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Individual preference functions exist without overall preference in a tropical jumping spider

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Female mate choice is a widespread and well-recognized phenomenon. Nevertheless, individual variation in female preference has not yet received the same attention, although such preferences can have important effects on evolutionary dynamics. Here we assess and compare population- and individual-level female preferences for male ornaments and size in the tropical jumping spider *Hasarius adansoni* in two sets of laboratory experiments. First, we paired females with a single male and quantified receptive behaviours (e.g. receptive posture, number of copulations) and unreceptive behaviours (e.g. attacking the male, running away from a male). We assessed whether these male traits were related to offspring quality and quantity to determine whether there was selection on female preferences. Then, we paired different females with three different-sized males, one per day, and scored similar behaviours to measure preference functions (relationship between male traits and female receptivity). Generally, the population of females did not show a consistent average preference for male traits, despite our finding that females mated to larger males produced more offspring. However, at the individual level, females showed different preference functions for male size, such that some females preferred larger males, while others preferred smaller males. We discuss these data in terms of the causes and consequences of individual preference functions, highlighting the importance of including individual preference functions in future studies that focus on sexual selection and how individual preference can maintain phenotypic variation in wild populations.

Sexual selection models predict that animals should not mate randomly (Andersson, 1994). As the sex that invests more heavily in each reproductive event, females are usually 'choosier' and, according to a number of theoretical models, are expected to mate nonrandomly with males in ways that will enhance their reproductive output or the fitness of their offspring (Andersson, 1994; Bateman, 1948). The evidence supporting nonrandom mating by females is remarkable and encompasses virtually all main taxonomic groups (Andersson, 1982; Candolin, 2003; Cotton, Small, & Pomiankowski, 2006; Kirkpatrick, 1982; Kokko, Jennions, & Brooks, 2006; Møller & Alatalo, 1999; Ronald, Fernández-Juricic, & Lucas, 2012; von Schantz, Bensch, Grahn, Hasselquist, & Wittzell, 1999). Much of this work examines average preferences that are expected to impose consistent selection on male traits, although these population-level patterns could be coincident with significant variation at the level of individuals (Wagner, 1998).

Individual sexual preferences are a less frequently explored facet of sexual selection. The idea that individuals consistently differ in the way they perform specific behaviours is now well recognized, and recent research has shown that such differences may be adaptive (Bell, 2007; Dall, Houston, & McNamara, 2004; Dingemanse & Réale, 2005; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004; Stamps & Groothuis, 2010; Wolf & Wessing, 2010). However, distinct behavioural types (i.e. consistent individual differences in behaviour) and different behavioural syndromes (i.e. suites of correlated behaviours across situations; Bell, 2007; Sih & Johnson et al., 2004), most recently called animal 'personalities' (Sih & Johnson et al., 2004), have been assessed in a relatively limited number of behaviours. Aggression, environment exploration and fear response to novel or threatening situations (usually called boldness) are among the most common behaviours assessed in the personalities paradigm (Carter, Goldizen, & Tromp, 2010; Castilho & Macedo, 2016; Dingemanse, Both, van Noordwijk,

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Rutten, & Drent, 2003; Møller, 2010; Rabaneda-Bueno, Aguado, Fernández-Montraveta, & Moya-Laraño, 2014; Smith & Blumstein, 2010; Zhao, Hu, Liu, Chen, & Sun, 2016). The influence of consistent differences in behaviour in a sexual selection context, however, has been relatively neglected (Schuett, Tregenza, & Dall, 2010). To date, there is some evidence that females may vary in their propensity to engage in copulations (Godin & Dugatkin, 1995; Keiser, Lichtenstein, Wright, Chism, & Pruitt, 2018; Kralj-Fišer, Schneider, & Kuntner, 2013), or extrapair copulations (Forstmeier, 2007) and in the direction of mate choice (Ah-King & Gowaty, 2016; Edwards, Melville, Joseph, & Keogh, 2015; Forstmeier & Birkhead, 2004; also see ; Jennions & Petrie, 1997). For instance, in the zebra finch, *Taeniopygia guttata*, some females prefer high song rates while others prefer low song rates, although song rate is related to average male attractiveness (Forstmeier & Birkhead, 2004). In other cases, such as brown-headed cowbirds, *Molothrus ater*, variation in female visual and auditory systems affects perception and links to individual preferences for multimodal male display traits (Ronald et al., 2017, 2018). The pattern of female receptivity as a function of male phenotype defines a preference function that indicates the rank order of preference for males with particular trait values (Jennions & Petrie, 1997). The causes of distinct mating preference functions may vary, but female past experience (e.g. previous sexual encounters) and assortative mating are among the most commonly reported (e.g. Baldauf, Engqvist, Ottenheym, Bakker, & Thünken, 2013; Bel-Venner, Dray, Allainé, Menu, & Venner, 2008; Fowler-Finn & Rodríguez, 2011; Hebets, 2003; Hoefler, Persons, & Rypstra, 2008; Johnson & Basolo, 2003; Keiser et al., 2018; Kralj-Fišer et al., 2013).

