



SYMPOSIUM

Perspective: Matching, Mate Choice, and Speciation

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Synopsis Matching was developed in the 1960s to match such entities as residents and hospitals, colleges and students, or employers and employees. This approach is based on “preference lists,” whereby each participant ranks potential partners according to his/her preferences and tries to match with the highest-ranking partner available. Here, we discuss the implications of matching for the study of mate choice and speciation. Matching differs from classic approaches in several respects, most notably because under this theoretical framework, the formation of mating pairs is context-dependant (i.e., it depends on the configuration of pairings in the entire population), because the stability of mating pairs is considered explicitly, and because mate choice is mutual. The use of matching to study mate choice and speciation is not merely a theoretical curiosity; its application can generate counter-intuitive predictions and lead to conclusions that differ fundamentally from classic theories about sexual selection and speciation. For example, it predicts that when mate choice is mutual and the stability of mating pairs is critical for successful reproduction, sympatric speciation is a robust evolutionary outcome. Yet the application of matching to the study of mate choice and speciation has been largely dominated by theoretical studies. We present the hamlets, a group of brightly colored Caribbean coral reef fishes in the genus *Hypoplectrus* (Serranidae), as a particularly apt system to test empirically specific predictions generated by the application of matching to mate choice and speciation.

Introduction

A practical problem arose when residency began to be implemented as part of the curriculum for medical students in the United States during the past century. Students wanted to undertake their residency in the best possible hospital, and hospitals wanted to attract the best students. Yet, there were more available positions than students, which generated intense competition among hospitals for residents. This resulted in the advancement of the date of the finalization of binding agreements between students and hospitals, up to 2 years before the position would be actually taken up. How can students and hospitals be matched in a way that is optimal for students? For hospitals? This is a classic problem of matching (see Roth 1984 for a review). Yet matching can be applied to a variety of questions, as for example, the matchings between students of colleges, men and women, buyers, and sellers, and—our focus

of interest here—males and females in the context of mate choice and sexual reproduction.

Matching is based on lists of preferences, whereby each participant ranks all potential partners according to his/her preferences and tries to match with the highest-ranking partner available, i.e., achieve the highest satisfaction. For example, in the case of residents and hospitals, each resident has a specific ranking of hospitals according to his/her preferences and each hospital has a specific ranking of students according to its needs and preferences. These rankings, referred to as “preference lists,” constitute the basic material upon which matching is built. Matching is said to be two-sided when members of two different groups are matched (e.g., residents and hospital), and one-sided when members of a single group are matched among themselves (e.g., roommates, the “roommate problem”). In both cases, matching constitutes a complex problem due to the

large number of possible matches. For example, in the roommate problem there are $(2N)!/[2^N(N!)]$ ways to match $2N$ individuals in pairs in two-bedroom apartments (Morrill 2010), which represents over 654 million possibilities for only 20 individuals.

An important achievement of matching has been its ability to address such complex problems with relatively simple algorithms. Gale and Shapley (1962) showed notably that a stable set of matching always exists in the “marriage problem,” in which men and women are matched in couples. A stable set of matching corresponds to a situation in which no new pair can form that would improve the satisfaction of both partners. Gale and Shapley (1962) pointed out that such a situation is always produced by the following algorithm: (1) each man proposes to his favorite woman, (2) each woman who receives more than one proposal rejects all but her most preferred man, who is accepted provisionally, (3) if a man is rejected he proposes to his next choice, and again each woman who receives more than one proposal (including a provisionally accepted man, if applicable) rejects all but her most preferred man, who is accepted provisionally. This procedure follows until no man is rejected, at which point all women accept their partner definitively. At the end of this algorithm, called the “deferred-acceptance procedure,” no new pair can form that would improve the satisfaction of both partners; the set of pairings is stable. This means that if a man was to propose to a woman he prefers more than his wife, she would not accept him because her husband ranks higher than him in her preference list. Conversely, if a woman was to propose to a man she prefers more than her husband, he would not accept her because his wife ranks higher than her in his preference list. Of course, the symmetric algorithm where women propose and men choose also leads to a stable set of matching, although as discussed below not necessarily the same one. Note that the deferred-acceptance procedure does not necessarily imply an equal number of men and women. In this case, a stable set of pairings also exists, with some individuals remaining single.

