An evaluation of the underlying causes of personality-based assortative mating

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Assortative mating by personality has gained increased interest in recent years. However, while the occurrence of personality-based assortative mating has started to be studied more often, the proximate causes behind this phenomenon remain unclear. By reviewing fourteen recent studies on personality-based assortative mating, I investigate three possible underlying mechanisms: mate choice, habitat matching, and plasticity. Mate choice appears to be the most significant mechanism underlying assortative mating, although its importance may be overestimated as it has received far more attention than the other two mechanisms. Few personality-based assortative mating studies consider habitat matching as a possible underlying mechanism, which is surprising as many studies have found a correlation between dispersal and personality differences. Plasticity does not appear to be as important a mechanism as mate choice, but as few studies have focused on plasticity specifically, the importance of this mechanism may be underestimated.

Assortative mating takes place when individuals with similar phenotypes mate with one another more frequently than would be expected by chance alone. This phenomenon has been observed to occur in the mating patterns of a large variety of animals (Jiang et al, 2013). The vast majority of assortative mating studies focused on pair similarity in morphological traits and ornaments. For example, water striders (Gerridae family of Heteroptera, Arnqvist et al, 1996) and curculionid beetles (*Diaprepes abbreviatus*, Harari et al, 1999) were found to mate assortatively by size, like many other animals. Other species, like the northern cardinal (*Cardinalis cardinalis*), were shown to pair up with partners whose bills and plumage had similar colours (Jawor et al, 2003). In contrast, few studies have examined assortative mating in relation to animal personality, defined as the consistent difference in behavioural tendencies among individuals across time or context (Wolf & Weissing, 2012). This is surprising, because like morphological traits, personality traits are heritable (Dochtermann et al, 2015) and exhibit large between-individual variation within populations, which means they can evolve under natural and sexual selection (Schuett et al, 2010; Wolf & Weissing, 2012). However, the role animal personality plays in evolution and assortative mating has received increasing interest in recent years (Schuett et al, 2010; Wolf & Weissing, 2012).

In 2010, Schuett et al reviewed studies on personality-based assortative mating. Many of those studies found that assortative mating was positively correlated with reproductive success, especially for pairs sharing extreme personalities on either side of the spectrum. These results suggest that mating assortatively by personality may thus be adaptive. To explain the adaptive nature of assortative mating, Schuett et al (2010) suggest pairs with similar individuals may be better able to coordinate their behaviour than dissimilar pairs. For example, partners with similar personalities are likely to forage closely together. This deters predators, and it also means that the intervals at which they feed their young are synchronized. The ultimate cause is clear, but while Schuett et al (2010) offered some possible explanations, the proximate causes of personality-based assortative mating had not yet received much attention. In this thesis, I will investigate whether recent studies have been able to shed light on these causes. Specifically, I will research three theoretical mechanisms through which personality-based assortative mating might occur: mate choice, habitat matching, and plasticity.

Mate choice, or intersexual selection, takes place when members of one sex, usually females, actively choose their mate from a selection of members of the other sex (Darwin, 1871). This choice can be based on morphological traits, such as the famous peacock's tail, but it can just as likely be based on personality traits (Schuett et al, 2010). There are two ways in which mate choice can cause animals to mate assortatively by personality. First and most straightforward, individuals might choose mates who exhibit personalities similar to their own. If similarity between partners is positively correlated with reproductive success, individuals might consider potential partners similar to them to be more attractive than those dissimilar to them. Alternatively, it is possible that one personality type is considered more desirable by all individuals. If both sexes are selective in their choice of mate, this will cause the individuals exhibiting the preferred personality to mate assortatively among themselves. When this happens, those with the least preferred personalities will have to settle for one another, and thereby also mate assortatively (Burley, 1983).

