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Mate choice as social cognition: predicting female behavioral and neural plasticity as a function of alternative male reproductive tactics

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Female mate preference behavior has traditionally been viewed as a sensory response, yet recent research supports the involvement of cognitive processes. Here we argue that cognition is likely to arise as a critical component of female mate choice in mating systems with alternative male reproductive phenotypes. In alternative male mating systems, selection should favor female recognition of, and adaptive response toward, different male behavioral strategies: avoid phenotypes incurring fitness costs and affiliate with phenotypes associated with fitness benefits. Here we review the behavioral, molecular and neural evidence supporting cognitive processes in female mate choice behavior across animals, and make predictions as to how the relative contribution of social cognition in mate choice decisions is likely to vary by mating system.

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Social cognition and mate choice behavior: the behavioral evidence

Cognition refers to the gathering and integrating of internal and external information to produce a context-specific response based on a set of decision rules [1]. Similar to general cognition, social cognition refers to neural processes that allow an animal to adjust its behavior based on social interactions. Put simply, social cognition is the differential recognition of, and the adaptive response toward, social agents [2–4]. Many social behaviors such as shoaling decisions and dominance interactions are recognized as products of social cognition [1,5]. Interestingly, one of the more fundamental social behaviors over the course of a lifetime, choosing a mate, has received relatively little attention in the social cognition arena.

Mate choice, the behavioral manifestation of a mate preference function, refers to the non-random and coercion-free selection of a mating partner, and should be distinguished from mating biases resulting from female resistance to unwanted attention [6]. It is an inherently social behavior, yet there is no general consensus as to whether it is an inherently cognitive process. Perhaps unsurprisingly, human mate choice has been recognized as a social cognitive task for several decades [7,8]. Evolutionary and cognitive psychologists have recognized that there are three inter-related subtasks involved in a mate choice process that include (1) perceiving sexual cues that provide information about potential mates, (2) integrating these cues to assess and evaluate the relevant properties of potential mates (e.g. health, status), and (3) searching for, discriminating amongst, and deciding to mate with specific individuals [8]. Clearly, many other animals are faced with this same set of social tasks.

Although most animals face the task of mate choice, how they process this task may vary. Some taxa may employ a simple sensory threshold response whereas others may employ an experience-dependent assessment of male phenotypes. As the decision rules across this continuum become more complex, they may demand greater investment in cognitive processing (Figure 1). For instance, early theoretical models have suggested that when males vary along a unidimensional sensory axis, genetically predetermined sensory biases may produce female preferences (e.g. mate with redder or brighter males) that are not modified over the course of a female's lifetime. Genetic divergence between opsin genes and correlated preference behavior between Lake Malawi cichlid populations is a potential candidate for this scenario [9]. Meanwhile, processing multidimensional signaling traits may require greater involvement of cognitive hardware. For example, female bowerbirds prefer to mate with males constructing higher quality bowers, an assessment that incorporates inputs on size, color, interior and exterior design elements [10]. Across bowerbird species, male and female brain volume increases with the complexity of the male's bower [11]; and female mate choice decision rules vary as a function of experience [10].

Experience-dependent mate choice decisions suggests that females are engaging in the cognitive process of