Given the possibility that animals can vary intrinsically in their sexual preferences, evaluating the parameters that reflect population-level preference functions may not accurately reflect the detailed processes of sexual selection that act within a species. A comprehensive understanding of sexual selection can only be achieved with the assessment of the full spectrum of sexual preferences, encompassing both population and individual levels, and considering possible individual variations that might influence mate choice and preference functions (Ah-King & Gowaty, 2016; Wagner, 1998).

Here, we explored the scope of sexual selection at population and individual levels in the tropical jumping spider *Hasarius adansoni*. Jumping spiders are excellent models to assess many aspects of behaviour, including sexual behaviour, since most species perform complex displays (Elias, Maddison, Peckmezian, Girard, & Mason, 2012), which usually imply mate choice (Busso & Rabosky, 2016; Girard, Elias, & Kasumovic, 2015), and are easy to capture and maintain in controlled conditions. *Hasarius adansoni* males have courtship displays with visual and vibrational signals, and females exhibit a stereotyped receptive posture when accepting a male for copulation (Castilho, Andrade, & Macedo, 2018). In the present laboratory experiment, we first paired each female with a randomly assigned, single male to test whether there was a population-level preference function for females based on male size or ornament dimensions. Then, we compared offspring quantity and quality as a function of paternal traits to determine whether there were any benefits for choosiness (i.e. if different males would convey different fitness benefits for the female). Finally, we paired females with multiple males in sequence to measure individual female preference functions (Wagner, 1998). We also assessed possible causes for such individual variation, by testing whether female size or mating experience influenced females' sexual preferences.

Since our study species performs sexual displays, we predicted that females would exhibit a population-level preference, being more receptive to males siring more and/or better offspring than others (e.g. larger males). Given that individual variation is common in animals, and individual variation in preference functions can coexist with a population-level preference (e.g. high versus low song rate in zebra finches; Forstmeier & Birkhead, 2004), we also predicted that individual females would differ in their preference functions.

METHODS

Morphology and Mating Behaviour

Hasarius adansoni (Salticidae: Araneae) is a common tropical spider with sexually dimorphic coloration. Females are black and brown, while males are primarily black with bright white patches on their palps (paired, anterior-most appendages, which are also the copulatory organs in male spiders; see Figure 1 in Castilho et al., 2018). The white patch is revealed to females during courtship and may be used as a visual signal (Castilho et al., 2018), as is typical for sexual ornaments used in courtship displays in jumping spiders (Foelix, 2011). Males also produce vibrational signals during courtship, classified as tremulation, a type of substrate-borne signal in which the male vibrates his abdomen without touching the substrate. The vibration energy is transmitted through his legs to the substrate and the receiver (Castilho et al., 2018). Male *H. adansoni* usually court in bouts, that is, a single couple may go through the whole process (i.e. courtship–copulation/rejection) many times in a few hours (Castilho et al., 2018).

Receptive females respond to the male's courtship by continually orienting towards the male as he courts, and eventually adopting a receptive posture (i.e. staying motionless with legs curled and vibrating the abdomen), which is required for mating to proceed (Castilho et al., 2018). Nonreceptive females may attack the male, rapidly retreat from the male, or simply ignore his copulation attempt by not adopting a receptive posture (Castilho et al., 2018). The former behaviours were classified as receptive behaviours, while the latter were classified as nonreceptive behaviours.

General Capture and Handling

A total of 161 animals (71 females and 90 males) were captured in the urban environment around the city of Brasília, in central Brazil (15°46′47″S, 47°55′47″W) and brought to the Laboratório de Comportamento Animal at the Universidade de Brasília main campus. Spiders were maintained in glass vials (9 × 4.5 cm) with a piece of wet cotton and were fed with 15 adult *Drosophila* spp. and one *Gryllus* sp. cricket nymph every 4–7 days. Males and females