Alternatively, it is possible for assortative mating to occur more passively. An individual's success may depend on how well it is able to perform in its environment, which in turn may depend on its phenotype. Given that there is a large variation of both environment and phenotypes, some phenotypes will be better adapted to certain environments than others. If an individual's phenotype does not match its environment, it may leave and find a more suitable habitat. This process is called habitat matching (Edelaar et al, 2008). While an individual might choose a habitat based on its morphological traits, its personality can be a factor as well (Edelaar & Bolnick, 2012). Personality determines how an animal interacts with its environment. For example, conspecifics with different personality-based foraging strategies will differ in their foraging success in different environments, which can lead them to prefer different habitats, and define their social network structure (Spiegel et al, 2017). In support to this hypothesis, individual dispersal tendency has been found to be correlated with personality differences in many species (Cote et al, 2010). When dispersal and settlement decisions differ between personality types, individuals are more likely to encounter conspecifics with similar personalities in their breeding habitat than they would if dispersal were random (Spiegel et al, 2017). As a consequence, individuals will pair with mates with personality type similar to their own even if mate choice is random, which means assortative mating will occur.

Finally, assortative mating can occur even when personality has not been selected for prior to mating. Animal personalities can exhibit some degree of plasticity: personality can change to be better adapted to the individual's social or physical environment (Schuett et al, 2010). For example, if a pair's personalities do not match, it is possible that one or both animals might alter their personality to resemble the other. Alternatively, both partners might adjust their personalities to their shared environment, resulting in their personalities becoming more similar over time. However, personalities are generally considered to be consistent over time, and to show only limited plasticity. Therefore, while some plasticity may occur, I do not expect to find it to be a prominent cause of assortative mating.

Do mate choice, habitat matching, and plasticity underlie personality-based assortative mating? I will strive to answer this question by reviewing studies that investigated personality-based assortative mating since the publishing of Schuett et al's (2010) paper. I will review which of the three mechanisms, if any, the studies proposed as being the cause underlying assortative mating, and evaluate whether this proposal is supported by the results of the study. In so doing, I hope to be able to ascertain whether these mechanisms hold true in practice, and which mechanisms, if any, are more significant than the others.

Analysis

Methods

To answer my research question, I have gathered fourteen studies on personality-based assortative mating, all of which have been conducted after Schuett et al's (2010) paper was published. The findings of these studies have been summarized in Table 1. I will review each of these studies separately. I will note whether the study has found assortative mating to occur if the study concerned a wild population, and I will note whether the study found assortative mating to be positively correlated with reproductive success. I will note which mechanism, if any, the study proposed to underlie assortative mating, and I will describe and evaluate the reasoning behind this proposal. Finally, in the discussion, I will use the findings of these studies to compare the three mechanisms that can underlie assortative mating, judge which mechanism is most important, and which mechanisms, if any, require more research.

Reference	**Research species**	**Location**	**Method**	*** Assortative**	**** Correlation**	**Proposed mechanism**	**Based on**
Kralj-Fišer et al, 2013	Bridge spider (*Larinioides sclopetarius*)	Lab	Experimental	+	O	Mate choice	Spiders were given a choice, and tended to mate assortatively.
Fox & Millam, 2014	Cockatiel (*Nymphicus hollandicus*)	Lab	Descriptive	O	-	NA	Birds were free to choose their partner, but no mechanism was proposed.
Laubu et al, 2016	Convict cichlid (*Amatitlania siquia*)	Lab	Experimental	NA	+	Plasticity	Reactive individuals changed personality to match their proactive partners.
Laubu et al, 2017	"	Lab	Experimental	O	NA	Plasticity, see 2016	Cichlids did not choose mates based on matching personalities.

