



## Study on mate choice in animals

Zhongyuan Shen<sup>a,1</sup>, Xixi Liu<sup>a,1</sup>, Kaikun Luo<sup>a</sup>, Liming Shao<sup>a</sup>, Jing Wang<sup>a</sup>, Wuhui Li<sup>a</sup>, Shennan Li<sup>a</sup>, Qianhong Gu<sup>a</sup>, Liang Guo<sup>a</sup>, Lei Zeng<sup>a</sup>, Shi Wang<sup>a</sup>, Chang Wu<sup>a</sup>, Qinbo Qin<sup>a,b,\*</sup>

<sup>a</sup> State Key Laboratory of Developmental Biology of Freshwater Fish, Engineering Research Center of Polyploid Fish Reproduction and Breeding of the State Education Ministry, College of Life Sciences, Hunan Normal University, Changsha, 410081, Hunan, People's Republic of China

<sup>b</sup> Nansha-South China Agricultural University Fishery Research Institute, Guangzhou, People's Republic of China

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### ABSTRACT

Sexual selection is critical to animal reproduction. Mate choice not only determines an individual's capacity for reproduction but is also the primary mode of selection in sexual selection. Mate choice behavior relies on social information, and animals can extract useful information (e.g., genetic quality, hormone levels, physiological status, habitat) about potential mates based on morphological and behavioral traits they observe or perceive and can modify their mate choice strategy by detecting and integrating this information. The information conveyed by potential mates is multimodal. This paper synthesizes the effects of several factors, including individual biological characteristics, sensory systems, hormones and genotype on mate choice, demonstrating that mate choice preferences in the traditional sense are generally more favorable for individuals with superior genes and phenotypes. And the paper also explores the limitations of these studies on mate choice and proposes the future major trend of the correlational research in this field. This work will provide helpful information for guiding the subsequent studies of mate choice in animals.

### 1. Introduction

In 1859, Darwin proposed the concept of sexual selection in "On the Origin of Species" [1]. Subsequently, in "Evolution and Sexual Selection," Darwin further developed the theory of sexual selection, and then extended it to the theory of mate choice [2]. The theory refers to the fact that an individual in a population has certain characteristic advantages over other members of the same or opposite sex of that species, and the advantages of these obvious features, such as special coloration, different body size, or eye-catching ornament, may enable individuals with these features to get greater success in mate choice. Thereafter, mate choice has been one of the hot topics in animal behavior research. Especially, with the expansion of human activities, the population size and reproductive population of many species in nature are constantly decreasing, and the reproductive activities of populations are under pressure, seriously affecting the survival and continuation of species. The biodiversity of the Earth is facing huge challenges. Therefore, it is crucial for studying mate choice of species.

Most individual organisms possess the ability to discriminate and

recognize distinctions between suitors, such as by choosing mates based on differences in body size, phenotype, genotype, and age of conspecifics. Male intertidal snails (*Echinolittorina malaccana*) [3] and African cichlids (*Pelvicachromis taeniatus*) [4] favor larger females over smaller females. Female common yellowthroats [5] and Atlantic salmon (*Salmo salar*) [6] prefer males that are heterozygous for the major histocompatibility complex (MHC) genes [7]. And female black grouse (*Lyrurus tetrix*) [8] and broad-horned flour beetles (*Gnatocerus cornutus*) [9] tend to mate with older males. Other factors, such as olfaction, chirping behavior, personality, and testosterone, can likewise be utilized as cue information for assessing potential mates. The Nereid polychaete (*Neanthes acuminata*) selects males with extensive paternity care experience for larval survival based on odor [10]. Male Savannah sparrows (*Passerculus sandwichensis*) with trill fragments in their call mates earlier [11]. The larger female Western mosquitofish (*Gambusia affinis*) prefer brave or active males, while larger males prefer females that are active swimmers [12]. The testosterone levels are positively correlated with male wild rock hyrax (*Procavia capensis*) mating success and negatively correlated with the reproductive success of females [13]. Individuals

\* Corresponding author. State Key Laboratory of Developmental Biology of Freshwater Fish, Engineering Research Center of Polyploid Fish Reproduction and Breeding of the State Education Ministry, College of Life Sciences, Hunan Normal University, Changsha, 410081, Hunan, People's Republic of China.