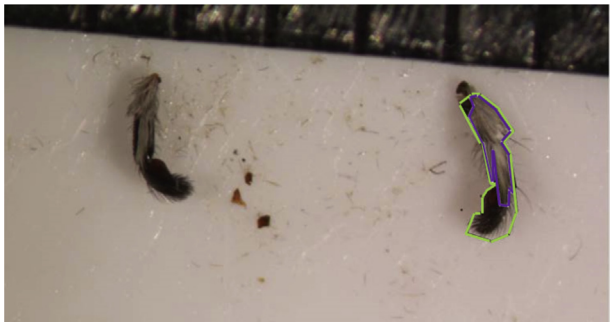

Figure 1. Paired copulatory organs (secondary sexual organs, or palps) of male *Hasarius adansoni* after dissection from the body to allow measurement. We measured the area of the whole palp (green outline) and the area of the white patch (potential ornament, purple outline).

captured as juveniles were reared until adulthood and experiments were conducted only with adult, sexually mature animals. We were able to distinguish between adult and juvenile females by the presence of a visible epigynum (adult female's external genital structure), assessed under a stereomicroscope. Adult males were identified by their fully developed palps. Animals captured as adults were used only in a subset of experiments (see below).

A pilot study showed that after a few copulations, females become globally less willing to copulate, even with males they had previously chosen. In the same pilot study, we found that males were still willing to copulate after many copulations. Given these pilot results, we reared virgin females for use in general preference mating trials in which females are paired with only one male (see below). However, since individual preference measures required assessing the difference in responses to multiple males from a single female, without actually mating (see below), and to avoid a very small sample size for these experiments, we allowed nonvirgin females to enter individual preference experiments. Our focus here was to examine individual females' responses to distinct males, while maintaining each female's willingness to copulate constant. This was achieved with our procedure, while allowing us to keep the sample size large enough to produce robust models. It is also possible that after the first copulation, females change their preference. We do not think this is the case, since we did not find any consistent difference in preference functions for females captured as adults versus those captured as young (although our design did not allow for formal tests of this hypothesis). Even if this were the case, it would not diminish the importance of a possible individual preference function variation and could be interpreted as the cause of such variation.

Permits for collection and maintenance of animals were issued by Instituto Chico Mendes (ICMBio), Brazil. Animals were handled as carefully as possible, and at the end of the project, all remaining animals were released in the same city where they were initially collected. All protocols described adhered to the legal requirements of Brazil and Canada.

Measuring Spider Phenotype

Before mating trials, we chilled all spiders inside a vial that was in contact with ice for a few minutes, until the spiders stopped moving. We took their weight with a 0.001 g precision balance and also photographed them with a ruler in the image to use as a scale to later determine absolute body size (i.e. carapace width) using the software ImageJ (Schneider, Rasband, & Eliceiri, 2012). Photographs were taken with a digital USB 2.0 stereomicroscope (manufactured by DigiMicro). Individual condition was also estimated using the residuals of a regression of animal mass on animal size. In spiders, well-fed animals are usually in better condition (i.e. larger and heavier), and this affects their ability to court and compete for mates, and might affect female choice (e.g. Cotton et al., 2006; Elgar & Fahey, 1996; Hoefler et al., 2008; Kasumovic & Andrade, 2006; Kasumovic, Brooks, & Andrade, 2009). Moreover, female condition (i.e. size, infection status, energy available, etc.) might affect choice (Cotton et al., 2006). Although the condition index we used has been criticized (Jordi & Andy, 2009), it has also been endorsed (Schulte-Hostedde et al., 2005), and has been considered the best condition index for spiders (Jakob, Marshall, & Uetz, 1996).

After the males' natural deaths, we photographed their palps to measure the percentage of the palp area covered by the white patch as an estimate of ornament elaboration (Fig. 1). Palps were amputated at the base to facilitate measurement, and the mean of both palps was used as our index except in a few cases where one palp was damaged by the procedure.

EXPERIMENT 1: GENERAL FEMALE PREFERENCES AND OFFSPRING QUALITY

Mating trials took place in a mating arena, which consisted of an acrylic square box, measuring 13 × 13 × 4 cm. The arena had two opaque dividers in opposite corners, so two animals could be held at the same time without visual contact until their release. Since our arena was made from a rigid acrylic material, any substrate-borne vibrations made by the spiders were likely to have been significantly attenuated while in the arena (e.g. see Elias, Mason, & Hoy, 2004). We are aware that using a softer substrate would have allowed females to better assess males' vibration signals, which could modify the shape of preference functions. Most of our spiders, however, were captured on the walls of buildings, so we believe our experimental set-up closely matches the conditions they encounter naturally.