Harris & Siefferman, 2014	Eastern bluebird (*Sialia sialis*)	Field	Descriptive	+	+	Plasticity / Mate choice	Speculation: did not test behaviour prior to pair formation.
Burtka & Grindstaff, 2015	"	Field	Descriptive	+	+	Mate choice	Conclusions of other studies. Considered plasticity, but found consistency.
Martin-Wintle et al, 2017	Giant panda (*Ailuropoda melanoleuca*)	Captivity	Descriptive	NA	- / O	Mate choice	Females prefer aggressive males. Aggressive females are more likely to mate.
Ariyomo & Watt, 2013	Guppy (*Poecilia reticulata*)	Lab	Experimental	O	+	Habitat matching	Conclusions of other studies: mate choice was not found to underlie assortative mating.
Rangassamy et al, 2015	Mound-building mouse (*Mus spicilegus*)	Lab	Experimental	NA	+	NA	NA
Scherer et al, 2017	Rainbow krib (*Pelvicachromis pulcher*)	Lab	Experimental	+ / -	NA	Mate choice	Females preferred males with similar consistency, but dissimilar boldness.
Gabriel & Black, 2011	Steller's jay (*Cyanocitta stelleri*)	Field	Descriptive	+	+	Mate choice	Conclusions of other studies.
Montiglio et al, 2016	Stream water strider (*Aquarius remigis*)	Captivity	Descriptive	+ / -	NA	Mate choice	Assortative mating did not arise from differences in partner availability.
Schuett et al, 2011a	Zebra finch (*Taeniopygia guttata*)	Lab	Experimental	NA	+	NA, but see 2011b	NA, but see 2011b
Schuett et al, 2011b	"	Lab	Experimental	+	NA	Mate choice	Intermediate and high-exploratory females preferred high-exploratory males.

Table 1: The studies summarized.

*** Did the research species tend towards personality-based assortative mating? + = assortative mating, - = disassortative mating, O = random mating**

**** Was personality-based assortative mating correlated with offspring fitness? + = positive correlation, - = negative correlation, O = no correlation**

Results

Kralj-Fišer et al (2013) studied mate choice based on aggression in bridge spiders (*Larinioides sclopetarius*). The spiders were ranked either aggressive or non-aggressive, and were then placed together in groups of six: two females, one aggressive and one non-aggressive, and four males, two aggressive and two non-aggressive. Aggressive females were more than three times more likely to mate with aggressive males than with non-aggressive males. Non-aggressive females were 1.45 times more likely to mate with non-aggressive males than with aggressive males. While aggressive males sired significantly more eggs than non-aggressive males, neither female personality nor assortative mating were correlated with any measure of reproductive success. The underlying mechanism behind assortative mating in this study turned out to indeed be mate choice, as males and females were not dispersed by habitat in any way. Aggression was measured before mate choice, ruling out plasticity.

Fox & Millam (2014) studied the effects of various personality traits on reproductive success in cockatiels (*Nymphicus hollandicus*). They studied 10 pairs that were formed through free choice, and showed no significant overall tendency towards either assortative or disassortative mating. Prior to pair formation, all individuals were scored for three personality traits: agreeableness, boldness, and affiliativeness. After pair formation, the pairs' behavioural compatibility was measured by recording the amount of aggressive interactions they showed. Reproductive success was measured by the ability to successfully hatch eggs. Pairs that hatched at least one egg were considered successful, pairs that did not manage to hatch any eggs were considered unsuccessful. Successful pairs showed significantly fewer occurrences of intrapair aggression, and were as such considered to be significantly more compatible, than pairs that were unsuccessful. Neither successful nor unsuccessful pairs showed a significant correlation between mates' scores on boldness and affiliativeness. However, successful pairs showed a significant negative correlation between mates' levels of agreeableness. Similarly, unsuccessful pairs showed a significant positive correlation between mates' levels of agreeableness. In conclusion, disassortative mating for agreeableness was positively correlated with reproductive success. As cockatiels showed no overall tendency towards assortative or disassortative mating, this study sheds little light on the mechanisms that underlie assortative mating.

