Review

You're Just My Type: Mate Choice and Behavioral Types

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Consistent individual differences in behavior [i.e., behavioral types (BTs)], are common across the animal kingdom. Consistency can make behavior an adaptive trait for mate choice decisions. Here, we present a conceptual framework to explain how and why females might evaluate a male's BT before mating. Because BTs are consistent across time or context, a male's BT can be a reliable indicator of his potential to provide direct benefits. Heritable BTs can enable informed mate choice via indirect benefits. Many key issues regarding patterns of mate choice, including sensory biases, context dependence, and assortative mating apply to BT-dependent mate choice. Understanding the relationship between BTs and mate choice may offer insights into patterns of variation and consistency common in behavioral traits.

BTs and Mate Choice

Mate choice is often a key factor influencing the evolution of traits [1,2]. While sexual selection via mate choice likely has a special role as a major explanation for highly elaborated ornaments, it is not only important for explaining exaggerated, sex-specific traits. A new insight is that the choosy sex (typically females) may also select a mate based on their own and their potential mate's **behavioral type** (BT) (see Glossary); for example, boldness, aggressiveness, exploratory tendency, or sociability [3]. An individual is said to have a BT if its behavior is consistent across time or contexts (e.g., an individual that is more aggressive than another in a foraging context, also tends to be more aggressive in the future and/or more aggressive in a mating context) [4]. If males have consistent BTs, then male behavior observed by a female at one time and context (e.g., during courtship) provides information about his likely behavior in the past and future (e.g., during parental care). Importantly, the time scale of this correlation is not part of the definition for either human or **animal personalities** [4,5]. More persistent BTs (e.g., over a lifetime) presumably have greater potential to be impactful, particularly for species with long-term mating associations, but even short-term consistency (e.g., from courtship to nesting or parental behavior a few weeks later) can be important [6–8].

With regard to mechanisms of adaptive mate choice, correlations between a potential mate's past, present, and future behaviors may determine the quality and quantity of expected **direct benefits** that he can provide (e.g., nuptial gifts, territory, or parental care) [3]. Within a breeding season, BTs allow a female to predict a male's future behavior towards her and her offspring, which may be particularly important for species that have paternal care, including territory defense and provisioning [9,10]. While consistency to the next breeding season is not necessarily important for all species, species that engage in long-term pair bonds may rely more heavily on BTs to determine long-term compatibility [11]. Furthermore, given that BTs are heritable (about half of BT variation is attributable to additive genetic variation [12]), BT may also be important for **indirect benefits** – offspring inheritance of adaptive traits – as it can serve as a predictor of the offspring's traits [13].

Highlights

Acknowledging the existence of consistent differences among individuals in behavior [i.e., behavioral types (BTs)] yields new insights on patterns of mate choice.

Because BTs are both consistent over time and context, and are heritable, mate choice based on the partner's behavioral type can be adaptive.

Choosing an individual's BT can affect its adaptive mate choice.

Due to complex interactions between the sexes, their BTs, and environmental context, BT-dependent mate choice may help to explain the maintenance of variation between individuals in behavioral type.

In addition, the social context and benefit of honest signaling that is a part of mate choice may contribute to why we see consistency within an individual in BT.

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Conversely, incorporating mate choice and individual consistency in behavior is insightful for understanding the ecological and evolutionary dynamics of BTs. BTs are inextricably tied to individual fitness [14,15]. Thus, changes in the mean value and variance of BT within a population can shape species interactions and the ecology of the system [16]. If the mean value and variance of BTs are partially influenced by BT-dependent mate choice, it is important to understand how mate choice influences the standing behavioral variation within a population and the evolution of behavioral consistency.

