striving for the best possible mating partner. However, both sexes show both intrasex competition and intersex mate choice — although these are frequently weighted differently in sexes and/or species. However, competition and strategic mate choice are only 2, albeit behaviorally conspicuous and, therefore, well studied mechanisms of sexual selection. In addition, less obvious strategies such as sperm competition or manipulative and exploitative behavior driven by sexual selection (e.g., deception, infanticide, and sexual violence) exist. Sexual competition results in winners and losers. If individual males are unlikely to succeed in the competition for sexual partners, but are most likely among the losers, it is often more advantageous for them to evade the unfavorable form of competition and instead try to achieve their fitness goals through "alternative tactics". These may include, for instance, strategies taking into account physical sex-specific dimorphism, the "social rank" of an individual, enhanced cognitive capabilities such as learning or remembering of food sources, using public information about the social and ecological environment, or a higher degree of behavioral flexibility. However, we are only beginning to understand the way in which sexual selection responds, interacts and, in turn, is influenced by other processes and phenomena.

Mate Choice and Cognitive Abilities

Mate choice occurs within a complex framework of an animal's social interactions that are markedly affected by factors such as environmental conditions, cognitive abilities, dominance hierarchies, family bonds, age, or sex of an interacting individual. Moreover, attention, motivational, sensory, and perceptual mechanisms (all of

which are known to exhibit substantial differences between sexes and species) that allow animals to survive, cooperate, and reproduce depend on the corresponding morphological and/or neuronal prerequisites innate to every individual. Mate choice has favored the development of a wide diversity of sexual signals to attract the choosy sex (Bateson 1983). For instance, given the great variety of beautiful male ornaments, it is difficult to deny the females any preference, as even a slight preference would allow sexual selection (Jones and Ratterman 2009). Hence, Darwin (1871) observed that "when we see many males pursuing the same female, we can hardly believe that the pairing is left to blind chance – that the female exerts no choice, and is not influenced by the gorgeous colours or other ornaments with which the male alone is decorated". But why should female preferences exist at all? Females receive both direct and indirect fitness benefits for their offspring by exploiting these signals to determine the best and most suitable partner (Kokko et al. 2003). However, there is often a wide, highly individual variation in the choosy sex' preferences, which is likely to affect the strength and direction of sexual selection on particular characteristics within a population (Brooks and Endler 2001). In the past, numerous studies have focused on determining behavioral and physical traits indicative of the quality of preferred partners (Andersson 1994; Schuett et al. 2010). More recently, research has shifted one focus toward the examination of the congenital cognitive or behavioral characteristics of choosing individuals as well as on those that are chosen, and how these initiate and/or influence mate choice of the choosy sex. For instance, it has recently been shown that problem-solving tasks (Chen et al. 2019), sensory characteristics (Ronald et al. 2018) as well as brain size (Corral-López et al. 2017) in females significantly affect mate choice and the ability to accurately assess the sexual signals of potential mating partners. In this context, individual cognitive differences may contribute to better explaining the varying preferences for one or another sexually selected trait, which, for instance, may be common within a particular population.

Recently, associations between an individual's mating success and cognitive skills (Shohet and Watt 2009; Keagy et al. 2009, 2011; Minter et al. 2017) and between its cognitive skills and sexual characteristics (Karino et al. 2007; Boogert et al. 2008, 2011; Mateos-Gonzalez et al. 2011; Keagy et al. 2012; Fabre et al. 2014) have indicated that sexual selection may possibly affect cognitive abilities (Andersson and Simmons 2006; Boogert et al. 2011; Sewall et al. 2013; Isden et al. 2013). Cognition is described in terms of the way individuals acquire, store, and use information (Shettleworth 2010). For instance, this information can be applied to decisions on potential mating partners and, thereby, possibly result in mate choice via learning. In this context, mate choice involves personal experience with others (i.e., private or personal information) or observing conspecifics (i.e., public information) and continues throughout an individual's entire life (reviewed in Hebets and Sullivan-Beckers 2019). Moreover, environmental — including social—influences on mating decisions have long been recognized (Jennions and Petrie 1997; Irwin and Price 1999). Throughout their lives, animals gather and process environmental information, that is, these individuals learn (cf. definitions of "learning" in Barron et al. 2015). Accordingly, their learning and decision-making processes can have a social component and may change to increase their chances of finding a high-quality partner. An individual's "cognitive style" comprises many aspects of cognition such as an individual's cognitive flexibility, decisiveness, or gathering of new information (Sih and Del Giudice 2012), and individuals within populations were observed to exhibit homogeneous differences in cognitive style (Matzel et al. 2003, 2017; Guillette et al. 2015; Boogert et al. 2018).