In addition to stability, an important concept in matching is optimality. A stable set of matching is said to be optimal if every participant is at least as well off under it as under any other stable set of matching. Gale and Shapley (1962) showed that the version of the deferred-acceptance procedure where men propose leads to a pairing configuration that is optimal for the men (i.e., every man is at least as well off under this set of matching as under any other stable assignment) and, conversely, that the

version in which women propose leads to a pairing configuration that is optimal for the women. These two stable sets of pairings differ unless a single stable assignment exists, in which case it is reached by both versions of the algorithm.

The deferred-acceptance procedure is a good illustration of this approach to matching, which has been largely dominated by the question as to whether stable sets of matching exist, if so which ones are optimal, and how to reach these assignments. These types of questions have been addressed from two fields, computer science and economics game theory, as illustrated by the two monographs *The Stable Marriage Problem: Structure and Algorithms* by Gusfield and Irving (1989) and *Two-sided Matching: A Study in Game-theoretic Modeling and Analysis* by Roth and Sotomayor (1990), respectively. Here, we discuss some implications of matching for the study of mate choice and speciation, and emphasize an approach that does not necessarily focus on stable or optimal sets of matching (Almeida and de Abreu 2003).

Implications for the study of mate choice and speciation

The application of matching to the study of mate choice presents several aspects that differ fundamentally from classic approaches. Most importantly, pairing is explicitly considered as a “context-dependant” process: it depends not only on the traits and preferences of two potential mates, but also on the traits, preferences and pairing configuration in the entire population. Two individuals may or may not end up pairing depending on whether preferred mates exist in the population, if so whether they have a partner, and if so whether they would be inclined to switch partners. When this is considered explicitly for all sexually mature individuals in a population, pairing becomes precisely the complex problem addressed by matching. This is in sharp contrast with classic approaches to mate choice and sexual selection in which pairing is considered largely out of its social context, typically by looking at the probability of mating between pairs of individuals without explicit consideration to what other members of the population are doing (Lande 1981).

In addition, matching considers explicitly the “stability” of mating pairs. The notion of stability defined above was considered at the level of the entire population, with a stable set of pairings corresponding to a situation in which no new pair can form that would improve the satisfaction of both partners. Stability can also be considered at the level of

individual pairs. For example, a pair in which both individuals rank first in the preference list of their partner is stable (these two individuals cannot form a new pair that would improve their satisfaction), even if the set of pairings is not stable (other members of the population can form new pairs that would improve their satisfaction). From a biological perspective, the concept of stability of mating pairs applies to all situations in which “spending time together” is required for successful reproduction. Spending time together could correspond to a variety of situations, as for example the time required for courtship, building a nest or raising offspring together. The stability of the mating pair is critical in these situations because reproductive success will be affected if one of the mates decides to switch partners during this time. On the other hand, two mates who have already invested a significant amount of energy in the process of pairing (and/or mating, raising young) may not be inclined to switch partners, even if preferred partners are available in the population. By considering explicitly the stability of pairings, matching provides an opportunity to address the consequences of pair stability for mate choice, sexual selection and speciation.

Another important aspect of matching is that mate choice is “mutual”: selection of males by females and of females by males. Mutual mate choice is known to occur in a variety of taxa including fish, birds, amphibians, insects, and rotifers (Kraaijeveld et al. 2007). In addition, while mate choice is often thought of as the familiar situation in which females choose among males, the significance of males’ mate choice for the maintenance of females’ ornamentation is receiving increasing attention and support, even in polygynous species (Amundsen 2000; Clutton-Brock 2007, 2009; Kraaijeveld et al. 2007). Thus, mutual mate choice does not appear to be a rarity in nature, and may even turn out to be more common than generally assumed. Note that matching does not necessarily imply that mutual mate choice is perfectly symmetric. As discussed above, a rather subtle level of asymmetry between the sexes arises when one sex proposes and the other sex disposes. Asymmetry in levels of choosiness between the sexes could also be implemented within the framework of matching, for example by applying a randomization procedure to the preference lists of individuals of one sex.

Additional implications of matching for the study of mate choice have been emphasized by Bergstrom and Real (2000). An important point is that since each individual is characterized by a specific preference list, matching provides an opportunity to

consider preferences that vary between individuals, as opposed to preferences that are uniform within a population. It is also to be noted that matching is quite flexible with respect to mating systems. As mentioned above, it does not necessarily require an equal number of individuals of both sexes or symmetric, mutual mate-choice. In addition, it does not necessarily imply the one-to-one matching between the two sexes addressed by the marriage problem. For example, in the case of residents and hospitals, more than one resident can be matched to each hospital. From a biological perspective, this situation of many-to-one matching corresponds to pairing in polygynous or polyandrous species, in which one male (female) can be paired to several females (males). The main concepts, used in matching and their implications for mate choice are summarized in Table 1.