A decade ago, Schuett *et al.* [3] created a framework and proposed the core ideas that: (i) mate choice might be based on the potential partner's BT; (ii) this might represent adaptive mate choice for direct or indirect benefits; and (iii) BT-dependent mate choice may be an important factor for the evolution and maintenance of behavioral differences. However, they acknowledged that, at the time, few empirical examples existed for nonhuman animals. In the past decade, dozens of empirical studies on BT and mate choice in nonhuman animals have emerged. Here, we first discuss how animals might evaluate a potential partner's BT (Box 1). We then re-examine some of the ideas of Schuett *et al.* [3] in light of new research, as well as review new ideas regarding, in particular, the importance of context in determining which BT is preferred. We present an updated conceptual overview (Figure 1) that highlights the mechanisms by which animals might choose mates based on their BT and explore the evolutionary and ecological consequences.

Mate Choice Mechanisms
Direct Benefits
The direct benefits hypothesis posits that females select mates based on indicator traits that honestly predict benefits to her future fitness, such as resource provisioning, parental care, or lack of sexual coercion [17]. Since BT is, by definition, repeatable across time or context [4], females can use behaviors exhibited before mating to predict a correlated future behavior and the expected rewards or costs [3,10].

Box 1. How to Choose

For a female to use behavioral type (BT) for mate choice she must be able to evaluate it. While females may use other traits that relate to BT [67], they can also evaluate the male's behavior directly. Females may assess a male's behavior over time or make a decision based on one interaction, such as a courtship display. Importantly, females should only pay attention to behavior during displays if that behavior indicates something about a male's future behavior, that is, if it is part of his BT.

In social species, with longer-term interactions, females may aggregate information over time. For example, in bluefin killifish (*Lucania goodei*), male aggressiveness towards other males is often correlated with his aggressiveness towards females [68]. A female could thus use aggression in one context (aggression towards other males) to avoid sexual coercion. If courtship displays are correlated with BT, as, for example, in great tits (*Parus major*), where singing activity is correlated with exploratory behavior [69], the courtship display alone could allow the female to predict future behavior. If song is a key part of a male's display and predicts exploratory behavior, which in turn relates to his ability to find food, females may not be directly making mate-choice decisions based on BT but are indirectly selecting for specific BTs. In other cases, females appear to evaluate a male's social responsiveness to her signals and prefer males that are more responsive [70]. While social responsiveness is not a classic axis of personality, it has been suggested as an important, understudied aspect of BT [71].

Females may not be making decisions based directly on behavior, but instead choosing based on physical traits that are correlated with BT [72]. Many of the sometimes arbitrary-seeming attributes that females use to make mate choice decisions have been theorized to indicate fitness-relevant traits via good genes or direct benefits. Many of these attributes, including coloration [73–75] and dewlap size [76], are also correlated to BT. Females may be selecting based on ornaments but if those ornaments are correlated to a male's BT, she will indirectly select BT.

Importantly, females are likely choosing based on several factors and are assessing the 'complete package'. Under multimodal signaling, females may be assessing behavior to indicate a male's BT and ornaments to indicate condition. Different traits may also indicate different aspects of direct and indirect benefits.

Glossary

Animal personality: a general term referring to the combination of between-individual differences and within-individual consistency in behavior across time or contexts.