Figure 1
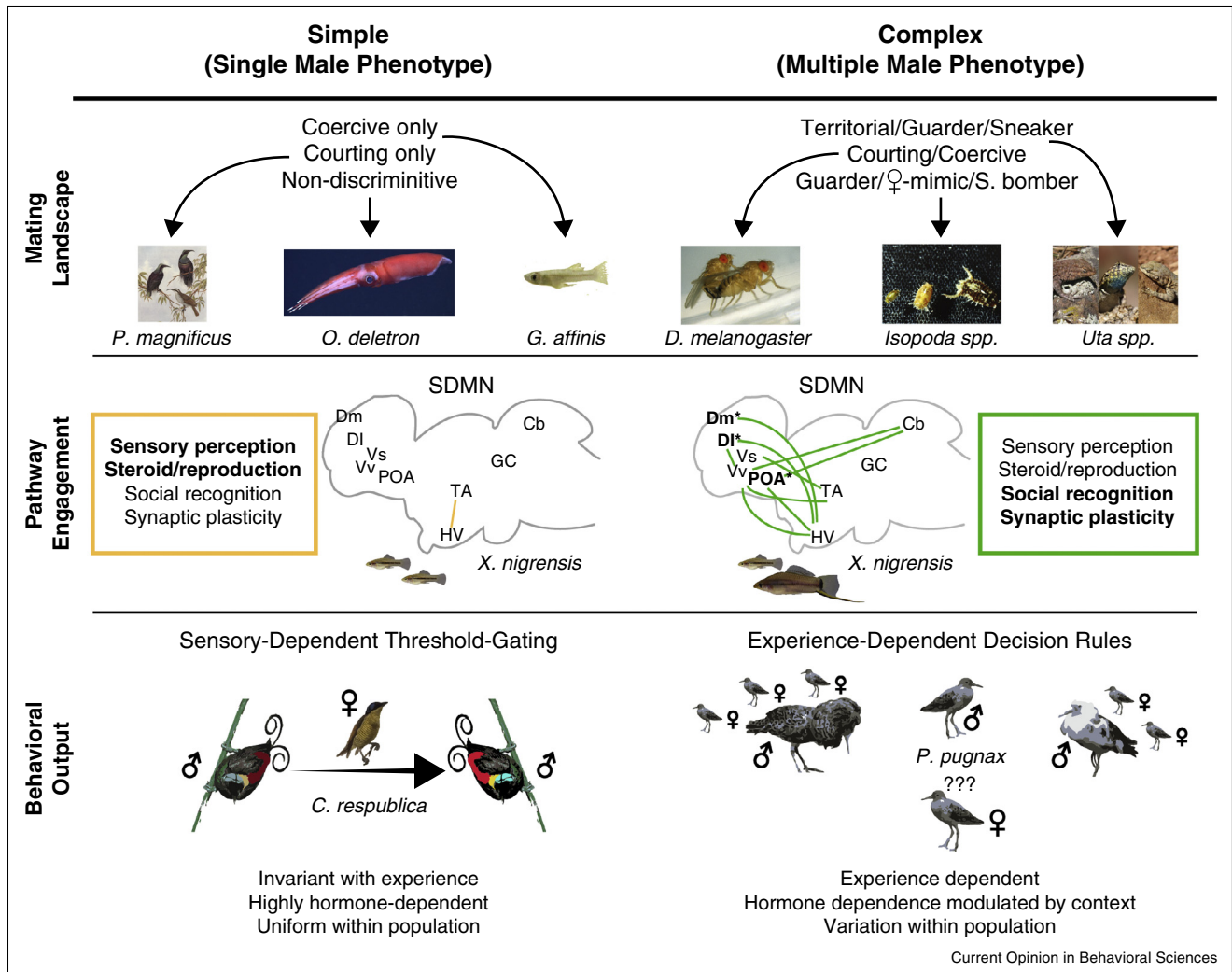
The cognitive requirements of female mate choice can be simple or complex based on the mating landscape a female must learn: single male phenotypes (e.g. coercive-only (*G. affinis*), courting only (*P. magnificus*), no discrimination (*O. deletron*)) versus multiple male phenotypes (e.g. territorial/guarder/sneaker males (*Uta* spp.), courting/coercive (*D. melanogaster*), guarder/female mimic/sperm bomber (*Isopoda* spp.)). In both mating categories, females might utilize inputs from sensory perception, steroid priming, social recognition and synaptic plasticity processes in making mating decisions. However, we propose that the relative complexity of the mating landscape is reflected in relative neural pathway engagement: single phenotype systems primarily require sensory perception and steroid/reproduction pathways over social recognition or synaptic plasticity-associated pathways while female mating decisions in a multiple male tactic/morph system would also require neural activation of social recognition and synaptic plasticity associated neural pathways in the Social Decision Making Network (SDMN). Example of differential synaptic plasticity gene expression (*neuroligin-3*) across the SDMN in *X. nigrensis* females exposed to single male phenotypes (coercive-only males, on left) versus multiple males (courting and coercive, on right) with a schematic sagittal section of fish brain (see [48,49] for brain region names). Each line between brain regions signifies unique significant positive correlations of *neuroligin-3* in female *X. nigrensis* exposed to different male contexts. Bolded brain regions with asterisks indicate regions that show significant increased synaptic plasticity gene expression (*neuroserpin, neuroligin-3*) and positive covariance with female preference behavior [48,49]. The differential cognitive complexity of mate choice also informs female behavioral output: from simple systems characterized by hormone and sensory-dependent threshold gating invariant with experience, to more complex systems with hormone dependence modulated by context and experience-dependent decision rules. Photo Credit: *O. deletron* (copyright 2011 MBARI), *Isopoda spp.* (courtesy of Dr. Stephen Shuster), *D. melanogaster* (T. Chapman in [57]), *Uta* spp. (courtesy of Robb Hannawacker).