In each trial, animals were placed inside the arena and separated by the dividers for 1 h (acclimation), after which the dividers were removed and the animals were allowed to see and interact with each other for 3 h. We videotaped all trials and, from the videos, collected the following variables to measure female receptivity: (1) number of copulations; (2) total copulation time across all successful copulations; (3) number of female unreceptive behaviours (i.e. attacking the male, running away from the male or not adopting receptive posture when in front of a displaying male); and (4) percentage of copulation attempts by the male that were unsuccessful. One copulation attempt was defined as a courting male getting close to a female and touching her (i.e. trying to engage in palp insertion). These variables were chosen based on our observations indicating that, in *H. adansoni*, no copulations occur if the male does not court and females control the total number of copulations (Castilho et al., 2018).

Before each trial, the arena was cleaned with soap, water and alcohol to remove any pheromonal cues that could have been left behind by previous animals. Since sexual ornaments of some jumping spiders reflect light in the ultraviolet spectrum (e.g. Bulbert, Hanlon, Zappettini, Zhang, & Li, 2015), we conducted experiments under a natural light-simulating lamp (Arcadia Bird lamp, Model FB 36). Trials in which it was clear that animals did not see each other ($N = 12$) were excluded from analyses. It was easy to detect the moment when animals saw each other, since they usually turned their median eyes to one another quickly to engage in eye contact, and visually followed each other using cephalothoracic movements following the initial contact.

After mating trials, females were kept in the same housing conditions as described above until they produced eggs. The number of eggsacs per female and the number of hatched offspring per eggsac were counted. After spiderlings emerged from the eggsac, they were kept individually in small glass vials (~5 × 1.5 cm). Half of each brood was left unfed, providing us with data to conduct survival analyses to assay juvenile provisioning and fitness under stress (Cox proportional hazard model, described below), and the other half was used in a feeding performance trial.

Since newly dispersed jumping spiders usually rely on their own predation ability to survive (Richman & Jackson, 1992), we measured feeding performance as an offspring quality indicator. We created a protocol to measure feeding performance in young jumping spiders, using springtails (Collembola) as the model prey. Feeding performance trials consisted of placing individual spiderlings in a petri dish with a single live springtail. We replaced the springtail if it died before being captured by the spiderling. Since static prey do not attract spiders, we kept the springtails moving by touching them with a paintbrush every time they were immobile. We kept the spiders within the petri dish by gently pushing them back inside with a paintbrush when they tried to escape. Such

protocol usually ended with the springtail being captured and eaten by the spider. One caveat to this methodology is that the paintbrush could alter the behaviour of the spider or the springtail. However, this seems unlikely for two reasons: (1) we did not observe any change in spider behaviour when the paintbrush was touching the springtail, in contrast to when the spider was stalking the springtail; and (2) although this method was used throughout the experiment, we found a decrease in predation performance in later broods (see Results), showing biological correlations were measurable using this technique.

Each feeding trial was videotaped, and the following variables were extracted from the videos as measurements of feeding performance: (1) latency to start moving towards prey, once oriented towards it; and (2) speed while approaching prey (in mm/s). Our springtail populations were obtained from an independent seller in Toronto, Canada. Springtails were kept in consistent housing conditions throughout our experiments and bred successfully under these conditions. They were held at room temperature in two small boxes with soil, and provisioned with water and food (live yeast) every other day.

Experiment 2: Individual Preference

We used a subsample of 23 adult males to establish the mean and standard errors of body size in the population. The same person measured all males, with repeatability of these measurements assessed on a subsample of males that were measured twice ($R = 0.92$, $F_{1,18} = 24.3$, $P < 0.0001$). Once all 23 animals were measured, we were able to classify any male in one of three body size categories: average males (between -1SE and +1SE of the average); small males (< −1SE); large males (> +1SE). Before each trial, we also measured the females.

We used standard errors as cutoff points to separate male sizes because this resulted in a more or less equivalent number of small, average and large animals for the experimental trial, which was our main goal with the size classification. On average, males in the large male group were larger than those in the average group, which in turn were larger than males in the small group (large: 2.21 ± 0.12 mm; average: 2.11 ± 0.09 mm; small: 1.89 ± 0.14 mm), and these differences were significant (ANOVA: $F_{2,46} = 29.2$, $P < 0.0001$). This shows that our classification correctly divided males into three distinct size groups.

Mating trials were similar to those described in experiment 1, however, each female was presented with three different-sized males (small, average and large) in random order and on three separate days (one male presented per day), to prevent excessive stress and fatigue from handling. Since one copulation may alter the chance of a female copulating again (Castilho et al., 2018), experiments were interrupted right before mating took place or after 1 h, if no copulations occurred.