Predictions

The application of matching to mate choice and speciation is not merely a theoretical curiosity; it can generate counter-intuitive predictions and lead to conclusions that differ fundamentally from classic theories of sexual selection and speciation. For example, in the marriage problem, the fact that the stable set of matching reached by the deferred-acceptance procedure is optimal for men when men propose and optimal for women when women propose is quite counter-intuitive; it implies that overall, what is most beneficial is not the ability to choose among individuals who propose, but the ability to choose the individuals to whom one proposes (Bergstrom and Real 2000).

To the best of our knowledge, a single (theoretical) study has used matching to study the role played by sexual selection in the process of speciation (Almeida and de Abreu 2003). In this model, preference lists are established with respect to a specific phenotypic trait (e.g., size, larger individuals are preferred) and pairs are formed following an iterative procedure similar to the deferred-acceptance procedure. At each iteration, every male proposes to a female ranking higher than his current mate in his preference list (or to any female if he is single) and females accept only males ranking higher than their current partner in their preference list. Only stable pairs do reproduce, with stable pairs defined as pairs for which no switching of mate occurs over T iterations of the pairing procedure. In this situation, in which mate choice is mutual (with the same trait used for mate choice in both sexes) and pair stability is critical for reproductive success, sympatric

Table 1 Main concepts of the matching approach and implications for mate choice

Concept	Implications for mate choice
Preference lists	The fact that each individual has a specific list in which all potential partners are ranked according to his/her preferences implies that preferences are hierarchical, and may vary between individuals
Reciprocal preferences	The fact that all individuals have a preference list also implies that mate choice is mutual (choice of males by females and of females by males). Note that this does not necessarily imply symmetric mate choice, one sex may be choosier than the other (see main text)
Context-dependant matching	Mate choice is a fundamentally context-dependant process within the framework of matching. It depends not only on the traits and preferences of two individuals, but also on the traits, preferences, and configuration of pairings in the entire population. Two individuals may or may not form a mating pair depending on the social context
Stability of matches	The stability of mating pairs is considered explicitly, with a stable set of pairings defined as a situation in which no new pair can form that would improve the satisfaction of both partners in terms of pairing with a preferred mate. Note that the notion of stability may also be considered at the level of individual pairs (see main text). From a biological perspective, the concept of stability of mating pairs applies to all situations in which “spending time together” (e.g., for courtship or raising young) is required for successful reproduction
Two-sided matching	Two-sided matching refers to a situation in which members of two different groups (e.g., men and women) are matched. From a biological perspective, this corresponds to pairing in species with separate sexes
One-sided matching	One-sided matching refers to a situation in which members of a single group (e.g., room-mates) are matched among themselves. From a biological perspective, this corresponds to pairing in simultaneous hermaphrodites
One-to-one matching	One-to-one matching implies that each individual is matched to at most one individual. From a biological perspective, this corresponds to pairing in monogamous species
Many-to-one matching	Many-to-one matching implies that each individual can be matched to more than one individual. From a biological perspective, this corresponds to pairing in polygynous or polyandrous species

speciation by sexual selection alone is a robust evolutionary outcome. This conclusion is in sharp contrast with the current view that speciation by sexual selection alone is unlikely in the presence of gene flow (Panhuis et al. 2001; Turelli et al. 2001; Bolnick and Fitzpatrick 2007; Ritchie 2007).

An interesting aspect of the study by Almeida and de Abreu (2003) is that contrary to the traditional matching approach, the authors did not focus on stable sets of matching. Unlike the deferred-acceptance procedure, the mating procedure implemented in their model does not necessarily lead to a stable set of pairings. Nevertheless, some mating pairs are more stable than others and if these more stable pairs are given a reproductive advantage, sympatric speciation follows. Thus, it is precisely the nonequilibrium pairing dynamics that contribute to speciation in their model. Considering the large number of pairing possibilities for a relatively small number of individuals (see numerical example above), it would actually be surprising to observe stable sets of matching in nature.