learning; yet the specific type of learning may impose different levels of cognitive demand. Minimal cognition may be involved in closed-ended learning processes such as sexual imprinting, where associations between stimuli and responses are made at an early developmental stage and are referenced later without significant modifications. On the other hand, open-ended learning where associations between stimuli and response are continually updated and refined through different social experiences may require greater cognitive demand. Evidence that

younger females deviate in mate preference functions from older, more experienced females is prevalent, including not just bower birds [10], but also flies, field crickets, treehoppers, butterflies, wolf spiders, and poeciliid fishes (reviewed in [12]). Further evidence of open-ended learning processes is found in mate choice-copying, wherein females use social learning to copy the mate choices of other females (as observed in birds [13], fish [14], and flies [15]). Overall, recognition that cognitive processes are important to mate choice decisions is gaining attention [2,16,17], yet there is very little discussion on whether the variation we observe in mate choice cognitive processing is predictive.

Do the cognitive demands of mate choice decisions scale with the complexity of the mating landscape?

To narrow the focus of our scope, we will concentrate on the diversity of mating systems as a predictive variable influencing the relative contribution of cognitive processing in mate choice behavior. Mating systems vary as a function of how males and females interact with each other, and the nature of these interactions may drive differential investment in cognitive processing. For example, in systems with a single male phenotype, mating interactions can range from no-choice or coercive systems (e.g. pupal mating male butterflies, elephant seals), to systems where males employ non-coercive display and ornamentation to attract females (e.g. female choice in lekking birds). For the majority of species, however, there is some mixture of these two types of interactions (coercion or choice), thereby increasing the dimensional complexity of male assessment. In some taxa, individual males employ discrete behavioral roles such as courtship display, sneak copulations, or coercive mating attempts, which we refer to as male mating morphs or strategies. In other taxa individual males may display one or all of these different roles depending on condition or context, which we refer to as male mating tactics. We expect selection on female mate choice behavior to favor increased investment in social cognition in systems characterized by multiple male mating strategies and/or tactics over those with a single male phenotype.

We recognize that focusing on the diversity of male phenotypes may be an over-simplification, as demand for cognitive processes is also likely to arise in taxa with single courting phenotypes that display multimodal signaling or vary in condition-dependent traits. However, restricting our focus to the number of male mating strategies or tactics provides a simple framework for broad phylogenetic comparisons, as well as ease of assigning costs and benefits to female mating decisions. In general, each alternative male reproductive strategy or tactic does not represent equal fitness costs and benefits to females, therefore selection should favor the ability of females to recognize and predict a male's likely behavioral action so

that she can mount the appropriate response to maximize her own fitness. Across many taxa, females have evolved behaviors to resist coercive males while also discriminating among courting males [6]. This discrimination should be particularly important in systems where male coercion of females during mating encounters inflicts costs to females [6,18,19], and mechanisms by which females choose mates have been shown to increase female fitness [6,20]. The fact that the evolution of resistance and choice behaviors is decoupled in some taxa suggests that females can recognize different social agents and respond with context-appropriate responses. In other words, there is good reason to think that under conditions where females experience multiple male phenotypes, females engage in social cognition during mate choice encounters.

Increasing evidence suggests non-human animals can adjust their cognitive effort based on cost/benefit decision-making [21], and humans show increased cognitive search effort with increased variation in the choice environment [7]. A logical extension of these examples suggests that as variation in male reproductive tactics or morphs. In increases in a species, there should be a concomitant increase in female cognitive processing demands. In taxa with a single male mating phenotype, females may mediate mate choice encounters with simple graded or threshold responses mediated by sensory systems or some varying level of cognitive demand depending on the complexity of the male display. Mating systems with both coercive and courting male phenotypes or males with mixed reproductive tactics represent a social landscape within which females must learn, discern, and react appropriately in a context-specific fashion. In taxa with multiple male mating phenotypes, interactions with *each* male tactic/morph require a unique set of evaluation processes and decision rules that may be influenced by experience as well as sensory processes.

In particular, we predict that the relative cognitive investment in mate choice decision-making will scale with the number of different male phenotypes a female must learn throughout her lifetime. Here we focus on poeciliids, a family of internally fertilizing fish with a diversity of mating systems, including taxa with up to 3 or more male phenotypes (including coercive, courting, and mixed strategies). Although learned preferences for some sensory cues are imprinted during juvenile social exposure [22], multiple lines of evidence in poecillid fishes point to females continuously altering their preference function as they age [23–25], with social experiences as a major contributor [26–29]. Unlike taxa where reproductive senescence may relax choosiness [30], in some poeciliid species females may become stronger discriminators as they age. Behavioral evidence for female preference toward the courting phenotype over the coercive

phenotype as an age-dependent function has been found in two different poeciliid species (*Xiphophorus multilineatus* [24,29]; *X. nigrensis* [25]). Is this link between experience and changing preference function due to chance or simple size-assortative mating? Or, is the shifting of preferences toward a particular mating phenotype an example of open-ended female learning?