From the videos, we recorded the following female behaviours as measurements of female receptivity: (1) number of unreceptive behaviours (i.e. attacking or running away from the male, even if he did not attempt copulation); (2) number of rejections (i.e. number of displays performed by the male that did not result in a receptive posture by the female); (3) percentage of copulation attempts by the male that were rejected; and (4) occurrence of copulations (coded as 1 or 0). If the animals tried to copulate, but were separated by us, we assigned the number '1'. If not, we assigned the number '0'. The occurrence of copulation was easy to observe, since a courting male would approach a female in receptive posture and mount her. As soon as she turned her abdomen up to facilitate palp insertion and the male was about to insert, they were separated. Trials in which males did not court females at least once were excluded from further analysis ($N = 2/51$ trials).

Statistical Analysis

Reducing variables' dimensionality

Principal component analyses (PCA) were used to reduce data dimensionality. Females' preference variables (e.g. number of attacks towards males, number of copulations, etc.) and offspring feeding performance variables along with eggsac number (to control for any early versus late brood effects) were reduced by PCA analysis (Tables 1–3). The number of principal components we used in our analyses was based on the percentage of total variance explained and consideration of the biological significance of the PCs. As a general rule, we were conservative and used PCs that together explained at least 75% of the total variance in our data sets.

General female preferences

General linear models were used to create female preference functions, with variables of female preference (extracted from the principal components) as response variables and the following male quality variables as predictors: male mass, size, condition and percentage of white patch cover on palp.

Young survival

A Cox proportional hazard rate model was used to perform a survival analysis of the offspring. The model uses brood number as a fixed effect and brood identity nested in female identity as random factors. Female Cox proportional hazard coefficients were then regressed on male quality variables to assess the influence of male quality on survival of each female's offspring.

Young feeding performance

Male quality, measured as male size and condition, was also inserted in linear models as predictors, with offspring feeding performance (extracted from the axes of the PCA) as response variables, to test for any effect of male quality on offspring predatory performance. We also regressed number of offspring produced against male quality, to assess the influence of male quality on offspring number.

Note, however, that for experiment 1, not every predictor was used in every analysis, since this would lead to collinearity problems in some models (e.g. male size, mass and/or condition were sometimes correlated). We also used percentage of white patch cover as a predictor variable, since total patch area was usually correlated with other variables, especially male size. To summarize, we used male weight, condition and percentage of white patch cover as predictors in a model that had female acceptance as response. The same predictors were used in another model with female rejection as response (this separation was due to the PCA results, see below). Another model had offspring feeding performance as response, and male size and condition as predictors. We also regressed number of young produced with male condition, size and percentage of white patch cover. Offspring survival was

Table 1
Component loadings from a PCA with different variables used to measure female *Hasarius adnasoni* preference for males

Variable	PC1	PC2	PC3	PC4
Number of copulations	0.92	0.32	0.16	0.18
Total copulation time	0.91	0.36	0.06	−0.18
Unreceptive behaviours	−0.32	0.84	−0.44	0.02
% Rejections	−0.64	0.55	0.54	−0.01
Cumulative % variance explained	55%	86%	98%	100%

Unreceptive behaviours include attacking or running away from the male or not adopting a receptive posture in the presence of a displaying male.

Table 2
Component loadings from a PCA with different variables used to measure feeding performance of *H. adansoni* young

Variables	PC1	PC2	PC3
Latency to move towards prey	0.28	0.96	−0.06
Speed moving towards prey	−0.79	0.22	0.57
Eggsac number	0.8	−0.12	0.58
Cumulative % variance explained	45%	78%	100%

regressed against male condition, size and percentage of patch cover.

Individual female preferences

To measure within-individual consistency and between-individual variation in mate preference, we used the reaction norms approach to build individual female preference functions for male body size (see details of this approach in Dingemanse, Kazem, Réale, & Wright, 2010). Female acceptance was included as a response variable, male size centralized by its mean was included as a fixed continuous variable and female identity was included as a random factor. With this approach, each female's intercept can be interpreted as the mean sexual responsiveness of that female, and each female's slope can be interpreted as the female's behavioural plasticity due to differences in male size (Dingemanse et al., 2010). Male size was chosen as a male quality of interest since it is easy to measure and compare between males and is strongly correlated with male weight (which is correlated with condition) and with palp white patch area.

Preference variation due to quality

To test for differences in preference functions due to female quality, we built regression models with the values of females' intercepts or slopes of the reaction norm model as responses, and female size as predictors. Since such relationships appeared to be nonlinear, we performed general additive models (GAM) with the local weighted linear regression (LOWESS) smoothing technique as described by Zuur, Ieno, Walker, Saveliev, and Smith (2009).