The model by Almeida and de Abreu (2003) predicts that when mate choice is mutual (with the same phenotypic trait used for mate choice in both sexes) and the stability of mating pairs is critical for successful reproduction, speciation in the presence of

gene flow is a robust outcome. How common is this situation in nature? The authors suggested that it could apply to a “wide variety of taxa” including yeasts, east-African cichlid fish (Seehausen et al. 1999), mammals, and plants. Identifying such taxa from the literature is not a trivial task because it implies a detailed knowledge of the reproductive biology of each group, and such a review is beyond the scope of this perspective. Instead we present the hamlets, a group Caribbean coral reef fishes in the genus *Hypoplectrus* (Serranidae), as one system particularly apt for applying the perspective of matching to the role played by sexual selection in the process of speciation.

A system to address the role of matching in mate choice and speciation empirically

The hamlets are characterized by a remarkable polymorphism in color pattern, with at least 12 different color morphs identified in the wider Caribbean (Fig. 1). Most color morphs have been named as species, and up to eight different color morphs can be found on a single reef (Puebla et al. 2007). Pairing and mating occurs on a daily basis before sunset. Hamlets are simultaneous hermaphrodites and mate



Fig. 1 Nine color morphs of hamlets. From upper left to lower right: barred hamlet (*Hypoplectrus puella*), black hamlet (*H. nigricans*), butter hamlet (*H. unicolor*), shy hamlet (*H. guttavarius*), golden hamlet (*H. gummigutta*), yellowtail hamlet (*H. chlorurus*), indigo hamlet (*H. indigo*), blue hamlet (*H. gemma*), and tan hamlet (*Hypoplectrus* sp.). Photographs with permission from Reef Fish Identification, New World Publications, © 2002, Paul Humann.

choice is mutual; individuals engage in an elaborate courtship and they spawn in pairs, alternating sex roles up to seven times during a single spawning session (Fischer 1980a). There is no parental care, fertilization is external and both eggs and larvae are planktonic.

From an empirical perspective, an interesting aspect of the hamlets is that pairing and spawning can be observed in the field, which provides an opportunity to document the entire pairing process, from courtship to spawning. Hamlets are predators and they can be captured relatively easily with hook-and-line using SCUBA. Once captured, individuals can be measured, fin-clipped for DNA analysis, tagged with Visible Implant Elastomer (Northwest Marine TechnologyTM) and photographed, all underwater (Fig. 2). By tagging and releasing all individuals of a given color morph on a given reef, pairing interactions can be described at the level of the entire population. In particular, the decisions of tagged individuals when confronted to a choice between two or more partners can be documented. By repeating these observations for all individuals with respect to as many other individuals as possible, it should be possible to establish whether

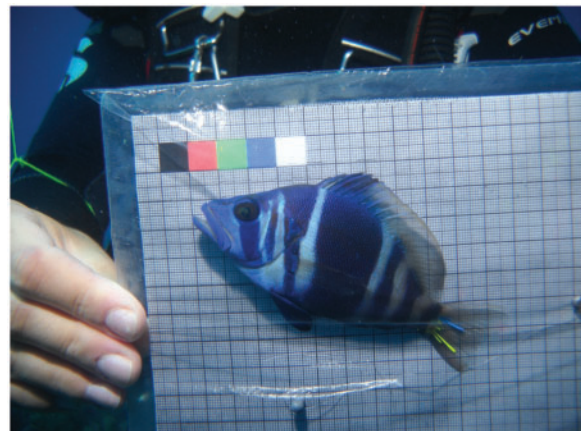


Fig. 2 Hamlets are predators and they can be captured relatively easily with hook-and-line using SCUBA and tagged underwater with Visible Implant Elastomer (Northwest Marine TechnologyTM). By tagging and releasing all individuals of a given color morph on a given reef, the pairing dynamics can be documented at the level of the entire population.

the hamlets have the equivalent of a preference list. If so, removing or adding specific individuals on the reef would provide an opportunity to test specific predictions about the rearrangement of pairings in the population.