Mate choice as social cognition: genomic predictions and molecular evidence

We propose that as females make decisions based on learned male phenotypes and their costs and benefits, they engage cognitive pathways in addition to responding to sensory or endocrine cues. Open-ended learning presupposes the ability to modulate neuronal connections (synaptic plasticity), similar to the requirement for synaptic plasticity processes in experience-dependent modification of courtship behavior in male drosophila [31•], or open-ended song learning birds [32]. Furthermore, as the number of male mating phenotypes increase, there is a concomitant need to recognize different types of social agents. Therefore, we predict differential engagement of synaptic plasticity-associated and social recognition pathways during mate choice conditions in females from species with multiple male morphs versus those with a single male morph (Figure 1).

Molecular evidence from our research using three poeciliid species with contrasting mating systems supports this prediction. Expression of *N-methyl-D-aspartate receptor* (*NMDAR*), the central mediator of synaptic plasticity signaling [33], is correlated with mate choice exposure in a species with alternative male mating morphs (swordtails, [34]) but not in females from a monomorphic, all-coercive male species (mosquitofish (*Gambusia affinis*); [35]). Blocking NMDAR signaling with an antagonist eliminates female preference for the courting class male in female swordtails, suggesting that NMDAR pathways regulate perception of the different male phenotypes in this system [36•]. Furthermore, expression of other synaptic plasticity-associated genes (*neuroserpin, neuroligin-3*) is positively correlated with increased mate preference when swordtail females are simultaneously exposed to courting and coercive male conspecifics [34]. These same genes are negatively correlated with mate preference behavior in the brains of female mosquitofish presented with a choice between two coercive conspecific males [35]. However, female mosquitofish exposed simultaneously to coercive and courting phenotypes (including conspecific and heterospecific males) reverse their species-typical negative covariance of synaptic plasticity genes and mate preference to a positive one [37]. This positive relationship is similar to the pattern found in the alternative male morph system of swordtails, and suggests that exposure to variable male phenotypes may induce engagement of cognitive processes.

We expect other genomic responses besides synaptic plasticity genes if social cognition is crucial for navigating complex mating landscapes. In particular, genomic pathways that facilitate social recognition are crucial. Evidence from another fish species with alternative male morphs, the medaka (*Oryzias latipes*), reveals that terminal-nerve gonadotropin-releasing hormone (TN-GnRH3) is a critical peptide in regulating female ability to recognize familiar from unfamiliar males [38••]. In the scramble competition of the polygynous medaka system, both sneaker and courting males compete for females [39] and female preference toward courting males increases with greater familiarity. Transgenic manipulation of the TN-GnRH3 neurons alters female receptivity toward familiar and unfamiliar courting males [38••].

The nonapeptides oxytocin and vasopressin (and their non-mammalian homologues isotocin, vasotocin) are also expected to play a role in mediating the social cognition of mate choice as they can mediate valence assignment (positive or negative) to different social agents [40,41•]. Although oxytocin and vasopressin are famous for regulating partner preference following co-habitation [40], their roles in pre-copulatory mate choice decisions are understudied. Voles are famous for their variation in mating systems across species, and also exhibit variable male reproductive tactics even within generally socially monogamous species (wanderer vs. territorial males; [42]). Recent research exploring alternative *female* mating tactics in meadow voles (pairing vs. remaining single) demonstrates predictive patterns of oxytocin and vasopressin receptor expression with female reproductive decisions in brain regions that are key to social decision-making (SDMN, [43] and see below).

Mate choice as social cognition: the neural network predictions

Both genomic and neural responses should underlie the context-specific recognition, evaluation, and behavioral response toward specific social agents that occurs during mate choice encounters. Hence, along with gene pathways associated with social recognition and gating (nonapeptides, NMDAR, TN-GnRH3) as well as learning (synaptic plasticity), we predict that the neural networks and region-specific neural activation within the female brain scales with complexity of mate choice decisions (e.g. number of male tactics/morphs to learn).

There is strong comparative evidence for conserved neural circuitry mediating social decision-making within the vertebrate brain [44,45••]. The Social Decision-Making Network (SDMN) as proposed by O'Connell and Hofmann comprises a set of interconnected brain regions including the mesolimbic reward system (involved in evaluating stimuli salience, valence as well as learning and memory) along with a set of steroid-sensitive brain regions involved in sexual and social

response (Social Behavior Network; [46,47]). Although numerous social cognition tasks have been shown to involve the SDMN (reviewed in [4]), relatively few studies have explored mate choice decision-making within this neural framework [48,49].