Behavioral syndrome: a suite of correlated behaviors across multiple contexts; for example, a positive correlation between boldness and aggressiveness. A characteristic of populations or species.
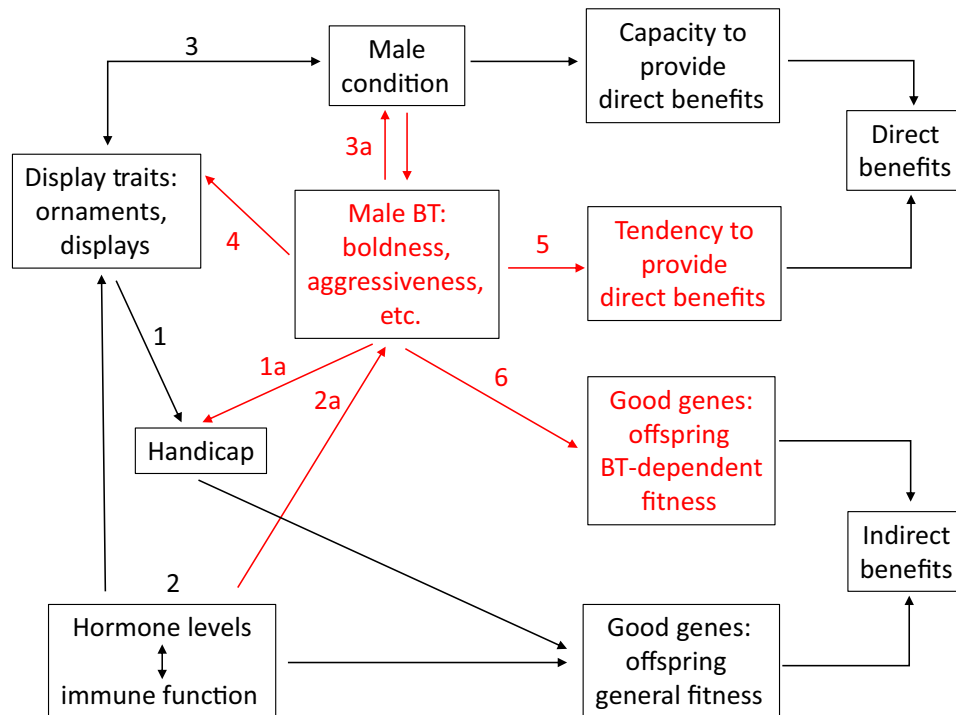
Behavioral type: characterization of an individual's consistent behavior (e.g., being consistently more aggressive versus less aggressive).

Direct benefits: mate-choice mechanism in which exhibiting a particular mating preference directly increases the chooser's reproductive fitness via material advantage of resources (e.g., access to high-quality territory, nuptial gifts, or help with parenting) or enhanced safety.

Handicap hypothesis: traits that are constrained to be honest because they are costly to produce so the production of the trait provides information to the chooser about the quality of the potential mate.

Indirect benefits: mate-choice mechanism in which benefits associated with choosing a particular mate indirectly increases the chooser's fitness by improving the fitness of her offspring (i.e., via good genes).

Sensory bias: preference for a trait that evolved in a nonmating context but has been co-opted to attract the choosy sex.

Trends in Ecology & Evolution

Figure 1. Relationship between Behavioral Type (BT) and Adaptive Mate Choice. Conventional paths, according to traditional sexual selection work, from male display traits to direct and indirect benefits are in black. Paths in red show how a male's BT might affect female fitness. Display traits can be honest indicators of good genes via (1) the handicap principle, or (2) connections through hormones and immune function. The display traits can indicate (3) the male's condition that relates to his capacity to provide direct benefits. A male's BT can provide alternative or more direct connections with each of these pathways. (1a) Being bold puts a male at risk. (2a) BTs are associated with hormones related to immune function. (3a) Variation in BTs connects to variation in condition. (4) BT can affect courtship behavior such that the fitness-relevant information in the display might be information about the male's BT. For direct benefits, females need honest indicators of the male's future behaviors. BT might be a good way to evaluate not only the male's capacity to provide direct benefits, but also (5) his tendency to provide direct benefits. Because BTs are moderately heritable, (6) a female can provide her offspring with good genes by choosing a male with an adaptive BT.

In species with biparental or solely paternal care, females have strong incentives to choose males based on traits that predict future caring investment. In species such as stickleback fish (*Gasterosteus aculeatus),* in which level of paternal care has been shown to be repeatable and important for offspring success [6], a male's BT may be associated with his ability to parent. Females could use behavior prior to mating to choose a mate who is likely to invest strongly into offspring in the future.

Aggressiveness is a key male BT that is often related to his parental care ability [7,9,10]. However, the effect of aggressiveness on parental care is context, task, and system dependent. For nest defense, we expect females to prefer more aggressive males. Aggressive males are often more likely to win territory contests and hold bigger or better territories [9] that should potentially provide more resources for offspring. Females could use their assessment of a male's aggressiveness (e.g., during courtship) to gain the benefits of a high-quality territory, information which may be hard to judge directly and quickly in a mate choice context, particularly if territories are large, resources are dispersed, or territory acquisition has not yet happened. In contrast, male aggressiveness tends to correlate negatively with offspring provisioning [10]. In house wrens

(*Troglodytes aedon*), aggressive males provide less for their young [7], suggesting that females should select less aggressive males.