Sex Differences in Cognitive Abilities in the Context of Mate Choice

Variations in the way cognition is associated with different sex roles potentially lead to differences in selection on cognition and possibly trigger sex differences related to cognitive abilities (Galea et al. 1996; Jacobs 1996; Lindenfors et al. 2007). In various species across all taxa, this "cognitive-sexual dimorphism" often reflects the observed differences in sex roles within a mating system. Male cognition has been identified as an important potential protagonist in sexual selection. Various studies have determined positive associations of male sexual signals with cognitive performance and/or significantly increased preferences of females for males that perform better cognitively. For instance, meadow vole males *Microtus ochrogaster, M. pennsylvanicus* dominate large home ranges and their reproductive success is strongly correlated with finding and convincing females to mate. To meet these challenges, meadow vole males developed an improved spatial learning ability compared with their conspecific females (Gaulin and Fitzgerald 1986, 1989; Galea et al. 1996). Likewise, male guppies *Poecilia reticulata* outperformed females in learning a complex spatial task (Lucon-Xiccato and Bisazza 2017) and made decisions faster (though not more correct) than females in visual color discrimination learning (Lucon-Xiccato and Bisazza 2016). Conversely, female guppies were observed to outperform males in a spatial orientation task to rejoin a group of conspecifics and in a numerical task requiring them to discriminate between 5 and 10 dots to obtain a food reward (Petrazzini et al. 2017). Another study examined western mosquitofish *Gambusia affinis* regarding the association between activity, exploration, anxiety, and sociability with the individual's associative learning performance in numerical discrimination experiments (Etheredge et al. 2018). The authors concluded that sexes differ in their cognitive-behavioral responses that could possibly be attributed to different sexual selection pressures, despite the convergence of their learning performance (Etheredge et al. 2018).

Cognition and Behavioral Flexibility

While many mating preferences have a genetic basis, the question remains as to whether and how learning and/or experience can alter an individual's mate choice decisions. The ability to learn from experience offers a certain degree of flexibility which is crucial to living in a variable, constantly changing environment (Dodson 1988). In this context, "behavioral flexibility" denotes the ability to better adapt the own behavior to altered environmental conditions or unpredictable resources (Bond et al. 2007). It requires individuals to rapidly shift from a no longer viable strategy to a new one to obtain new associations as environmental demands change (Rayburn-Reeves et al. 2017a,b). Therefore, assessing an individual's behavioral flexibility allows to indirectly examine its level of "cognitive flexibility". Cognitive flexibility has been defined as the ability to channelize attention between different tasks, for instance, in response to an alteration of rules or demands (Scott 1962). Accordingly, it is the aptitude to adapt the own rational to new situations and/or to overcome the habitual thinking and decision-making processes (Deak 2003; Moore and Malinowski 2009; Rayburn-Reeves et al. 2017a,b).

In several mammalian, avian and fish species, females were observed to show a higher performance than males in tasks requiring cognitive flexibility such as the discrimination reversal learning. For instance, female guppies appeared to be more innovative and interested in problem solving when given a novel foraging task involving spatial exploration (Laland and Reader 1999). Likewise, females solved learning flexibility tasks faster compared with their male conspecifics. In these studies, individuals were challenged either with a detour reaching task to join a group of conspecifics (Lucon-Xiccato and Bisazza 2017) or with a series of color discrimination reversal learning tasks (Lucon-Xiccato and Bisazza 2014).

To widen our understanding of the ways in which learning, other neurobiological aspects, and mate choice interact, coincide or differ between males and females within or between species, the topical collection of this Special Issue comprises a number of exciting contributions: Keagy et al. (2019) observed cognitive sex differences and their relationship to male mate choice. To do so, they repeatedly presented male and female three-spined sticklebacks *Gasterosteus aculeatus* with a detour task to assess initial inhibitory control and improvement over time, and examined, whether male mate choice was associated with female inhibitory control. Since males consistently outperformed females, there seemed to be suggestive evidence that males learned the task better than their conspecific females, although sex-specific differences in neophobia played an important role as well. Rystrom et al. (2019) have examined the flip side of the same coin. They challenged female three-spined sticklebacks with a dichotomous mate choice task using computer-animated males differing in breeding coloration. They examined their results with regard to the females' spatial learning and reversal learning ability and possible correlations between an individual's spatial learning ability and its mate assessment. Females spending more time to evaluate potential partners in a dichotomous mate choice task made fewer errors during both the initial and reverse spatial learning task. However, these females made more consecutive errors at the very beginning of the reversal phase, indicating that they were not quickly adapting to environmental changes, but quickly forming strict routines during the learning tasks.

