CellPress

Current Biology
Dispatches

Mate Choice: Charting Desire's Tangled Bank

Gil G. Rosenthal
Department of Biology, Texas A&M University, College Station, TX 77843, USA and Centro de Investigaciones Científicas de las Huastecas "Aguazarca", Calnali, Hidalgo, Mexico
Correspondence: grosenthal@bio.tamu.edu
http://dx.doi.org/10.1016/j.cub.2016.02.016

Choosing a mate requires a way to turn sexual arousal into sexual action. A recent paper identifies a hormone receptor that acts as a molecular gatekeeper in reproductive decisions. Focusing on mate-choice mechanisms may clarify longstanding evolutionary puzzles in sexual selection and speciation.

Long after he had formulated evolutionary explanations for complex structures like the vertebrate eye, elaborate ornaments like the peacock's intricate plumage made Darwin "sick" with perplexity [1]. His proposed agent of selection to account for such extravagances — the peahen's ineffable "taste for the beautiful" [2] — is as close as Darwin ever gets to mysticism. He punted on the nature of mating preferences for good reason: if the beauty of the plumage was vexing in the face of natural selection, how much more so the 'taste' that drove its evolution? For well over a century, a Darwinian mix of sensibility and good ol' androcentrism kept the focus firmly on male ornaments, with little attention to what's going on inside the peahen. A surge of recent work has begun unraveling the complexity of mate-choice mechanisms, causing us to reevaluate their evolutionary history and role.

As reported in this issue of *Current Biology*, Juntti and colleagues [3] studied the neuromolecular regulation of mating behavior in females of a mouthbrooding Rift Lake cichlid fish, *Astatotilapia burtoni*. If a female is sufficiently impressed by a courting male, she follows him to his territory, where the pair swim in tight circles with the female releasing eggs and picking them up in her mouth. She then has the male fertilize the eggs by mouthing his urogenital region as he releases sperm. Previous work had shown that circling — the last stage of female mate choice before egg release — depended on a prostaglandin hormone [4]. Juntti and colleagues combined functional neuroanatomy, hormone manipulations, and CRISPR/Cas9 inactivation of the prostaglandin receptor *Ptgfr* to show that female mating behavior depends on the activation of *Ptgfr*+ neurons in distinct brain regions.

A series of neuroanatomical studies by Hoke and colleagues [5] identified a similar 'gate' in túngara frogs: sexual responses to an acoustic stimulus predicted brain activity of sensorimotor regions that, as in this study, connect external inputs to motor responses. *Ptgfr*+ neurons might act as a gate in cichlids, initiating motor activity only when appropriate signals are received. These sensorimotor gates, however, involve different stages of mate choice in each study organism: the sensorimotor regions in túngara frogs determine which displaying male she moves towards, whereas *Ptgfr*'s gating comes into play once a female cichlid is already in intimate contact with a male, determining whether a female transitions from courtship to coordinated release of eggs. Such a mechanism can be key to mate choice, as Juntti *et al.* suggest. This is especially likely if female *A. burtoni* deposit eggs with multiple males like other mouthbrooding cichlids [6], giving females the opportunity to bias the distribution of eggs unevenly among males [7]. In mammals, prostaglandin receptors are critical to pregnancy [8], and they may play a similar role in modulating mate choice through differential abortion or resource allocation. Prostaglandins similarly stimulate oviposition in orthopteran insects [9]. Across animals, common neuroendocrine mechanisms may underlie female decisions about allocating reproductive resources before, during, and after mating.

Juntti *et al.* suggested that *Ptgfr* could serve specialized functions in distinct parts of the brain, with some responding to circulating prostaglandin and others responding to brain-synthesized prostaglandin. This finding reinforces the point that mate-choice mechanisms, like most organismal processes, are evolutionarily constrained by function across multiple contexts. One such function is as a sensory receptor in the nose. Classes of odorant receptor neurons in another teleost fish are highly sensitive both to the *Ptgfr* agonist and to prostaglandin metabolites produced by females [10]. If females release more (or less) prostaglandin in the presence of a preferred mate, the sensory functions of *Ptgfr* could mediate mate copying, whereby females incorporate public information about the preferences of other females [11].