Previous sexual experience

To evaluate the effect of previous sexual experience on female preference functions, we also tested the effect of male presentation order on the intercepts and slopes of female preference functions through analysis of variance (ANOVA).

All analyses were performed in R (R Core Team, 2014) using the package 'nlme' and 'nlme4' to build GLMs and the package 'gam' to build GAMs.

RESULTS

General Female Preference

The PCA of female general mate preference resulted in a first principal component heavily and positively loaded on number of copulations and total copulation time and negatively loaded on percentage of failed copulation attempts. The second component loaded heavily only on unreceptive behaviours. Together, both components explained 86% of the total variance (Table 1). Since the first component did not explain a large percentage of variance, and the second only loaded on unreceptive behaviours, we used the first principal component as a measure of female acceptance and the raw values of unreceptive behaviours as a measure of female rejection.

Female acceptance was not related to male mass, condition or percentage of white patch cover (GLM: $\beta_{weight} = 154.98$, $P = 0.15$; $\beta_{condition} = -44.13$, $P = 0.81$; $\beta_{patch} = -0.86$, $P = 0.85$, $N = 11$). Similarly, female rejection was unrelated to male weight or condition, and only weakly affected by percentage of white patch cover (GLM: $\beta_{weight} = 437.83$, $P = 0.48$; $\beta_{condition} = 1968.50$, $P = 0.13$; $\beta_{patch} = -0.73$, $P = 0.053$, $N = 11$). A closer evaluation of the percentage of white patch cover revealed no further relationship with female rejection (Spearman rank correlation: $r_S = -0.27$, $N = 11$, $P = 0.42$).

Offspring Quality and Quantity

We had access to a total of 53 eggsacs, with an average of 21 spiderlings per sac. The PCA with offspring feeding performance variables yielded a first principal component heavily and positively loaded on eggsac production order and heavily and negatively loaded on spiderlings' speed towards prey. The second component loaded heavily and positively on spiderlings' latency to start moving towards prey (Table 2). The two principal components explained 78% of the total variance.

Male quality and the first and second principal components for offspring feeding performance yielded no significant relationships (PC1: $\beta_{male\ size} = -1.32$, $P = 0.14$; $\beta_{male\ condition} = -30.64$, $P = 0.67$, $N = 18$; PC2: $\beta_{male\ size} = -0.05$, $P = 0.91$; $\beta_{male\ condition} = 24.12$, $P = 0.55$, $N = 18$). The only male quality variable related to the total number of offspring was male size, with larger males producing more offspring (GLM: $\beta_{male\ condition} = -151.1$, $P = 0.94$; $\beta_{patch} = -64.2$, $P = 0.38$; $\beta_{size} = 159.5$, $P = 0.0007$, $N = 17$). We found that quality of adult males did not influence offspring survival, since the female random coefficients, extracted from the Cox proportional hazard mixed model, were not related to male condition, size or percentage of white patch cover ($\beta_{condition} = 105.894$, $P = 0.14$; $\beta_{size} = 0.55$, $P = 0.5$; $\beta_{patch} = 0.19$, $P = 0.93$, $N = 17$).

Individual Female Preferences

The first principal component for individual female preference explained 63% of the total variance and was strongly and positively correlated with number of unreceptive behaviours, number of rejections and percentage of rejections. The first component was also moderately and negatively correlated with the presence of copulations. Then, we considered this first component as a measure of female rejection. The second component explained another 21% of the variance and was moderately and positively correlated with presence of copulations and only weakly related to other variables (Table 3). Since the first component did not explain a large part of the variance, and the second was highly influenced only by presence of copulations, we used the first principal component in one behavioural reaction model and the raw values of presence of copulations in a separate behavioural reaction model.

The first model, using the first component, had no significant general effect of male size on female rejection ($\beta = 0.09$, $N = 46$, $P = 0.89$). This shows that, overall, females did not choose males based on their size. However, significant differences in slopes (likelihood ratio test: $\chi^2_1 = 13.20$, $P = 0.0014$) showed that females differed in how much they preferred different-sized males (Fig. 2). However, these preference functions slopes cancelled each other out at the level of the population (or general preference) because some females preferred larger males while others preferred smaller males.