Plath et al. (2019) have also focused on mate assessment to which they added the exciting aspect of the attendances or absences of predators. They assigned wild-caught (predator-experienced) and laboratory-reared (predator-naïve) Western mosquitofish *G. affinis* to 2 mate choice tests, during one of which different animated predators were present. They aimed to investigate whether (innate) mating preferences would change under immediate predation threat and whether potential predator-induced changes in mating preferences would differ between sexes or depend on the choosing individual's personality and/or body size. Wild-caught fish altered their mate choice decisions most when exposed to co-occurring predators whereas laboratory-reared individuals responded most to coevolved predators, suggesting that both innate mechanisms and learning effects were involved. The effects were stronger in bolder individuals, likely because those phenotypes face an overall increased predation risk.

Within the scope of this Special Issue, sex-specific differences, visual discrimination ability, and aspects of spatial orientation, although in different contexts have been studied in túngara frogs and 3 poeciliid species. Ventura et al. (2019) tested male and female túngara frogs for their place learning capabilities by using a 2-arm maze featuring 2 differently marked doors (red, yellow, or achromatic cues), one of which was rewarded with return to the home cage. They examined whether the type of door marking (chromatic or achromatic) had a sex-specific effect on the individuals' place learning behavior. Frogs rewarded to choose the yellow door showed an increase in correct choices and an increased preference for the yellow door in the course of training. However, authors found no evidence for a sex difference in learning. Fuss and Witte (2019) performed one of the first comparative studies dealing with behavioral flexibility in the context of (cognitive) sex-specific differences in 3 related poeciliid species (*P. latipinna*, *P. mexicana*, and *P. reticulata*). They assessed male and female individuals for their ability to exploit previously gained knowledge using a simple color discrimination paradigm (red, yellow, or green cues) and, subsequently, for their behavioral flexibility in a series of reversal tasks. While no sex differences were observed in sailfin mollies, male Atlantic mollies learned to solve the initial color discrimination task significantly faster than their conspecific females. Surprisingly and contrasting our expectations of a reflection of the results of a previous study on guppies (Lucon-Xiccato and Bisazza 2014), only females solved the initial task in our study, whereas males failed to learn any of the tasks they were assigned to. Regarding the expected sex differences in accuracy and behavioral flexibility during serial reversal learning, different results for the 3 species under investigation were observed. Compared with previous studies or other vertebrate taxa, the hitherto apparently universal pattern (i.e., females showing higher behavioral flexibility) seemed to be inverted in the 2 examined molly species.

Sexual Selection and Neurobiological Substrates

Mate choice may involve any sensory modality (Halfwerk et al. 2019). Choosers often attend to a courter's traits by exploiting every modality they possess. However, prior to a chooser expressing a preference for any particular aspect of a courter's phenotype, the chooser (i.e., the recipient) has to be capable of recognizing it (Levine 2000); anything outside a chooser's range of sensitivity is imperceptible to it, for example, invisible, inaudible, or odorless (Rosenthal 2017). A stronger sensory stimulation often translates into a stronger preference of a certain trait. In short, sensory biology is of major importance to mate choice and to its evolutionary effects.

Vocalization plays an outstanding role in mate recognition and selection in a number of taxa, especially, but not limited to, orthopterans, frogs, birds, and certain fish species. The ability to unambiguously identify a conspecific by its vocalizations alone, the so-called "individual voice recognition", allows a fast, turning communication in a crowd (e.g., Bee and Micheyl 2008). For instance, in a social context, such as a cocktail party, it might be of vital importance to recognize the voice of the spouse. Individual voice recognition is widely spread amongst animals of various taxonomic groups — especially, but not limited to orthopterans (e.g., Greenfield 2002), frogs (e.g., Ryan 2001; Gerhardt and Huber 2002), birds (e.g., Keen et al. 2016; D'Amelio et al. 2017), and some fish species (e.g., Amorim et al. 2015). Many mammalian and bird species are even capable of vocally recognizing their partners, relatives or group members (e.g., Lambrechts and Dhondt 1995; Frommolt et al. 2003; Insley et al. 2003; Sharp et al. 2005; Deecke 2006; Börner et al. 2016; Stoeger and Baotic 2017). It is known, however, that several species generate a large number of different acoustic signals that allow individuals to flexibly convey information in different contexts with a large vocal repertoire (e.g., Bradbury and Vehrenkamp 2011). The acoustic information presented in a sound signal needs to be decoded and processed by the recipients, which