E-mail address: [qqb@hunnu.edu.cn](mailto:qqb@hunnu.edu.cn) (Q. Qin).

<sup>1</sup> These authors contributed equally to this work.

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tend to choose mates with morphologies and genes that are attractive to them as a means of obtaining direct or indirect fitness benefits to ensure the species continues [14]. Then, it is vital to explore the influencing factors of mate choice. In this paper, the effects of individual characteristics, age, genotype and on mate choice are reviewed, which provides important reference for understanding and studying mate selection and mating systems in animals.

## 2. Mate choice and individual biological characteristics

### 2.1. The individual physical characteristics factor in mate choice

Individual physical traits, which represent an individual's phenotypic characteristics, body shape characteristics, and body mass, are heritable. Some of the exaggerated physical features of males are secondary sexual traits that evolved due to female preference, and these secondary traits may reflect the ability of males to provide high-quality genes and high-quality material resources. Downer-Bartholomew et al. demonstrated that female Japanese medakas (*Oryzias latipes*) were more responsive to red and orange objects than to objects of other colors under nonmating conditions; under mating conditions, females showed less resistance to males with distinct long wavelength (LW)-colored stripes, suggesting that medaka have a clear mate choice preference for males with LW colors (yellow, orange, and red) [15]. In addition, during mate choice in the order Passeriformes (Oriental greenfinch), males preferred heavier females, possibly because heavier females have more fat stores and longer incubation times, thus reducing the risk of hatching predation. In turn, females favored mating with males that had larger beaks because these males have better foraging ability [15].

The physiological condition of an individual is reflected in its body size, with larger individuals typically displaying higher levels of competitiveness and the ability to fend off predators. The study of body size as a selection criterion in male competition and female reproduction has been recognized. Mature male ladybirds (*Menochilus sexmaculatus*) with larger body sizes have greater mating success, and larger female ladybirds produce more eggs [16]. Lau et al. investigated the biological mechanisms of mate choice in an intertidal snail (*Echinolittorina malaccana*) through multiple-choice experiments and concluded that the intensity of snail mate choice decreases in small populations and increases in large populations [3]. Female Western mosquitofish (*Gambusia affinis*) with opposite sexual size dimorphism exhibit a preference for large males for protection, which may be a means of female selection in a coercive mating system [17]. Studies on amphibians have indicated that body size may be positively correlated with reproductive time, clutch size, egg size, and hatching success [18].

### 2.2. The age factor in mate choice

Age is a key factor influencing the reproductive success of a species, determining fundamental processes related to survival, mate choice, and reproduction [19]. Middle-aged males have a greater reproductive capacity and generate more sperm than older or younger males in the female mate choice. For instance, females prefer middle-aged males to younger males because middle-aged male ladybirds take longer to mate than younger males [20]. And 3-day-old male hawthorn spider mites (*Amphitetranynchus viennensis*) have better reproductive traits and competitiveness, as well as longer mating durations, and are able to obtain a greater number of mating opportunities than 5-day-old and 1-day-old males [21]. Most species do not select younger mates but tend to mate with older heterosexuals, possibly because older individuals have good social status, mating experience, and higher genetic quality. Aich et al. revealed experimentally that older males produced more offspring than younger males, regardless of whether male mosquitofish had a history of mating [22]. However, In the male mate choice of the hawthorn spider mite, experienced males were found to prefer 5-day-old unmated females; however, inexperienced males preferred 1-day-old

first-time mated females [21]. In addition, some animals have a preference for younger individuals of the opposite sex. For example, female *Pachycrepoideus vindemniae* prefer to mate with younger males that have had multiple mating experiences and are large enough to produce a large number of female offspring, and female offspring of *P. vindemniae* can attack certain fly species for biological control purposes [23]. Cotto and Day noted a time-lapse model in which individuals spend time searching for better quality mates to increase mating benefits and reduce reproductive costs, a process that is contingent upon the individual's own physiological state and external risks [23]. Despite the older age of middle-aged individuals compared to younger individuals, their ability to assess external risks is greater than that of younger individuals, resulting in longer waiting times and lower accidental mortality before accepting a mate among middle-aged individuals [24].