The effect of male BT on direct benefits and costs for females can also come via sexual harassment and coercion. Females may be able to assess whether a male is likely to engage in sexual coercion by evaluating how aggressive he is in other contexts [18] (i.e., aggression towards other males may indicate aggression during mating [8]). Females should then prefer less-aggressive males if sexual coercion carries significant costs [18,19]. In contrast, females might prefer more-aggressive males if the key is the male's ability to protect her from harassment by other males [20].

The above discussion illustrates two recurrent themes of the interplay between BT and mate choice: (i) female choice is context-dependent – female preferences for male BTs are expected to vary depending on mating system; and (ii) variation in female choice for different BTs depending on her BT and state (see How the Chooser's BT Matters) may help to explain both maintenance of variation and consistency in BTs (Box 2).

Indirect Benefits

According to the indirect benefit hypothesis, females select mates based on traits (e.g., 'flashy' ornaments or songs) that increase offspring fitness via the inheritance of beneficial genes [2,21]. Mate choice via indirect benefits can result whenever observable male traits reliably reflect genes that can increase offspring survival, attractiveness to the opposite sex, or reinforce preferences for these traits. We posit that a male's heritable BT might often provide a relatively straightforward indicator of indirect benefits for a female.

For BTs to serve as traits indicating indirect benefits via good genes, they must fit the following criteria: (i) BTs, or traits tightly associated with BTs must be heritable; (ii) inherited BTs influence the fitness of offspring; (iii) and females show a preference for males with heritable BTs that

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Box 2. Variation and Consistency

Despite the putative benefits of behavioral types (BTs), variation in many behavioral traits are maintained and we rarely see extreme BTs. There are several proposed reasons for this [77], but BT-dependent mate choice may offer insight [3]. Different individuals may benefit from different BTs [78]. Selection in different directions on the same trait in different sexes, for example, can increase population level variation [79,80]. Additionally, if different females prefer different BTs (see "How the Chooser's BT Matters"), variation can be maintained. Further, context matters – both in terms of the female's preferred BT and what BT is favored selectively [64] (see "Context Dependence"). The interplay between context and the BT of both the chooser and the chosen further maintains variation. Different selective pressures in different contexts can prevent directional selection of BTs; for example, if females prefer active males, but active males pay a cost when predators are present [13].

A complementary question is: why are individuals ever consistent relative to the situation (or mate) at hand? Numerous positive feedback loops have been proposed as mechanisms for maintaining behavioral consistency [77], including BT-dependent mate choice [3]. The social niche hypothesis posits that behavioral consistency is maintained because social partners constrain each other to maintain stable roles [81,82]. There is some evidence for this; in Australian field crickets (*Teleogryllus oceanicus*), for instance, the heritability of repeatability is higher when crickets are given social cues [83]. Mate choice may be a particular type of social environment that encourages consistency. If there is pre-existing variation in both behavioral consistency in a population (for example due to developmental constraints on plasticity) and partner choice sensitivity for consistency, then assortative mating should lead to increased fitness of mates who prefer consistent individuals and individuals who behave consistently [84]. Particularly if the consistent behavior is beneficial to the chooser, this should lead to the joint evolution of both increased consistency and preference for consistency [85]. Mate choice may put more evolutionary pressure on males to be repeatable than females [3]. There is some evidence for this [86–89], including a meta-analysis confirming that for parental behavior, males are significantly more consistent than females [3]. However, the specifics of the ecology of the species is likely to affect the importance females put on consistency. In systems where partners do not interact after mating, there may be less reason to expect differences between the sexes in terms of consistency [90,91].

enhance offspring fitness. Numerous studies have shown that BTs have a genetic basis and are heritable [22]; indeed, BTs appear to be more highly heritable than behavior per se [12]. BT can have important fitness consequences [14,15,23–25]. Male BT can thus serve as a reliable signal of his and his offspring's genetic quality, and females should prefer males with those beneficial BTs [3]. For instance, in the presence of predators, female common lizards (*Zootoca vivipara*) prefer males that are less active – a heritable behavior that can reduce risk of predation [13].