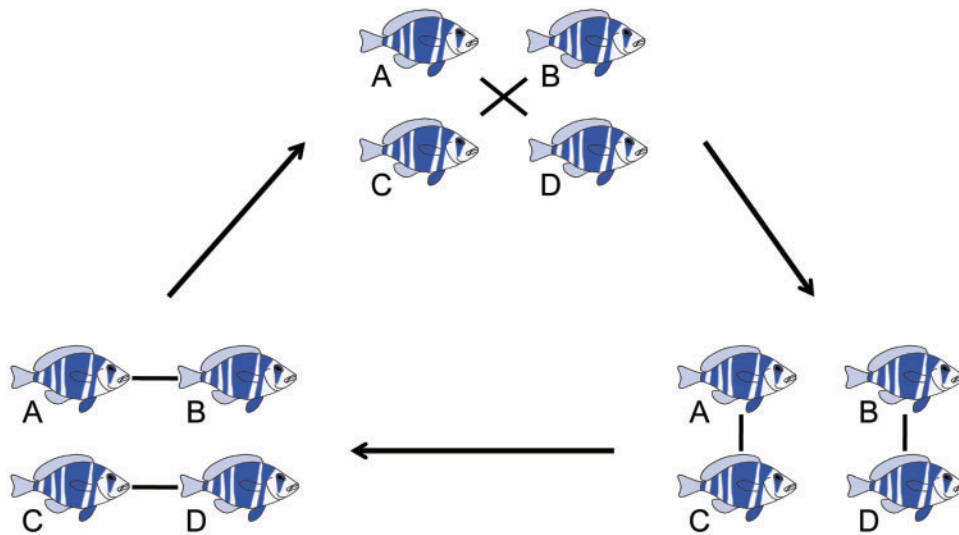


Fig. 3 Illustration of a situation in which no stable set of pairings exists. In this example, individual A prefers B then C then D, individual B prefers C then A then D, individual C prefers A then B then D, and individual D prefers A then B then C. The reader can confirm that there is no stable set of pairings in this situation, and that the pairing configuration will cycle indefinitely following the black arrows.

Pairing is one-sided in the hamlets since they are simultaneous hermaphrodites, i.e., an individual can mate with any other sexually mature individual. From the perspective of matching, this situation corresponds to the “roommate problem” briefly mentioned above, where pairs of individuals are matched in two-bedroom apartments. Gale and Shapley (1962) noted that contrary to the case of the marriage problem, there is not necessarily a stable set of matching in the roommate problem. This can be shown with a simple example, as illustrated in Fig. 3. Thus, the set of pairings in hamlet populations is not necessarily expected to be stable. Since hamlets spawn on a daily basis, the stability of mating pairs can be documented by repeating spawning observations every evening, providing an opportunity to establish whether a stable set of pairings has been reached in the population.

Hamlets spawn largely between members of the same color morph (Fischer 1980b; Domeier 1994; Barreto and McCartney 2007; Puebla et al. 2007), and the paragraph above illustrated how mate choice within color morphs can be addressed from the perspective of matching. Yet pairings and spawnings between different color morphs do occasionally occur in the field (Fischer 1980b; Barreto and McCartney 2007; Puebla et al. 2007), suggesting that there is ongoing gene flow between color morphs. This hypothesis is further supported by the lack of intrinsic barriers to fertilization between color morphs (Whiteman and Gage 2007), the occurrence of individuals with intermediate color

patterns in the field (Puebla et al. 2008), and the low levels of genetic differentiation between sympatric color morphs (Graves and Rosenblatt 1980; McCartney et al. 2003; Puebla et al. 2007). Thus, the hamlets also provide an opportunity to address the role played by mate choice in the process of speciation in the presence gene flow (i.e., sympatric speciation). In particular, hybridization can be studied within its social context in the field using the perspective of matching. For example, if individuals rank members of different color morphs lower than members of their own color morph in their preference lists, it is predicted that hybridization will occur only when mates of the same color morph are not available in the population.

As mentioned above, Almeida and de Abreu (2003) predicted that when mate choice is mutual and the stability of mating pairs is critical for reproductive success, the evolution of assortative mating in the presence of gene flow by sexual selection alone is a robust evolutionary outcome. Could the pairing dynamics of the hamlets explain speciation in this group? This question can be addressed empirically by testing whether some mating pairs are more stable than others and if so, whether individuals involved in stable pairs have a higher reproductive success than do individuals involved in unstable pairs.

Conclusion

In conclusion, matching provides a largely overlooked theoretical framework for the study of mate

choice and speciation. This approach presents several aspects that differ from classic theories of sexual selection and speciation, notably the context-dependent approach to the process of pairing, the explicit consideration of the stability of mating pairs, and mutual mate choice. Since natural populations are not necessarily expected to present stable sets of matching, the consequences of non-equilibrium pairing dynamics for mate choice and speciation are of particular interest. Additional theoretical work integrating realistic settings based on empirical systems such as the hamlets are needed to validate the relevance of matching for the study of mate choice and speciation.