Whether before or during mating, the *Ptgfr* system in *A. burtoni* has the capacity to modulate a central property of mate choice — choosiness (Figure 1). The choosier a female, the more selective she is among potential mates, rejecting all but a lucky few [12]. A plausible and economical, but so far entirely hypothetical, scenario is that choosiness at this stage of courtship involves modulating sensitivity of *Ptgfr*+ neurons to upstream stimulation from male signals, and therefore the likelihood that a female will spawn with a male. There are numerous ways this system could modulate the electrical activity of *Ptgfr*+ neurons to produce variation in choosiness: females should be choosier, rejecting all but the most preferred males, if their *Ptgfr* receptors have lower binding affinity to the hormone, produce less *Ptgfr* protein or prostaglandin in specific brain regions, or respond differently to other incoming signals (Figure 1).

The *Ptgfr* system provides an appealing mechanism for modulating choosiness, but it remains to be seen whether individual or interspecific variation in

choosiness is predicted by regulatory or structural variation at *Ptgfr*. One may be sobered by efforts to unravel the molecular underpinnings of another mate-choice mechanism, pair-bonding, in mammals. Male meadow voles are pair-bonded and monogamous, while male prairie voles are unpaired and polygynous. Targeted manipulation of a nonapeptide receptor in specific brain regions is sufficient to reverse the pair-bonding behavior of these two species [13]. Despite enthusiasm about the 'monogamy gene', subsequent inter- and intraspecific studies showed that monogamy varied through other, more complex means [14,15].

Similarly, *Ptgfr* is likely to be only one of multiple mechanisms underlying the decision to mate, let alone a female's overall choosiness throughout the process of mate choice. Specifically, the perceptual discrimination of variation in body coloration [16] surely plays a role in the early stages of choice. This caveat notwithstanding, identifying a molecular mechanism for gating of brain reproductive responses points the way for understanding proximate and evolutionary responses of mate choice to environmental variation. Choosiness can vary both positively and negatively with external stressors. Of central evolutionary importance is the extent to which choosiness covaries with physiological receptivity: are individuals non-choosy because they are sexually active and mating at random, or because they're unreceptive and not mating at all? A main finding of Juntti *et al.*'s work is that the *Ptgfr* system functions as a mechanism to modulate sexual response, and therefore choosiness, independently of sexual receptivity. This means that even though females are reproductively primed, they can forgo mating opportunities unless *Ptgfr*+ neurons receive the appropriate internal and external signals.

Choosiness independent of reproductive state may be important in both the formation of new species, and in species' collision through hybridization. *A. burtoni* is one of hundreds of haplochromine cichlids that have originated in the Rift Lakes over a few tens to hundreds of thousands of years. Seehausen and colleagues [16] showed that mate-choice mechanisms allow species to form at close quarters,