Laubu et al (2016) studied plasticity in convict cichlids (*Amatitlania siquia*). Cichlids were characterized as either proactive or reactive, using four different behavioural traits: aggression, exploration, maintenance activity, and food neophobia. These four measures were all repeatable, and strongly correlated. Cichlids that scored high on aggression and exploration, and low on maintenance activity and food neophobia were considered proactive. Cichlids that scored high on maintenance activity and food neophobia, and low on aggression and exploration, were considered reactive. These personality types were evenly distributed among the sexes. The cichlids were then paired up according to their personality type: eight pairs had two reactive partners, seven pairs had two proactive partners, six pairs had a reactive female and a proactive male, and seven pairs had a proactive female and a reactive male. Reproductive success was measured as the time until the start of spawning, and the amount of fry that hatched. Assortatively matched pairs did not significantly differ from each other in the amount of fry they hatched, regardless of whether the pair was proactive or reactive. Assortative pairs did, on average, hatch more fry than disassortative pairs. Assortative pairs also exhibited fewer intrapair conflicts than disassortative pairs did. However, all disassortative pairs showed some degree of plasticity. While proactive personalities remained consistent, cichlids with reactive personalities would become more proactive if they had a proactive mate. On average, the originally disassortative pairs that managed to converge the most managed to reproduce as fast as the assortative pairs did, and managed to spawn as many fry as assortative pairs as well. The disassortative pairs that did not manage to fully match their personalities reproduced later, and did not hatch as many fry as the assortative and converging disassortative pairs. Plasticity clearly at least partially underlies assortative mating in convict cichlids.

Later, Laubu et al (2017) studied whether convict cichlids engage in assortative mate choice, in addition to exhibiting plasticity. In this study, cichlids were scored only for aggression, which, as had been found in their 2016 study, is correlated positively with exploration, and negatively with maintenance activity and food neophobia. Mate choice was tested for in two ways. The first experiment focused on mutual mate choice. Up to 24 cichlids were brought together in one tank, with an equal distribution of males and females. In this tank, the cichlids were free to choose mates among themselves. The cichlids were given six days to find a mate, to avoid underestimating the strength of assortative mating by having cichlids that were unable to find a mate eventually settle for a second-choice partner. The second experiment focused on individual mate choice. In this experiment, a single cichlid was given a choice between two potential mates, one with a similar aggression score, and one with a dissimilar score. Both experiments had the same result: convict cichlids did not choose to mate assortatively based on their aggression score. The authors proposed that the costs of finding a matching partner are higher than changing one's personality after pairing, and that cichlids therefore exhibit plasticity rather than mate choice. Neither study considered, or tested for, habitat matching.

Harris & Siefferman (2014) studied the effects of interspecific competition on assortative mating. To this end, they studied a population of 63 pairs of eastern bluebirds (*Sialia sialis*) in the southern Appalachian Mountains, on a site that had recently been colonized by tree swallows (*Tachycineta bicolor*). The personality trait they studied was aggression in territorial defence, tested with a simulated territorial intrusion. Reproductive success was quantified by the number of fledglings, and nestling mass at an age of 14 days. Assortative mating was found to be significantly positively correlated with nestling mass, with pairs that were mated assortatively on both extremes producing the heaviest nestlings. No correlation was found between assortative mating and number of fledglings. The authors proposed both mate choice and plasticity as possible underlying mechanisms. However, because they did not measure aggression before mate selection occurred, they were unable to provide evidence for either mechanism. Habitat matching was not considered. While the authors note that bluebirds appear to suffer from competition with tree swallows, they did not comment on dispersal. I therefore think it is possible that aggressive bluebirds are less common in areas with high interspecific competition, and that this has led to assortative mating.

Burtka & Grindstaff (2015) also studied eastern bluebirds. While not solely an assortative mating study, they looked at aggression in nest defence, and proposed three hypotheses on how aggression might lead to reproductive success. (1) The individual personality hypothesis, where individuals with aggressive personalities will have greater reproductive success, (2) the pair coordination hypothesis, where assortatively mated pairs have greater reproductive success, and (3) the pair intensity hypothesis, where both partners in an assortatively mated pair, both with aggressive personalities, have greater reproductive success. As in Harris & Siefferman (2014), aggression was measured using simulated territorial intrusions. Reproductive success was indicated by the amount of fledglings in a nest. Nest defence scores were found to be significantly positively correlated within pairs. While the results did not support for the individual personality hypothesis and the pair intensity hypothesis, they did support the pair coordination hypothesis: pairs that mated assortatively had more nestlings fledge than pairs that did not. Eastern bluebirds tended towards assortative mating overall: 63 pairs were mated assortatively, compared to 30 pairs that were not. The authors considered that plasticity might underlie assortative mating, but noted that individuals were shown to be fairly consistent in nest defence behaviour over time. They did not test personality before pair formation and so could not rule out that plasticity might occur, but considered it unlikely as they had found that bluebirds that changed mates were still consistent in their behaviour. They therefore concluded, based on other studies, that mate choice is likely to be the underlying mechanism. Habitat matching was not considered.