For the behavioural binomial reaction norm using presence of copulation as the response variable, we included female size as a fixed effect in the model to ensure normality of random effects. The effect of slopes was nonsignificant (likelihood ratio test: $\chi^2_1 = 4.2$, $P = 0.12$), while the effect of the intercept was significant ($\chi^2_1 = 4.9$, $P = 0.02$). Thus, we further analysed the model with random

Table 3
Component loadings from a PCA with different variables used to measure female *H. adansoni* preference for distinct sized males

Variables	PC1	PC2	PC3	PC4
Unreceptive behaviours	0.83	0.38	−0.35	0.23
Rejections	0.87	0.39	0.1	−0.3
% Rejections	0.83	−0.25	0.48	0.16
Presence of copulations[a]	−0.63	0.7	0.3	0.1
Cumulative % variance explained	63%	84%	96%	100%

Unreceptive behaviours included attacking or running away from the male or not adopting a receptive posture in the presence of a displaying male.
[a] Coded as 1 or 0.

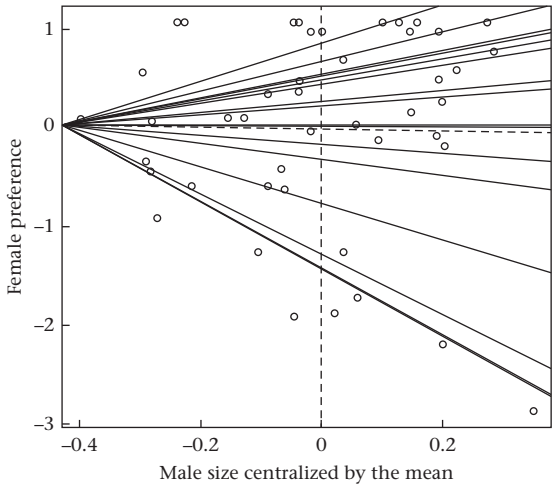

Figure 2. Preference functions for individual *Hasarius adansoni* females as a function of male size. Each dot represents a distinct mating trial. Each female underwent three trials with different males, and each male was classified in one of three size categories (small, average or large). Thus, each continuous line represents the preference function for a specific female. Male size is centralized by its mean, so the intercept (vertical dotted line) represents the preference of the females for an average-sized male. The horizontal thick dotted line represents the population preference function.

intercepts only. Similar to our first reaction norm model, we had no significant effect of male or female size on the probability of copulation (male size: $\beta = 2.6$, $P = 0.3$; female size: $\beta = -13.9$, $N = 38$, $P = 0.11$). This shows that, overall, male size did not affect the probability of copulation, but females differed intrinsically in their probability of copulation. Although the difference in slopes was nonsignificant, the correlation between slopes and intercepts was positive and high ($R = 0.9$), showing a pattern similar to that found in our first model: females differed in their propensity to copulate with different-sized males, but some females preferred large males while others preferred small males, which could mask female preferences if one measures only population-level correlations.

Preference Variation due to Quality

Our GAMs did not reveal any relationship between female size and female average sexual responsiveness ($F_{1,7.5} = 1.5$, $P = 0.24$) or between female size and female sexual behavioural plasticity. ($F_{1,7.5} = 1.5$, $P = 0.25$). This shows that female preference functions cannot be predicted by female quality as assessed by body size. Also, these nonsignificant effects are probably not very conservative. Female sexual responsiveness and plasticity were extracted from random terms of mixed modes. Since there is an intrinsic uncertainty in those terms (Houslay & Wilson, 2017), which we did not account for, our results probably overestimate the relationship between female size and sexual behaviour.

Previous Sexual Experience

Previous female interaction did not affect sexual responsiveness or plasticity of females, since females first presented to large, small or medium males did not differ in their intercepts or slopes in the behavioural reaction model (ANOVA: slope: $F_{2,14} = 0.51$, $P = 0.608$; ANOVA: intercept: $F_{2,14} = 0.517$, $P = 0.607$). This shows that different sexual experiences (within the experimental paradigm) did not dictate preferences of individual females. Similarly to our GAMs, the values of intercept and slope were extracted from a mixed model and have an intrinsic uncertainty related to them, which was not accounted for. Thus, our nonsignificant *F* values are probably overestimated.

DISCUSSION

We found that female *H. adansoni* did not prefer any particular male trait at the population level, despite the fact that larger males produced more offspring. However, we found that females strongly preferred males of different sizes at the individual level. These individual preferences, however, were arranged in a way that cancelled each other out, eliminating any general preference function. Variation in female preferences may arise from assortative mating (reviewed by Bel-Venner et al., 2008; Cotton et al., 2006), variable social and life history (Bierbach, Sommer-Trembo, Hanisch, Wolf, & Plath, 2015; Dukas, 2005; Fowler-Finn & Rodríguez, 2011; Gaskett, Herberstein, Downes, & Elgar, 2004; Johnson & Basolo, 2003; Place, Todd, Penke, & Asendorpf, 2010; Rundus, Biemuller, DeLong, Fitzgerald, & Nyandwi, 2015), variation in female perception of male traits (Ronald et al., 2012) or selection for genetically compatible mates (Landry, Garant, Duchesne, & Bernatchez, 2001; Tregenza & Wedell, 2000; see Kelly, 2018 for a review of all these topics), although we have not tested these ideas directly. The effect of individual preferences could be significant, including the maintenance of variation in male size due to sexual selection (Kelly, 2018), despite higher fitness of larger males.