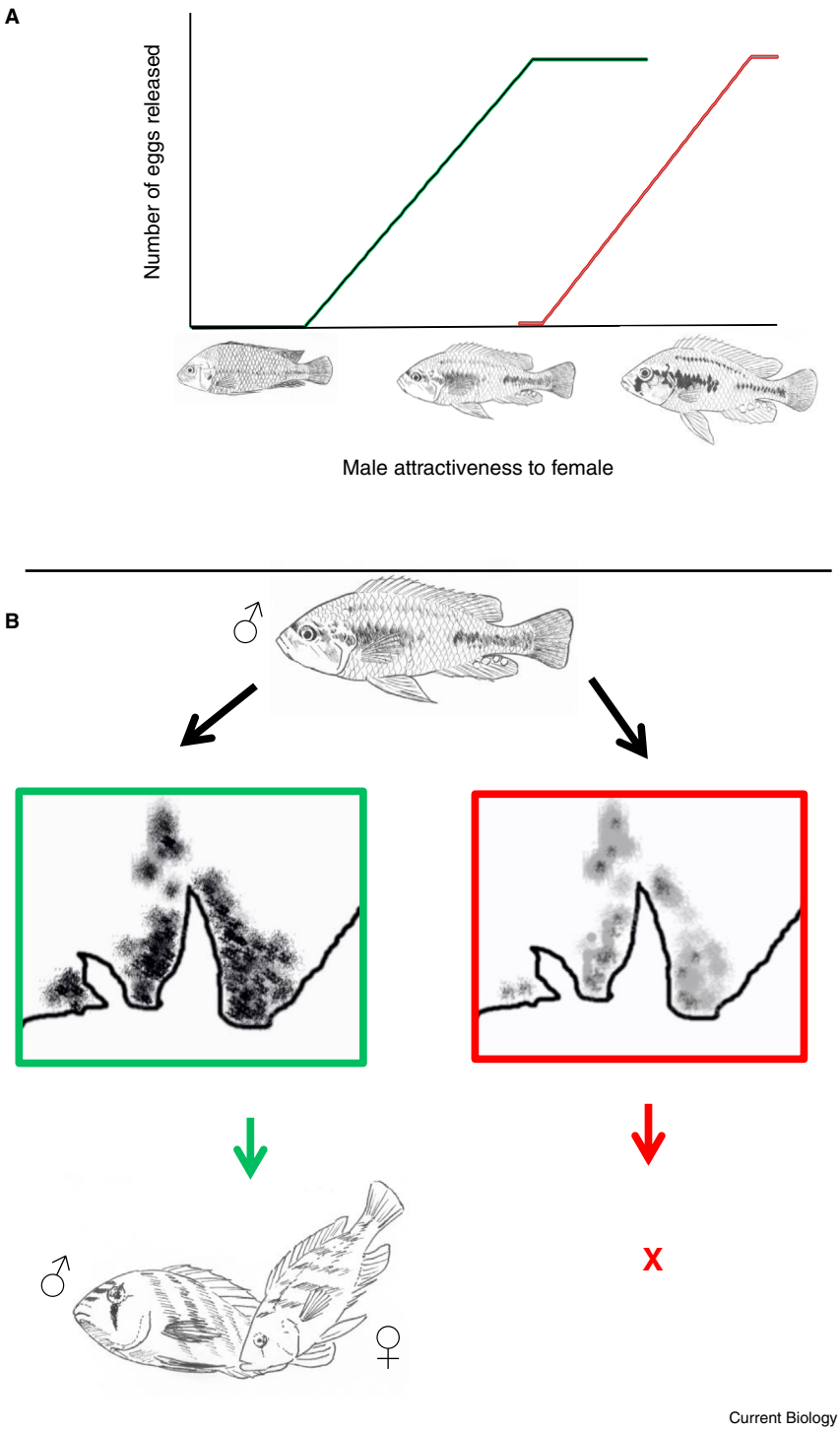

Figure 1. Modulating choosiness in mate choice.
(A) Mate-preference functions differing in choosiness. A female with the curve in red is choosier, accepting a smaller set of suitable mates, than a female with the curve in green.
(B) A hypothetical mechanism modulating variation in choosiness. A moderately attractive male elicits an upstream signal of intermediate strength. In a less choosy individual (green), this signal produces a response from sensitive Ptgfr+ neurons that in turn leads to circling and egg deposition. For a choosier individual (red), Ptgfr+ neurons are less sensitive and respond only to stronger inputs. Line drawings by Matt Stephens.

in this case along a depth gradient, through a process called sensory drive. Ecological selection on sensory function — here, color sensitivity — leads to divergent mating traits and preferences, and thereby to red and blue sister species. Intriguingly, however, allelic variation in color sensitivity failed to explain much variation in preferences [16]. This suggests that differential attractiveness of red and blue males resides beyond the sensory periphery. In the red species, non-color cues from red males could, for example, elicit stronger responses from *Ptgfr*+ neurons than those of blue males.

Conversely, modulation of *Ptgfr* provides a candidate mechanism to account for numerous behavioral experiments showing that sexually receptive females are frequently non-choosy. Under social isolation, ecological disturbance, or predation risk, females relax their preferences and will mate with males of a different species [17]. The evolutionary history of east African cichlids is characterized by recurrent, pervasive hybridization, which is likely a major contributing factor to phenotypic diversification [18] and reproductive isolation [19] in this and other adaptive radiations. In Rift Lake cichlids, environmental effects on choosiness, or lack thereof, lead females to mate with heterospecifics and allow gene flow between lineages [16]. The modulation of choosiness via *Ptgfr* may play a role in both the formation of reproductive barriers, through increased choosiness, and their episodic interruption when choosiness is relaxed by environmental factors.

Juntti and colleagues have identified a molecular mechanism that turns preferences into choices, and will hopefully spur others to focus on prostaglandin-mediated systems [4] and sensorimotor centers in the brain [5] as mate-choice mechanisms. The radiation of African cichlids provides an ideal natural experiment for evaluating and generating functional predictions about mate-choice evolution, particularly now that genetic manipulation enables direct tests of hypotheses about gene function.