Martin-Wintle et al (2017) studied the effect of personality matching on mating success in giant pandas (*Ailuropoda melanoleuca*). Giant pandas, an endangered species, are famous for being slow to reproduce in captivity, which may partially be caused by poor personality match-ups. Caretakers rated 19 female and 10 male giant pandas according to 23 personality traits, such as aggression, excitability, and fearfulness, to find out which combinations of traits are likely to increase reproductive success. To get an indication of fearfulness, the pandas were also tested for consistency in their responses to four novel objects. Reproductive success was measured by number of successful mating attempts, as well as whether cubs were born. Reproductive success was not correlated with assortative mating according to aggression: high-aggressive males paired with low-aggressive females had the highest reproductive success, followed by high-aggressive males paired with low-aggressive females. Aggressive males had the highest reproductive success overall. Reproductive success was not correlated with assortative mating according to fearfulness either: low-fearful males paired with low-fearful females had the highest reproductive success, followed by low-fearful males paired with high-fearful females. Reproductive success was significantly negatively correlated with assortative mating according to excitability, however: high-excitable males paired with low-excitable females had the highest reproductive success, followed by low-excitable males paired with high-excitable females. For all three personality traits listed here, pair combinations other than the ones listed had fairly low reproductive success. While no mechanisms were tested for, the authors propose that mate choice may underlie assortative mating among pandas, as they reported that aggressive females are more likely to exhibit sexual behaviour towards males than non-aggressive females, and that females generally prefer aggressive males. In the wild, this may lead to aggressive pandas mating assortatively among themselves, leaving non-aggressive pandas to mate with one another. Neither plasticity nor habitat matching have been considered.

Ariyomo & Watt (2013) studied mate choice in guppies (*Poecilia reticulata*). Specifically, they investigated whether female guppies prefer males who exhibit levels of boldness similar to their own. The boldness levels of 80 guppies of each sex were tested, and the 30 boldest and 30 shyest guppies of each sex were selected to partake in the mate choice experiment. During these experiments, female guppies were presented with randomly selected bold and shy males. The female guppy was free to approach both males, who were confined to 6.5 x 6.5 x 17.5cm cages, and preference was indicated by the amount of time the female spent in proximity to either male over two 10-minute periods. To measure reproductive success, males and females were randomly paired up according to their boldness, and given three days to reproduce. Pairs were scored on whether they produced offspring, the time until their offspring was born, and the amount of offspring that was born. Assortative pairs were more likely to produce offspring and produced more offspring than disassortative pairs. Neither bold nor shy females showed any significant preference for either bold or shy males. The authors therefore concluded that mate choice does not underlie assortative mating in guppies. They proposed habitat matching as an alternative explanation, as bold and shy guppies are adapted to different social and physical environments. This was speculative, however, as this study was performed in a lab. The authors did not consider plasticity. However, I consider plasticity to be unlikely to underlie assortative mating in the guppy, as boldness was found to be consistent in both males and females. Furthermore, I am unsure whether this experiment properly tested the effect of mate choice, and thus whether the authors were correct in their conclusion that mate choice does not underlie assortative mating. While the female was free to move around and explore during the mate choice experiment, the males, who were confined to fairly small cages, were not. The study does not describe how the female is able to tell which male is bold, and which is not. If the males are not free to explore, move around, and show off how bold they are, it is possible that the female does not know which male's personality is most similar to her own. If that were the case, I would not expect female guppies to show any significant personality-based preference. Which is exactly what this study found.