sometimes can be a complex cognitive task (Zatorre and Schönwiesner 2011). To understand the communication processes of a particular species, the (sexually dimorphic) characteristics of the entire vocal repertoire, the morphological structures that generate or perceive the sounds, as well as the recognition thresholds and the underlying neural substrates evaluating the sensation need to be taken into account. For instance, the effects of both natural and sexual selection can be traced back by observing (sex-specific) acoustic communication in many anuran species. Within the scope of this Special Issue, Taylor et al. (2019) aimed to investigate the threshold for signal salience of female túngara frogs detecting male acoustic sexual displays. To do so, they compared differences among behavioral signal recognition thresholds, midbrain multiunit electrophysiological thresholds, and neural auditory brainstem thresholds of female túngara frogs in response to simple tones and complex male advertisement calls. They revealed substantial differences among signal recognition thresholds, electrophysiological thresholds, and auditory brainstem thresholds. Fittingly, McClelland et al. (2019) focused on 2 main aspects of the laryngeal and ear structures of cricket frogs *Acris crepitans* — the potentially sexually dimorphic anatomical characteristics and the differences between populations living in different habitats — in the context of allometric effects of body size. Both sexes showed size differences in the larynx related to selection for larger body size in dry, open habitats. However, the observed selection on males for larger larynx size related to the production of lower frequency calls in those habitats did not result in correlated changes in the female larynx.

Future Perspectives

The topical collection of this Special Issue opens new exciting perspectives on the wide field of sexual selection and mate choice both in the context of sex-specific cognitive abilities and flexible behavioral adaptations, and in the context of sex-specific sensory–neurobiological characteristics. The various contributions can only scratch the surface of the diversity of ways in which learning, morphology, and neuronal activity can interact with mate choice and sexual selection. Hence, various aspects are brought together allowing the drawing of well-deserved attention to this key issue of behavioral and evolutionary biology.

With this Special Issue, we provide further evidence to Darwin's hypothesis that mate choice has an intriguing influence on the evolution of cognitive abilities in nonhuman individuals. Unquestionably, it is and will continue to be fascinating to unravel how superior cognition offers an evolutionary advantage, especially in terms of potential benefits for reproductive fitness. In mammals and birds (González-Lagos et al. 2010; Minias and Podlaszczuk 2017), those comparatively larger-brained individuals alleged to have superior cognitive abilities, were observed to be more long-lived compared with their smaller-brained conspecifics. For fish, a bigger brain will also come at a price: larger-brained individuals were observed to be smarter, but had about one-fifth less offspring than those with smaller brains (Kotrschal et al. 2013). On the contrary, they might still be able to reproduce better (and increase their reproductive success) because cognitive abilities contribute beneficially to survivorship in terms of foraging, mate choice, or escape from predators. Although a considerable body of studies has provided an impressive array of indirect evidence that cognition and attractiveness interrelate closely, the ultimate proof for the choosing sex judging cognitive abilities in potential mates just as outwardly visible physical traits is still lacking. In a thoroughly planned and well-performed

study on budgerigars, Chen et al. (2019) attempted to bridge the gap between mate choice and cognitive traits, a link urgently needed and often neglected in the fields of cognition and sexual selection. In this study, female budgerigars altered their preference for males after observing these males' ability to open 2 different so-called "problem boxes" to get access to food. This shift did not occur in control experiments, neither when focal females observed females solving the same task, nor when focal females observed males having free access to food. However, when interpreting these results, cognition cannot serve as the only explanation. Since females were not given the opportunity to explore the foraging task themselves to be able to judge the males' cognitive performance. They could also have attributed a male's problem-solving ability to its physical strength or subtle behavioral differences elicited by the extensive training paradigm (Keagy et al. 2019; Striedter and Burley 2019). Thus, in the context of this study and the studies in this Special Issue, it will remain a fascinating challenge to explore why and how learning and cognition do indeed influence mate choice and the dynamic processes in sexual selection and how (social) environmental conditions may affect the underlying neural substrates.

Acknowledgments

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