We predict that there will be variation in SDMN engagement during female mate choice behavior that varies as a function of male reproductive phenotypic diversity. Specifically, mate choice decision-making across vertebrates is likely to involve the engagement of sensory processing centers along with steroid-sensitive regions that modulate sexual activity (e.g. preoptic nucleus, POA). However, as the social cognition task of mate choice increases (with increasing male morph/tactic complexity) females should show a concomitant increase in activation of the learning and memory neural structures of the SDMN to allow access to decision rules and gate the appropriate behavioral response. Although earlier researchers did not evaluate learning and memory centers during mate choice responses, many have shown that mate choice behavior does involve differential activation of sensory processing centers [50,51], as well as steroid-sensitive regions [e.g. 52]. Recent work with cichlids supports the proposition that social cognition pathways are engaged during mate evaluation. Gravid females observing their preferred partners either win or lose a fight with a rival resulted in differential immediate early gene expression within nodes of the SDMN [52].

We have begun to test the hypothesis of differential SDMN engagement as a function of alternative male phenotype in poeciliid fishes. Swordtail females exposed to mate choice conditions with two alternative morphs (large courter vs. small coercive) show differential expression of synaptic plasticity and immediate early gene expression along with covariation with preference behavior in 3 out of 10 brain regions examined across the SDMN [48,49]. Two of these brain regions are associated with SDMN reward areas linked to learning and memory in teleosts (Dm and Dl; see Figure 1) and the third is linked to sexual activity (POA). Furthermore, analyses of neurogenomic networks (significant gene expression correlations between brain regions) show that co-expression of synaptic plasticity genes across SDMN regions increases when females are exposed to a mixed social landscape relative to coercive only phenotypes (Figure 1). A complete test of this hypothesis will require comparing activation of SDMN circuitry across taxa with different levels of alternative male complexity. Poeciliid fishes are a promising system for this examination as there are taxa with single male phenotypes (all coercives (*Gambusia* sp), all courting (e.g. *Xiphophorus variatus*), multiple discrete phenotypes (courters, coercers or mixed strategy males, e.g. *X. nigrensis*, *X. multilinatus*, and *Poecilia latipinna*), and species with males that employ multiple tactics (e.g. *Poecilia reticulata*).

Where do we go from here?

The exploration of female mate choice as social cognition is at an exciting stage. Neurogenomic tools can now be applied to behaviorally diverse taxa that until recently have remained outside the genomic purview. Parallel research exploring the genomic underpinnings regulating plasticity across male reproductive phenotypes reveals substantial differences in transcriptome profiles across alternative male phenotypes [53–55], and our research has revealed strikingly different neurogenomic responses within females exposed to different male types [2,34,56]. With female choice behavior, we have some early clues (behavioral and neurogenomic) that variation in female response to different male phenotypes may involve learning and other pathways related to social cognition in the brain.

Further studies are required to explicitly test the decision-rules (and the neurogenomic responses that regulate them) arising from different social experiences with a diverse range of male phenotypes. For example, side-blotched lizards (*Uta* spp.) are a famous example of a species with multiple male morphs and tactics, with genetically based color morphs and discrete male strategies (territorial, guarder, sneaker; Figure 1). These would be an ideal group to test if the contrasting molecular and neural patterns found in female poeciliids are also found in other taxa with complex and simple (e.g. another Phrynosomatidae species with a single male morph) mating systems. Another appealing direction would be a comparison in female cognitive processes (and their behavioral and neural correlates) in the ruff (*P. pugnax*), a species with multiple male morphs and experience-dependent mating decision rules (Figure 1) with its close relative the great snipe (*Gallinago media*), a closely related sandpiper with a lek mating system but no known alternative male morphs or tactics. Species that have traditionally been outside established genomic model systems can now be used to integrate some of the crucial behavioral experiments (e.g. common garden rearing under controlled social conditions; robust behavioral assays for mate choice and social cognition) with next-generation neurogenomic tools to test these hypotheses. We foresee a social cognition framework as key to understanding the behavioral, genomic and neural complexities of mate choice decision-making, as well as the relative contributions of cognitive, sensory, and endocrine influences in females encountering alternative male tactics/morphs.

Conflict of interest

We authors have not been paid for this work; and we have disclosed all of our funding for this research in the Acknowledgements section of our manuscript.

Acknowledgements

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