Alternatively, female preference for a particular BT may be because of the **handicap hypothesis**. Here, costly male BTs serve as an honest signal of general genetic quality [26]. Boldness, a commonly measured axis of animal personality, may fit the handicap principle well. Being bold in the presence of a predator is clearly dangerous, so bold males that are still alive are likely of high quality. Male lesser wax moths (*Achroia grisella)* sing to attract mates, however they also attract eavesdropping predators. Males that are bolder (i.e., continue to sing in the presence of predators) are indeed more attractive to females [27].

Alternatively, we may not always expect high-quality males to possess bold BTs. According to the asset protection principle, high-quality individuals have more to lose by engaging in risk-taking behavior and should be more cautious than low-quality individuals [28,29]. In western field crickets (*Gryllus integer)*, males that sing longer are more shy in male–male fighting bouts and more cautious following a predator cue [30]. Whether a high-quality male should exhibit risky (handicap principle) or safe (asset protection principle) BTs likely depends on the species' evolutionary history and factors like background mortality rate [31].

Indirect benefits of female preferences based on male BTs may also be associated with runaway or chase away selection. In runaway selection, females acquire an initial preference for a given trait (here, a male BT), which need not have either a selective benefit or a cost. Positive covariance between the preference and the trait builds up and is reinforced through positive feedback in subsequent generations [32]. BT has not been extensively studied through this lens, perhaps because pure runaway selection based on BTs is unlikely due to the clear correlation between BTs and fitness demonstrated in many taxa [14,15]. Additionally, because BTs are often under conflicting selection in different contexts (e.g., bold individuals favored with low risk, but cautious ones favored under high risk), we are unlikely to see runaway to extreme elaboration of BTs. It remains possible though that mate choice has led to more extreme BTs than would be favored otherwise.

Chase-away selection extends the logic of runaway selection by considering male traits that enhance male mating success in ways that are costly for females [33]. A sexual arms race results in evolution increasing both the costly male trait and female resistance against those males, where mating with males with this trait has a direct cost but an indirect benefit [34,35]. Female Japanese quail (*Coturnix japonica*) avoid mating with more aggressive males to avoid potentially injurious courtship behavior even though aggressive males are more successful at male–male competition [18]. When coerced to mate with aggressive males, females pay a direct cost but benefit by producing coercive sons.

Parasites

Avoiding parasites is often proposed as an important factor affecting mate choice via both direct and indirect mechanisms [36]. Both males and females gain a direct benefit by avoiding partners that carry socially transmitted parasites. Avoiding infected individuals is easier if parasitized individuals are perceivably in poorer condition. However, avoiding infected males is more difficult if males are infectious but do not exhibit clear symptoms [37]. In that case, females can rely on traits, notably BT, that predict a male's overall susceptibility to pathogens and parasitism risk.

The connection between BT and parasite load depends on how the host's BT interacts with the mode of parasite transmission [38,39]. For environmentally transmitted parasites, the key may be host BT-dependent space use [40] where bolder or more exploratory individuals are more likely to encounter parasites [41,42]. In contrast, for socially transmitted parasites, the key BT can be aggressiveness (for bite-transmitted parasites) or sociability (for those transmitted via affiliative behaviors).