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References

- Almeida CR, de Abreu FV. 2003. Dynamical instabilities lead to sympatric speciation. *Evo Ecol Res* 5:739–57.
- Amundsen T. 2000. Why are female birds ornamented? *Trends Ecol Evol* 15:149–55.
- Barreto FS, McCartney MA. 2007. Extraordinary AFLP fingerprint similarity despite strong assortative mating between reef fish color morphospecies. *Evolution* 62:226–33.
- Bergstrom CT, Real LA. 2000. Towards a theory of mutual mate choice: lessons from two-sided matching. *Evol Ecol Res* 2:493–508.
- Bolnick DI, Fitzpatrick BM. 2007. Sympatric Speciation: models and empirical evidence. *Ann Rev Ecol Evol Syst* 38:459–87.
- Clutton-Brock T. 2007. Sexual selection in males and females. *Science* 318:1882–5.
- Clutton-Brock T. 2009. Sexual selection in females. *Animal Behav* 77:3–11.
- Domeier ML. 1994. Speciation in the Serranid fish *Hypoplectrus*. *Bull Mar Sci* 54:103–41.
- Fischer EA. 1980a. The relationship between mating system and simultaneous hermaphroditism in the coral-reef fish, *Hypoplectrus nigricans* (Serranidae). *Animal Behav* 28:620–33.
- Fischer EA. 1980b. Speciation in the hamlets (*Hypoplectrus*: Serranidae)—a continuing enigma. *Copeia* 298:649–59.
- Gale D, Shapley LS. 1962. College admissions and the stability of marriage. *Am Math Month* 69:9–15.
- Graves JE, Rosenblatt RH. 1980. Genetic relationships of the color morphs of the serranid fish *Hypoplectrus unicolor*. *Evolution* 34:240–5.
- Gusfield D, Irving RW. 1989. The stable marriage problem: structure and algorithms. Cambridge: The MIT Press.
- Kraaijeveld K, Kraaijeveld-Smit FJL, Komdeur J. 2007. The evolution of mutual ornamentation. *Animal Behav* 74:657–77.
- Lande R. 1981. Models of Speciation by Sexual Selection on Polygenic Traits. *Proc Natl Acad Sci USA* 78:3721–5.
- McCartney MA, Acevedo J, Heredia C, Rico C, Quenoville B, Bermingham E, McMillan WO. 2003. Genetic mosaic in a marine species flock. *Mol Ecol* 12:2963–73.
- Morrill T. 2010. The roommates problem revisited. *J Econ Theor* 145:1739–56.
- Panhuis TM, Butlin R, Zuk M, Tregenza T. 2001. Sexual selection and speciation. *Trends Ecol Evol* 16:364–71.
- Puebla O, Bermingham E, Guichard F. 2008. Population genetic analyses of *Hypoplectrus* coral reef fishes provide evidence that local processes are operating during the early stages of marine adaptive radiations. *Mol Ecol* 17:1405–15.
- Puebla O, Bermingham E, Guichard F, Whiteman E. 2007. Colour pattern as a single trait driving speciation in *Hypoplectrus* coral-reef fishes? *Proc Royal Soc B* 274:1265–71.
- Ritchie MG. 2007. Sexual selection and speciation. *Ann Rev Ecol Evol Syst* 38:79–102.
- Roth AE. 1984. The evolution of the labor market for medical interns and residents: a case study in game theory. *J Polit Econ* 92:991–1016.
- Roth AE, Sotomayor MAO. 1990. Two-sided matching: a study in game-theoretic modeling and analysis. Cambridge: Cambridge University Press.
- Seehausen O, van Alphen JJM, Lande R. 1999. Color polymorphism and sex ratio distortion in a cichlid fish as an incipient stage in sympatric speciation by sexual selection. *Ecol Lett* 2:367–78.
- Turelli M, Barton NH, Coyne JA. 2001. Theory and speciation. *Trends Ecol Evol* 16:330–43.
- Whiteman EA, Gage MJG. 2007. No barriers to fertilization between sympatric colour morphs in the marine species flock *Hypoplectrus* (Serranidae). *J Zool* 272:305–10.