Selection preferences change with age as a result of trade-offs between the costs of reproduction and direct or indirect benefits to organisms. As male ladybugs age, there is a trade-off between longevity and mating, and females will be selective, choosing suitors of moderate age and rich in male attributes to maximize their benefits [25]. For species that mate only once, mate selection criteria will be relatively lax to reduce the cost of mate selection due to the limited time available for mating. The older the male is, the lower the fecundity and quality of offspring usually are, but some females still choose older males, probably because older males provide direct benefits to females, such as sexual experience and high-quality breeding sites [26]. The factor of male mating history is often taken into account when exploring the effect of age on mate choice in certain species. Aich et al. experimentally manipulated the mating histories of older or younger male eastern mosquitofish controlled for various factors and also recorded the mating behavior of males in mate-choice competitions and their affinities with their offspring; they concluded that, relative to younger and more experienced males, older and inexperienced males devote more of their time to mating with females and that older males benefit from previous mating experience to have more offspring. In this experiment, age and mating experience also affect the ejaculatory status of male mosquitofish, with inexperienced individuals producing more sperm than experienced individuals among older males, whereas the opposite is true for younger males [27].

### 2.3. The personality factor in mate choice

Personality is defined as a stable behavioral difference exhibited by an individual in a given situation [28], and individual animals can assess the quality of potential mates with the help of behavioral traits [29]. Personality occurs in a variety of animal groups [30] and is closely linked to biological evolution and natural selection. Faust and Goldstein investigated the effects of exploratory, aggressive, and social behaviors on pairing in zebra finches and showed that the birds tended to choose individuals of the opposite sex with exploratory personalities similar to their own [29]. However, female Java sparrows (*Lonchura oryzivora*) favored more exploratory males [31]. Sommer-Trembo et al. explored whether females of the livebearing fish *Poecilia mexicana* that chose adventurous mates gained a reproductive advantage and whether females chose mates based on their own risk-taking intensity. They found that females preferred more adventurous males and that the degree of preference for adventurous males was influenced by their own personality [32]. That is, risk-taking females have a stronger preference for adventurous males than risk-averse females.

The activity of female mosquitofish (*Gambusia affinis*) influences male mate choice tendencies, with males spending more time in contact with active females [33]. Aggressive male jumping spiders (*Siler semiglaucus*) exhibit increased reproductive performance and are dominant in both male competition and female choice [34]. The personality of the European green lizard (*Lacerta viridis*) is related to age and body size, with young lizards being more exploratory than older lizards and less exploratory males being able to socialize with more females [35]. Thus,

personality is present in various biological groups, including birds, fish, arthropods, and reptiles, and plays a significant role in mate choice as well as in offspring growth and development.