In addition, the pace-of-life syndrome hypothesis posits that because bolder, more-aggressive individuals exhibit a 'live-fast-die-young' strategy, they have a lower or more general immune response [43,44] and might generally have more parasites compared to less-bold individuals that have a stronger or more specific immune response. The relationship between BT and immune function may be mediated by hormones. BT is related to hormone levels including testosterone [45], and serotonin [46]; both of which are related to immune function [47,48]. Females may thus prefer males of a particular BT for the indirect benefit of producing offspring with increased immune function. Alternatively, BT may serve as a handicap signal for indirect benefits. If females use other signals (i.e., ornament quality) to assess actual parasite load, males with at-risk BTs (e.g., aggressive) but a low parasite load could indicate that they have high-quality genetic resistance to parasites [36].

Importantly, parasites can also change host behavior. Sometimes these changes alter a host's behavior to make it bolder or more aggressive [49]. In the short term the increased boldness or aggressiveness may make parasitized males more attractive to females if these BTs are favored in other contexts; however, in the longer term, if parasitism is a major driver for mate choice, we would expect a shift in preference to shy males.

Sensory bias

Mate choice based on **sensory biases** posits that males exploit pre-existing sensory preferences in females [50]. These preferences are usually assumed to have evolved by natural selection in a nonmating context [51]. The logic extends easily to BTs. For example, visual systems in many taxa have movement detectors [52]. A vigorous display or active behavior takes advantage of this bias, and behaviorally conspicuous males will be more likely to attract a female's attention. Displaying more vigorously likely entails some risks, and so can be viewed as a bold behavior. In extreme cases, this may favor males that are bolder and more aggressive, and produce offspring that are bolder and more aggressive, than would be favored by natural selection alone.

Even sensory biases for ornaments rather than behaviors, as originally considered in the classic guppy (*Poecilia reticulata*) system [51], are easily viewed in the context of BTs. The brightness of a male guppy's orange spot, and thus its effectiveness in attracting females, is a function of the amount of carotenoids he obtains from the environment [53]. If bold or active males are more successful at obtaining carotenoids [54], then females will inadvertently select for that BT via the classic sensory exploitation mechanism. If the BT associated with the ornament is adaptive, the ornament may work as an attractant because it is an indicator of an underlying trait. Alternatively, a female could be more likely to mate with bold or active males not because she prefers boldness or activity per se but because those males spend more time displaying and she is thus exposed to them and their ornaments more often. The result could be indirect female choice for bold personalities through sensory exploitation.

How the Chooser's BT Matters

The personality of the choosy sex can also affect mate choice: one BT may not be universally preferred by all females [3]. An area of recent interest has been the study of how and why choosers

with different BTs prefer partners of different BTs, and the resulting patterns of assortative or disassortative mating by BT (Box 3).

A simple mechanism that can result in a BT × BT interaction in mate choice (i.e., assortative mating by BT) is when females and males exhibit similar BT-dependent habitat use so each BT mainly encounters potential partners with a similar BT. A parallel mechanism emerges when choosing a bold male increases predation risk by drawing attention to the female. Bold females may be the only ones willing to make risky mate choice decisions and choose bold males [55].

A female's BT may also affect how she weighs different types of information when making a mate-choice decision. Females that are more exploratory or social may come into contact with more potential mates [56]. Broadening of her options may allow her to make a more informed assessment of a male's quality. In nonmonogamous species, mate copying (selecting a male that has been chosen by previous females) can be an effective way to choose a desirable mate. In guppies (*P. reticulata*), more-social females are more likely to switch their mate choice to match choices made by a model fish [57].

However, in some species, females that are less exploratory may be able to make better decisions even though they may not be able to gather information on as many males. While it appears that different BTs excel at different cognitive tasks, in general, less-exploratory individuals appear to 'take better notes'; they gather information from fewer sources but gain more information from a given source [58]. Slower exploring female black-capped chickadees (*Poecile atricapillus*) are more sensitive to differences in a vocal discrimination task, an important part of mate choice [59].

Box 3. Assortative and Disassortative Mating

Assortative/disassortative mating occurs when individuals with similar or dissimilar phenotypes mate more frequently than expected by chance. This pattern can arise through indirect mechanisms (e.g., BT-dependent habitat choice results in BT-dependent mate choice [92–96]) or direct choice for mates with a specific complementary BT. This latter scenario has received considerable attention in the context of parental behavior. Positive assortative mating by BT may lead to improved cooperation and coordination within a pair, which could increase reproductive success [11,97,98]. Positive assortment by BT has been found in many bird species [60,98–103].