Rangassamy et al (2015) studied the effect of assortative mating on reproductive success in mound-building mice (*Mus spicilegus*). Two personality traits were studied: exploratory tendency and anxiety. Exploration and anxiety scores were found to be consistent in both males and females. Mice were then paired randomly, into a total of 41 pairs. Reproductive success was quantified by the onset of reproduction. Early onset was considered to be an indicator of high reproductive success. Pairs that mated assortatively for anxiety showed significantly higher reproductive success than pairs that did not. Assortative mating for exploration was not significantly correlated with reproductive success. This study did not investigate the underlying mechanisms behind assortative mating, and the authors did not propose any.

Scherer et al (2017) studied personality-based mate choice in rainbow kribs (*Pelvicachromis pulcher*). Specifically, they studied the effect of male and female boldness on female mate choice. The study considered both an individual's level of boldness, as well as its consistency. Boldness was measured by studying the way kribs interacted with a simulated predator. Kribs were shown an animation of a predator, and boldness was quantified as their activity in the predator's presence. The boldness tests were conducted three times, and mate choice tests were conducted at the same time as the first two male boldness tests. A female watched two males undergo their test, while the males could not see the female. Afterward, the female was allowed to approach the two males, and preference was measured by the amount of time she spent near each of the males. The males were characterized as 'bold' (the bolder of the two males) and 'shy' (the less bold of the two). Definitions of bold and shy therefore seem to be relative to each other: even if both males were bold overall, one was necessarily considered shy. Males were tested for boldness unrelated to mate choice on the 33rd day, but whether these results were considered in the mate choice experiment is unclear. Overall, females did not show significant preference for either bold or shy males, nor did they show significant preference for either consistent or inconsistent males. Preference for bold males was significantly negatively correlated with female boldness. Preference for consistent males was significantly positively correlated with female consistency. The authors therefore concluded that mate choice underlies disassortative mating for boldness, and assortative mating for consistency. However, I doubt whether the design of this study was truly fit to measure assortative mating for boldness. For example, while shy females generally preferred the bolder male, the study does not answer whether they necessarily preferred bold males in general. I therefore doubt whether mate choice truly underlies disassortative mating for boldness. As the kribs in this study did not mate, plasticity was not considered. Habitat matching was not considered in this study.

Gabriel & Black (2011) studied a population of Steller's jays (*Cyanocitta stelleri*) on the border of a redwood (*Sequoia sempervirens*) forest in northern California. They studied two personality traits, exploratory behaviour and risk-taking behaviour, in pairs over three years (34 in 2006, 46 in 2007, and 44 in 2008). Long-term exploratory behaviour was measured as a jay's maximum travel distance from its nest, and short-term exploratory behaviour was measured as a jay's willingness to explore a novel environment. Partners' long-term exploratory behaviour showed a significant within-pair positive correlation over all three years. Short-term exploratory behaviour showed significant within-pair positive correlation in 2006, and within-pair risk-taking behaviour showed significant within-pair positive correlation in 2007. Jays exhibited a tendency to mate assortatively overall, even when the strong correlation between long-term exploratory behaviours was removed from the meta-analysis. Pairs that mated assortatively for at least one trait showed significantly greater reproductive success than non-assortative pairs, as was quantified by a pair's nest initiation date, where an early initiation date indicated high reproductive success. The authors proposed jays might choose to mate assortatively, but this proposal was based on the conclusions of earlier studies. This study did not investigate mate choice. While it is unclear whether the personality traits were measured before or after pair formation, the authors do note that these personality traits are consistent within individuals over time. I therefore consider plasticity to be unlikely to underlie assortative mating in Steller's jays. The study did not find a correlation between personality traits and habitat quality, which excludes habitat matching as an underlying mechanism.