### 3. Mate choice and sensory systems

#### 3.1. The olfaction senses factor in mate choice

Odor is an important chemical cue for mate choice, and many species rely on olfaction to determine the identity, developmental stability, and social status of potential mates. Fish have a well-developed olfactory system and often use odor information for mate selection. For example, Bacterially infected Nile tilapia emit more attractive odors to increase mating rates [36]. Female three-spined sticklebacks (*Gasterosteus aculeatus*) rely on their sense of smell to recognize females and males, different characteristics of the same species, and males with high-quality nests [37]. And mature male zebrafish (*Danio rerio*) prefer the odors of unfamiliar females, suggesting that the species avoids inbreeding [38]. The olfaction senses factor in mate choice also exists in insects. Boehm et al. reported that odors in the environment in which mating occurs impair the olfactory system of *Drosophila* females; for example, the pheromone cVA reduces the preference for polyamines by females during mating [39]. During mate choice in vertebrates, the body odor cues the major histocompatibility complex (MHC) signaling. The study found that mice select mates with heterozygous MHC alleles based on specific olfactory neuron responses to MHC peptide ligands [40]. Volatile compounds in bird feathers encode MHC information, reflecting the diversity of MHC alleles [41]. Similar to vertebrates, the odor information associated with MHC genes also affects mate choice preferences in humans, and humans usually prefer the opposite sex, which has greater MHC differences from themselves. Nevertheless, Havlicek et al. investigated the effects of MHC genes on human mate choice from a variety of perspectives and did not uncover a link between MHC dissimilarity and odor preferences [42]. In the future, the sample size should be expanded, and additional research should be conducted on the mechanism of odor preference based on human MHC alleles.

#### 3.2. The auditory senser factor in mate choice

Animals such as insects, batrachians, and birds produce sound during courtship and, like olfaction courtship. Mate choice is related to song, with males emitting calls or other sensory signals to attract females, who rely on these signals to select high-quality mates. The male East Asian cicadas (*Platypleura kaempferi*) emit high-frequency calls to attract distant females and ensure mating success by lowering the frequency of their calls [43]. The male groups of a chorusing cicada, *Mogannia formosana*, call in unison to attract females to mate, and females are typically more willing to approach males with low-frequency calls [44]. Acoustic signals indirectly reflect certain characteristics of males, including genetic status (genetic diversity), physiological status, morphological features, and age. For most species, including humans, symmetry indicates good genetic quality of an individual. Vijendravarma et al. revealed that *Drosophila melanogaster* relies on auditory cues to recognize the asymmetry of potential mates during courtship and that males with asymmetrical wings emit asymmetrical courtship calls, while females of *Drosophila* refuse to mate with such males [45]. The ability to transmit or perceive acoustic signals may be disrupted when an individual's social environment is altered. Sun et al. showed that *Rhacophorus rhodopus* may increase the complexity of their vocal signals by changing the dominant frequency, syllable duration, syllable spacing, and syllable count of their vocalizations under different environmental conditions, thus winning the mating competition [46]. Bent et al. white noise and traffic noise reduce the stimulus intensity of courtship chirps, which alters female *Gryllus bimaculatus* mate choice preferences under natural conditions, leading to decreased compatibility between male and female mates [47]. Jablonszky et al. investigated the “audience

effect” on the courtship song characteristics of a male collared flycatcher (*Ficedula albicollis*) and concluded that female stimuli altered the complexity of the song only, whereas male stimuli altered the duration and frequency of the song [48]. Changes in the social environment usually result in the adaptation or evolution of an animal's song behavior, yet signaling can still proceed smoothly; hence, song behavior is plastic, which has significant implications for mate choice.

### 4. Mate choice and hormones and intrinsic genotype

#### 4.1. The hormones factor in mate choice

From the perspective of biological evolution, individuals who choose mates with reproductive advantages are more likely to have more offspring, which can better sustain the gene pool. Thus, individuals with reproductive advantages have greater sexual attraction to the opposite sex. It is well known that an individual's reproductive health is related to their sex hormone levels, such as the hormone testosterone. The expression of certain traits in males is influenced by the androgenic hormone testosterone (T), and typically, males with higher plasma T levels exhibit more attractive ornamentation and exploratory behavior. Testosterone concentrations in male gray whales (*Eschrichtius robustus*) are significantly elevated throughout the breeding season, which may be a physiological adjustment prior to mating in these whales [49]. Larger male African cichlid fishes (*Astatotilapia burtoni*) release more testosterone during reproduction than do smaller males [50]. The red feather trait associated with carotenoids is an important sexual signal in male red-backed fairywrens (*Malurus melanocephalus*), and testosterone increased the expression of genes such as CYP2J19, ELOVL6, and ABCG, all of which have been implicated in the transport, metabolism, and uptake of carotenoids in male tissues [51]. Gomes et al. noted that a positive correlation between testosterone and antler size and body size could indirectly increase the reproductive success of white-tailed deer (*Odocoileus virginianus*); that is, the greater the hormone concentration is, the greater the antlers and body size are, and the greater the reproductive success is [52]. Similarly, increased testosterone concentrations drive human sexual selection. Wu et al. reported that healthy young males given exogenous testosterone exhibited greater sexual impulsivity [53]. Welling et al. found a positive correlation between male testosterone levels and their preference for feminized faces [54].