Conversely, disassortative mating by BT could be favored if each parent fulfills a different role (e.g., provisioner vs protector). Choosing a male with a complementary BT could allow a female to balance out shortcomings in her own parental care. Although the effect of different BTs on parenting behavior was not considered, this could explain the behavior of female rainbow krib (*Pelvicachromis pulcher*) that prefer males that are dissimilar in terms of level of boldness but similar in terms of consistency [104].

In addition to coordinating parental behavior, assortative mating may have other consequences for the offspring [105]. Assortative mating in species that do not have parental care has been less studied, but evidence suggests that it still occurs [106]. In guppies (*P. reticulata*), males only provide sperm, but pairs that are more similar in terms of boldness have higher parturition success than dissimilar pairs [107].

Importantly, observing that pairs have similar BTs does not necessarily imply assortative mate choice. Mismatched convict cichlids (*Amatitlania siquia*) become more similar after pairing. This increases reproductive success but they do not initially pair based on behavioral similarity [108,109]. To conclusively show assortative or disassortative mating, individual BTs needs to be assessed both before mate selection and after pairs have mated [3].

Laboratory studies may also not reveal the benefits of assortative mating if these benefits are only seen in unfavorable conditions. Eastern bluebirds (*Sialis sialis*) enjoy higher reproductive success when paired assortatively for aggression only under high levels of interspecific competition with tree swallows (*Tachycineta bicolor*) [101].

BT-based assortative mating preferences could be a first step towards reproductive isolation and subsequent speciation. Ingley and Johnson [110] proposed that BT could lead individuals to specialize in different habitats and evolve different overall suites of behaviors. Assortative mating (both via choice and location) could then facilitate divergence and speciation.

Similarly, females with different BTs may vary in how choosy they are. Only exploratory female zebra finches (*Taeniopygia guttata*) show a preference for male exploratory behavior [60]. This may be because being choosy is cognitively demanding and some BTs may be better able to cope with this challenge. In guppies (*P. reticulata*) that have been selectively bred for brain size, large-brained individuals perform better than small-brained individuals on a variety of cognitive tasks and are also bolder and more exploratory [61]. Large-brained, bold females prefer more colorful males; small-brained females fail to show a preference [62].

Importantly, if BT affects a female's mate choice and females differ in their preferences, this should facilitate the maintenance of variation in male traits. For example, if *Poecilia mexicana* females from nonsulfidic habitats preferred residents over alien sulfide-adapted males, local adaptation to harsh conditions could be increased. However, only bold, exploratory, females preferred resident males [63]. Female mate choice decisions may thus be important for predicting speciation events.

Context Dependence

Not only can a female's BT affect the type of BT she selects in a mate, but the current context may shape her preference. If females are selecting mates for the indirect benefits they provide to offspring, they may select males with a BT that is optimal in the current context so that the offspring are also likely to possess that BT. Higher activity (driving higher feeding and growth rates) is favored under low predation risk, but lower activity is favored under high risk [64]. Female common lizards (*Z. vivipara*) unexposed to predator cues preferred males that were highly active but shifted their preference when exposed to predators [13]. Similarly, if females select mates primarily based on direct benefits, the environmental context may modulate how BTs are valued. In times of food scarcity, females should prefer males with BTs associated with the ability to procure food [65]. During years of food shortage, shy African penguins (*Spheniscus demersus*) produce chicks that grow faster than chicks of bold parents [66]. Traisnel and Pichegru [66] suggest that this is because while bold penguins may be more successful at defending against predation or intraspecific aggression, they invest less time in foraging for young. In a changing environment where food shortages are predicted to become more intense or more common, shy individuals should be favored. Importantly, the time scale of behavioral consistency and change within the environment becomes important here as well. While different BTs are favored under different ecological contexts, each context must have enough stability that favoring a specific BT is useful. If the environment is changing too fast, then there is no point in choosing a male that exhibits behavioral consistency.