The preeminence of sexual selection theory, developed not to understand the evolution of mate choice but to understand the evolution of display traits, has led us away from studying this most consequential of processes on its own terms. The sensorimotor gate between desire and consummation may be a principal theater in the evolution of mate choice, or it may be a conserved mechanism for synchronizing egg release and social behavior during spawning. Either way, we will surely learn more about sexual selection and speciation by focusing on how mate-choice mechanisms work rather than on the putative information content of courtship signals. Juntti and colleagues are among the vanguard of a renewed focus on decision mechanisms as evolving phenotypes in their own right.

REFERENCES

1. Ryan, M.J., and Cummings, M.E. (2013). Perceptual biases and mate choice. Annu. Rev. Ecol. Evol. Syst. *44*, 437–459.

2. Darwin, C. (1859). On the Origins of Species by Means of Natural Selection (London: Murray).

3. Juntti, S.A., Hilliard, A.T., Kent, K.R., Kumar, A., Nguyen, A., Jimenez, M.A., Loveland, J.L., Mourrain, P., and Fernald, R.D. (2016). A neural basis for control of cichlid female reproductive behavior by prostaglandin F2α. Curr. Biol. *26*, 943–949.

4. Kidd, M.R., Dijkstra, P.D., Alcott, C., Lavee, D., Ma, J., O'Connell, L.A., and Hofmann, H.A. (2013). Prostaglandin F2α facilitates female mating behavior based on male performance. Behav. Ecol. Sociobiol. *67*, 1307–1315.

5. Hoke, K.L., Ryan, M.J., and Wilczynski, W. (2010). Sexually dimorphic sensory gating drives behavioral differences in tungara frogs. J. Exp. Biol. *213*, 3463–3472.

6. Immler, S., and Taborsky, M. (2009). Sequential polyandry affords post-mating sexual selection in the mouths of cichlid females. Behav. Ecol. Sociobiol. *63*, 1219–1230.

7. Eberhard, W.G. (2009). Postcopulatory sexual selection: Darwin's omission and its consequences. Proc. Natl. Acad. Sci. USA *106*, 10025–10032.

8. Sugimoto, Y., Yamasaki, A., Segi, E., Tsuboi, K., Aze, Y., Nishimura, T., Oida, H., Yoshida, N., Tanaka, T., and Katsuyama, M. (1997). Failure of parturition in mice lacking the prostaglandin F receptor. Science *277*, 681–683.

9. Arnqvist, G., and Rowe, L. (2005). Sexual Conflict (Princeton, NJ: Princeton University Press).

10. Sorensen, P., Hara, T., Stacey, N., and Goetz, F.W. (1988). F prostaglandins function as potent olfactory stimulants that comprise the postovulatory female sex pheromone in goldfish. Biol. Reprod. *39*, 1039–1050.

11. Danchin, É., Giraldeau, L.-A., Valone, T.J., and Wagner, R.H. (2004). Public information: from nosy neighbors to cultural evolution. Science *305*, 487–491.

12. Reinhold, K., and Schielzeth, H. (2015). Choosiness, a neglected aspect of preference functions: a review of methods, challenges and statistical approaches. J. Comp. Physiol. A *201*, 171–182.

13. Young, K.A., Gobrogge, K.L., Liu, Y., and Wang, Z. (2011). The neurobiology of pair bonding: Insights from a socially monogamous rodent. Front. Neuroendocrinol. *32*, 53–69.

14. Ophir, A.G., Wolff, J.O., and Phelps, S.M. (2008). Variation in neural V1aR predicts sexual fidelity and space use among male prairie voles in semi-natural settings. Proc. Natl. Acad. Sci. USA *105*, 1249–1254.

15. Fink, S., Excoffier, L., and Heckel, G. (2006). Mammalian monogamy is not controlled by a single gene. Proc. Natl. Acad. Sci. USA *103*, 10956–10960.

16. Seehausen, O., Terai, Y., Magalhaes, I.S., Carleton, K.L., Mrosso, H.D.J., Miyagi, R., van der Sluijs, I., Schneider, M.V., Maan, M.E., Tachida, H., *et al*. (2008). Speciation through sensory drive in cichlid fish. Nature *455*, 620–626.

17. Rosenthal, G.G. (2013). Individual mating decisions and hybridization. J. Evol. Biol. *26*, 252–255.

18. Seehausen, O. (2013). Conditions when hybridization might predispose populations for adaptive radiation. J. Evol. Biol. *26*, 279–281.

19. Schumer, M., Cui, R., Rosenthal, G.G., and Andolfatto, P. (2015). Reproductive isolation of hybrid populations driven by genetic incompatibilities. PLoS Genet. *11*, e1005041.