However, selection for high testosterone levels may be inhibited when these conspicuous features are detrimental to female reproduction. Some studies indicate that reduced sexual attractiveness in females may result from elevated testosterone concentrations. For instance, testosterone was negatively correlated with the extrapair copulation rate in female blue tits (*Cyanistes caeruleus*) [55]. The recognition of high-quality males by testosterone-treated female dark-eyed juncos (*Junco hyemalis*) was significantly reduced [56]. And testosterone-treated female budgerigars (*Melopsittacus undulatus*) were sexually biased in favor of males and were at a disadvantage in mate choice [57].

#### 4.2. The genotype factor in mate choice

Females benefit indirectly by selecting high-quality males to improve the genetic quality and heterozygosity of their offspring. Offspring with high-quality genes exhibit a dominant appearance, greater disease resistance, and good fertility. However, in the process of evolution, organisms choose mates for the transmission of their own genes or genetic benefits, which requires continuous provision of advantageous genetic variations in the population to maintain this picky motivation. Hamilton and Zuk proposed that co-evolution with parasites can maintain the supply of genetic variations that influence preferred traits [58]. As one of the most polymorphic gene clusters in vertebrates that can maintain diversity through pathogen mediation, major histocompatibility complex (MHC) class II genes have the potential for mate selection and evolution. Ekblom et al. investigated the impact of MHC genes on mate

choice in the great snipe (*Gallinago media*) from a number of perspectives and did not observe an MHC preference in this species or a preference for a rare allele; however, certain allelic lineages were common in males with successful mating [59].

In recent years, with the development of genetic technology, additional studies have been conducted on the mechanism of mate choice using MHC genes as markers. More and more evidence are proving that the MHC, a large family of genes with a high degree of polymorphism present in vertebrates, is an important measure of an individual's immunocompetence and plays an important role in mate choice in animal populations. Landry et al. used MHC and microsatellite loci to explore mating patterns in Atlantic salmon (*Salmo salar*) and test the heterozygote dominance hypothesis, and they proposed that Atlantic salmon do not select mates based on their relatedness to potential mates or the MHC but rather select heterozygous individuals that increase heterozygosity in the MHC peptide-binding region of their offspring [6]. Whitcomb et al. also supported the study of silver salmon that parental pairing is more likely to be selected in larger MHC class II gene diversity, thereby increasing the survival rate of offspring [60]. Mate choice between two genetic haplotypes of *Harmonia axyridis* is random, but *H. axyridis* of Haplotype-I is dominant relative to *H. axyridis* of Haplotype-II, and haplotype-II males have the lowest egg-laying hatch rate when mated to haplotype-II females [61]. Mingju et al. examined the effects of the morphological characteristics and genetic similarity of individuals with MHC class IIB (MHC IIB) exon 2 on the mating of the sexually dimorphic yellow-rumped flycatcher (*Ficedula zanthopygia*) and discovered that the MHC similarity of social mates was significantly lower than that of random mates and that mate choice in females may be based on the maintenance of a certain level of MHC diversity in the offspring [62]. Petersen et al. reported that polymorphisms in the class II MHC locus are linked to kin recognition and that olive baboons (*Papio anubis*) usually choose opposite sexes with large differences in MHC alleles to avoid inbreeding [63].