Concluding Remarks and Future Directions

Mate-choice decisions are important choices in an animal's life as they determine the direct and indirect benefits she and her offspring will receive. Females likely take many traits into account but one important, previously underappreciated [3] trait is the BT of the male. Even short-term correlations between present and future behavior can make BT based mate choice adaptive. Because an individual's BT relates to many aspects of its ecology, these mate choice decisions can also have far ranging effects. The connections between BT and performance in many important survival contexts [15] means there is likely no one answer for how BTs evolved; however, mate-choice decisions may contribute to both the variation between individuals and the consistency we see within an individual. While we now know that in many systems females choose mates based, in part, on BT and that a male's BT can relate to the quality of direct and indirect benefits he provides, this field is still in its infancy (see Outstanding Questions). More research that addresses the complete set of paths outlined in Figure 1 will help to elucidate just how large a role BT plays in mate-choice decisions and outcomes. Cross-species comparisons will

Outstanding Questions

How do females' behavioral type (BT)-dependent mate-choice decisions affect offspring fitness?

Do females make decisions about multiple BT traits (potentially to maximize both direct and indirect benefits), which may relate to the emergence of **behavioral syndromes**?

In cases where mutual mate choice plays a role in mate choice dynamics, does selection for behavioral consistency of both partners increase patterns of consistency?

What is the full pattern of context-dependent mate choice and in what instances are these decisions adaptive, particularly in light of human induced rapid environmental change?

What are the evolutionary implications of BT-dependent mate choice, particularly in regard to the maintenance of consistency in behavior?

Box 4. Captive Breeding Considerations

Human-induced environmental change has resulted in declines in the populations of numerous species. In response, many conservation initiatives include captive-breeding programs. However, changes in the average behavioral type (BT) of captive populations – including those bred for research [111], and production per se (e.g., fish hatcheries [112]) – is an established problem. Some personality types (e.g., proactive individuals who cope better with the stress associated with captivity) may be more successful breeders [113,114], leading to a decrease in variation in subsequent generations. McDougall *et al.* [115] argue that changes in BT in captive populations as a result of sexual and artificial selection are reducing diversity and have potentially damaging effects for reintroduction efforts.

These programs typically focus on genetic compatibility to minimize inbreeding. While these are important goals, considering the BT of the individuals may improve reproductive success [116] and increase behavioral variation. Considering whether individuals 'get along' behaviorally is particularly important because many programs fail to produce enough animals to replace wild populations.

While zoos have begun to consider BT in their management decisions [117,118], it has not been taken into account to improve captive breeding until relatively recently [116]. Initial work with the endangered Columbia Basin pygmy rabbits (*Brachylagus idahoensis)* found that when females were given the choice between two genetically compatible male neighbors, they were more likely to produce a litter and produced bigger litters when paired with preferred compared to nonpreferred neighbors [119]. This suggests that there are traits beyond just genetic quality that affect female choice and willingness to mate [120].

Similarly, giant pandas (*Ailuropoda melanoleuca*) paired with preferred partners had significantly higher copulation rates and birth rates. When both partners preferred each other, reproductive outcomes increased further [121]. Pairs that were similar in terms of neophobia and dissimilar for food anticipatory behaviors had higher reproductive success than other pairings [116]. Additionally, pairs in which the male scored higher than the female in terms of aggression also had high reproductive success. While further research in other species is needed, this offers promising evidence that considering BT could be used to improve reproductive outcomes in captive breeding programs.

be useful for understanding whether there are particular aspects of an organism's ecology, like parental care, that are related to BT-dependent mate choice. Relating mate choice by BT to differences in behavioral consistency between sexes will further help us to understand the evolutionary pressure that results in BTs [3]. Finally, understanding mate choice for BTs has potential applied benefits; for example, being cognizant of BTs in mate choice may be important for increasing captive-breeding outcomes (Box 4).

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