Montiglio et al (2016) studied the effects of mate choice and habitat matching on assortative mating in stream water striders (*Aquarius remigis*). The study investigated assortative mating by level of activity, as well as by size. To control for the effect of mate availability, the water striders were kept in artificial outdoor pools, each of which contained either 24 males and 24 females, or 32 males and 16 females. Activity was measured by recording each individual's actions each hour. If it was mating, the partner's identity was also noted, which was used to get an indication of who chose to mate with whom. Mating patterns were not found to be significantly influenced by mate availability. Water striders were found to mate assortatively by size, as well as by level of activity overall. However, water striders with extremely high and extremely low levels of activity were found to mate disassortatively for level of activity. The study did not note whether activity was correlated with body size in any way, and it is therefore unclear whether assortative mating by size influenced assortative mating by level of activity. The authors proposed mate choice underlies assortative mating in water striders, as mate availability was not found to influence mating patterns. The study did not consider plasticity, and did not note whether water striders were consistent in their level of activity. It is therefore unclear whether plasticity may have been an underlying mechanism.

Schuett et al (2011a) studied the effect of assortative mating on foster offspring fitness in zebra finches (*Taeniopygia guttata*). To this end, zebra finches were randomly paired up into 31 pairs and allowed to breed. Whole clusters of eggs were then cross-fostered shortly before hatching, to remove possible effects of heritability and focus solely on the effect of parental care. Zebra finches were tested for exploratory behaviour prior to breeding, and for aggression after breeding. Zebra finches underwent each test twice, and were found to be significantly consistent overall for both traits. Offspring fitness was quantified by the chicks' growth rate. Neither parents' exploratory behaviour nor their aggression were correlated with their genetic offspring's fitness in any way. Pairs that were mated assortatively for exploratory behaviour, aggression, and consistency, all raised foster offspring with significantly higher fitness than pairs that were not mated assortatively for any of these traits. However, while high-exploration females were more successful when paired with high-exploration males, and less successful when paired with low-exploration males, low-exploration females raised moderately successful young regardless of their mate's exploratory behaviour. This study did not investigate the underlying mechanisms of assortative mating.

Schuett et al (2011b) then studied the role of mate choice in assortative mating in zebra finches. As in their earlier (2011a) study, finches were scored on exploratory behaviour. The finches were tested twice, and found to be significantly consistent in their behaviour overall. In the mate choice experiment, 51 females each observed a unique brother pair, whose apparent exploratory behaviours were experimentally manipulated. The males were released into a novel environment. Apparently exploratory males were free to explore this environment, while apparently un-exploratory males, who were confined to a plexiglass box, were not. Females were presented with either two apparently exploratory males, two apparently un-exploratory males, or one apparently exploratory male and one apparently un-exploratory male. The female observed both males for 10 minutes, after which the males were placed in cages, and the female was free to approach them. Preference was measured as the amount of time the female spent near each male. While apparently un-exploratory males showed significantly greater activity than apparently exploratory males when approached by the female, this did not have a significant effect on the female's preference. The study found that medium- and high-exploratory females significantly preferred apparently exploratory males over apparently un-exploratory males. Low-exploratory females showed no significant preference for either apparently exploratory or apparently un-exploratory males. These results are consistent with Schuett et al's (2011a) findings that medium- and high-exploratory females are more successful at raising young when paired with high-exploratory males, while low-exploratory females raise moderately successful young regardless of their mate's exploratory behaviour. This study clearly shows that mate choice underlies assortative mating in zebra finches. Considering zebra finches were significantly consistent in their behaviour overall, it is unlikely that plasticity is an underlying cause. Habitat matching was not considered.

Discussion

I have summarized 14 studies on assortative mating. 7 of these studies (Burtka & Grindstaff, 2015; Gabriel & Black, 2011; Kralj-Fišer et al, 2013; Martin-Wintle et al, 2017; Montiglio et al, 2016; Scherer et al, 2017; Schuett et al, 2011b) proposed mate choice as the mechanism underlying assortative mating, 5 of which (Kralj-Fišer et al, 2013; Martin-Wintle et al, 2017; Montiglio et al, 2016; Scherer et al, 2017; Schuett et al, 2011b) found evidence to support their proposal. 2 studies (Laubu et al, 2016; Laubu et al, 2017) proposed plasticity as the mechanism underlying assortative mating. Both found evidence to support their proposal, but both were conducted by the same people. 1 study (Harris & Siefferman, 2014) proposed both mate choice and plasticity as possible underlying mechanisms, but had found evidence for neither mechanism. 1 study (Ariyomo & Watt, 2013) proposed habitat matching as a possible mechanism, because they did not find mate choice to have an effect. However, I question the validity of this result, and believe the study may have missed the effect of mate choice due to a flaw in their method. 3 studies (Fox & Millam, 2014; Schuett et al, 2011a; Rangassamy et al, 2015) did not propose any mechanism.