Currently, the mate choice strategy associated with the MHC gene has not been determined [64]. According to most related studies, the MHC gene may be correlated with the phenotype of the animal as well as with several other behavioral traits [65]. Milinski noted that potential mates signal the MHC allele through body odor, and certain females rely on their sense of smell to screen the sperm of males as a way to produce the best-adapted offspring [40]. Leach's storm petrel (*Oceanodroma leucorhoa*) uses olfaction to identify heterosexual individuals with high-quality MHC genes because volatile chemicals in bird feathers encode MHC information [41]. Although these are reflected in olfactory related mate choice, they exhibit clear preferences in genotypes. Furthermore, Pikus et al. tested for associations between the diversity of MHC class I and II genes and adaptive traits in an urban population of Eurasian coots (*Fulica atra*) and reported that individuals with a greater diversity of MHC alleles were more susceptible to disease and reproduced later in life, possibly because excessive diversity of MHC genes can lead to autoimmune diseases [66]. Other features, such as bright plumage color, complex calls, large body size, and large horns, in deer and cattle can be employed as informative markers of quality genes by which females can judge the quality of males.

## 5. Conclusion

In summary, this work reviews several studies and highlights potential influencing factors of animal mate choice, demonstrating that mate choice preferences in the traditional sense are generally more favorable for individuals with superior genes and phenotypes. Mate choice behavior relies on social information, and animals can extract useful information (e.g., genetic quality, hormone levels, physiological status, habitat) about potential mates based on morphological and behavioral traits they observe or perceive and can modify their mate choice strategy by detecting and integrating this information. The information conveyed by potential mates is multimodal. Most of the

studies on mate assessment mechanisms reviewed in this work have limited their focus to the main behavioral modes of experimental species, but as individuals communicate and interact with each other, other modalities will also play an increasingly important role in animal mate choice. However, regardless of the situation, the depth of research on mate choice is mostly limited to the description of natural reproductive behavior and the speculation and verification of macro ecological hypothesis concepts. Research on the molecular mechanisms that affect mate choice mainly focuses on mammals, birds, and insects, while research on fish is scarce.

In over 40 years of research on the molecular mechanisms of mate selection influenced by MHC, it has been shown that these evolutions may occur through various mechanisms, including increasing offspring immune gene diversity through preferred mating with individualities with specific inheritable immune gene characteristics ("good genes"), immune genetically dissimilar or distant relationship, and so on. In summary, it can be mainly divided into four categories: heterozygous mating, heterozygous dominance, hypothesis of good genes, and phylogenetic identification (or inbreeding avoidance) [63,67–69]. Although the occurrence of these mechanisms has been proposed, due to incomplete sample size, population data, and MHC genotyping, most studies are limited to specific research systems that raise questions and speculate on analysis, and cannot solve the decision-making problems caused by multiple mechanisms. The understanding of the spouse selection mechanisms affected by them is still limited. Especially, little is known about the potential role of MHC genes in mate choice and their role in mating, or their relative importance to whole genome mating preferences (such as avoiding inbreeding). Therefore, the mate choice related to the influence of MHC genes in fish and the effects of multiple behavioral cues on individuality mate choice and interactions (synergistic or competitive) between different cues can be explored in the future.

## Compliance and ethics

Qinbo Qin is an editorial board member for Reproduction and Breeding and was not involved in the editorial review or the decision to publish this article. All authors declare that they have no conflict of interest.

## CRedit authorship contribution statement

**Zhongyuan Shen:** Writing – review & editing, Writing – original draft, Funding acquisition. **Xixi Liu:** Writing – original draft, Data curation. **Kaikun Luo:** Data curation. **Liming Shao:** Formal analysis, Data curation. **Jing Wang:** Writing – review & editing, Formal analysis. **Wuhui Li:** Writing – review & editing. **Shennan Li:** Data curation. **Qianhong Gu:** Writing – review & editing. **Liann Guo:** Formal analysis. **Lei Zeng:** Data curation. **Shi Wang:** Writing – review & editing. **Chang Wu:** Data curation. **Qinbo Qin:** Writing – review & editing, Funding acquisition.

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