Mate choice

Mate choice is clearly an important mechanism underlying assortative mating. Half of the studies I have summarized concluded their observations of assortative mating were caused by mate choice, and most of them found evidence to support this conclusion. However, I believe the importance of mate choice relative to habitat matching and plasticity may be overestimated. Mate choice was by far the most researched mechanism, and was the only mechanism proposed by studies that had not found evidence for any mechanism themselves (Burtka & Grindstaff, 2015; Gabriel & Black, 2011), that based their conclusion on the findings of other studies. Therefore, while mate choice is definitely an important mechanism in assortative mating, I am hesitant to consider it the most important mechanism until habitat matching and plasticity have been researched just as thoroughly. Evidence has been found for the theory that animals choose mates who exhibit personalities similar to their own (Kralj-Fišer et al, 2013; Scherer et al, 2017), as well as for the theory that assortative mating happens when a specific personality trait is considered attractive by most individuals (Martin-Wintle et al, 2017; Schuett et al, 2011b). We can therefore conclude that both these forms of mate choice contribute to personality-based assortative mating.

Habitat matching

Habitat matching was badly underrepresented in the studies I have summarized. Only one study (Montiglio et al, 2016) accounted for the availability of mates with different personalities, and found no effect on assortative mating. The fact that few studies considered habitat choice is unsurprising, as many studies were carried out in a lab or captivity. However, of the three field studies, only one (Gabriel & Black, 2011) considered the influence of habitat variation. This study did not find a significant correlation between personality and habitat quality. While few assortative mating studies considered the influence of the environment on the dispersal of different personalities, however, many studies that did not focus on assortative mating did. For example, giant sea anemones (*Condylactis gigantea*) were found to be dispersed among different habitats according to different responses to disturbance in their physical environment (Hensley et al, 2012). Dispersal of great tits (*Parus major*) was found to be influenced by their social environment, as male great tits assort by personality during the mating season (Johnson et al, 2017). Furthermore, fast-exploring great tits are favoured in low population densities, while slow-exploring great tits are favoured in high population densities (Nicolaus et al, 2016). Dunnocks (*Prunella modularis*) have been found to actively disperse among different habitats according to their boldness (Holtmann et al, 2017). All these studies have found a correlation between personality differences and dispersal. I therefore find it remarkable that so few assortative mating studies consider the possible effect of habitat matching, and believe that this mechanism definitely deserves more attention.

Plasticity

As I expected, plasticity was not often found to underlie assortative mating in personality studies. While few studies explicitly considered the influence of plasticity, most tested for consistency in the trait they researched. However, few studies tested personality traits both before and after mating, which makes it difficult to draw proper conclusions on the occurrence of plasticity as a result of pair formation. I would therefore recommend that more assortative mating studies explicitly focus on investigating this mechanism. Laubu et al's (2016) study provides a good example of how this could be done. Until plasticity is studied further, however, I do not believe it is as important a mechanism as mate choice has shown to be, and habitat matching has the potential to be.

Conclusion

Mate choice has been shown to be an important underlying mechanism behind personality-based assortative mating in many animal species.

While plasticity has been shown to underlie personality-based assortative mating in some animals, it does not appear to be an important mechanism behind personality-based assortative mating overall. More research is required, however, as plasticity has been fairly underrepresented in assortative mating studies.

Habitat matching may potentially be an important mechanism underlying personality-based assortative mating. As it has barely been studied in relation to assortative mating, more research is required.

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