Different mating preferences may result from variation in female quality, and females of high quality are expected to choose males of similar high quality in many species, either because they can more easily bear the cost of choosiness or because they are more capable of choosing high-quality males (Cotton et al., 2006; Kelly, 2018). However, our results suggest that neither female average sexual responsiveness nor the direction of female preference for male traits was predicted by female size (which is correlated with mass, and thus could be a measure of 'quality'; L. Castilho, personal observation). Thus, we believe differences in female quality do not explain the highly variable preference functions we observed in this study. It is possible, however, that less ephemeral female characteristics guide female preferences. For instance, females might prefer males that best match their personalities (e.g. Kralj-Fišer et al., 2013; Pogány et al., 2018), if male size is somehow correlated with these characteristcs. Also, other factors that might influence individual quality, such as age, parasites and mutation loads, have been shown to change female preference functions (Cotton et al., 2006).

Across taxa, one plausible reason for variation in female preference is a difference in benefits provided by males, when females face different environmental or social contexts. For instance, in a study with the wax moth (*Achroia grisella*), females that copulated with more attractive males produced faster-growing and heavier

offspring when food was abundant and temperature was close to optimum (Jia & Greenfield, 1997). However, when food availability was reduced and temperatures were not optimal, females that mated with less attractive males produced higher-quality offspring. Other taxa are known for mate choice that varies based on their own genotypes, and traits that indicate the genotype of a potential mate. Disassortative mating leads to mating with partners with dissimilar, but compatible genes, which in turn enhances offspring heterozygosity (Landry et al., 2001; Tregenza & Wedell, 2000). These examples may help explain why individual preference functions evolve and are maintained in animals, including *H. adansoni*, since different choices may yield alternative benefits, given the female's genotype and her environment.

Such changes in the benefits provided by males could also help explain the initially counterintuitive result showing that larger males were not generally preferred, although they sired more offspring. If female fitness is not entirely dependent on offspring quantity, then females might choose smaller males if the benefits generated by such a choice outweigh the risk of producing fewer offspring.

The results of our study with *H. adansoni* may reflect the predictions of some models, which suggest that females should constantly alternate between strategies of producing numerous versus better offspring, especially when environmental conditions vary (Fischer, Taborsky, & Kokko, 2011; Sinervo, Svensson, & Comendant, 2000). Although our experimental conditions were stable, the conditions each animal experienced while developing are unknown. In addition, we measured offspring survival and feeding performance and could not detect such a trade-off. However, trade-offs could occur relative to other factors influencing offspring quality. For instance, predator avoidance could be an important aspect of the quality of offspring (Johnson & Basolo, 2003) that could trade off with quantity.

We did not find an effect of previous sexual experience on female preference function. It is plausible, however, that experiences earlier in life could have an effect in this regard (Kelly, 2018). For instance, Dukas (2005) found that *Drosophila* courted by large males early in life became less choosy; while Fowler-Finn and Rodríguez (2011) showed that female treehoppers became choosier after having been exposed to male vibrations in their preferred frequency. Since some of our females were captured after the last instar, we cannot rule out the possibility that males encountered by these females earlier in life may have affected adult mate preference and choosiness (Bierbach et al., 2015; Dukas, 2005; Fowler-Finn & Rodríguez, 2011; Place et al., 2010; Santangelo, 2015; Schuett et al., 2010; Swaddle, Cathey, Correll, & Hodkinson, 2005).

The consequences of individual variation are as important as the reasons for which they evolve. Forstmeier and Birkhead (2004) provided evidence that, in the zebra finch, some females prefer orange-beaked males and others prefer red-beaked males. Similarly, some females prefer more aggressive males, while others prefer less aggressive ones. The variation in the preferred traits was so high that the authors could not detect a general population preference for beak colour or aggressiveness (but they did find one for song rates). Such contradictory findings could have led to the wrong conclusion that such characters are not being targeted by sexual selection, had the authors not also assessed individual preferences. In the present study, we found a similar pattern in female preference for male size in the jumping spider *H. adansoni*. Female preferences are related to male size, however, some females prefer small males, while others prefer large males. The individual preference functions were arranged in a way that cancelled each other out, so that the net selection for size was close to zero (e.g. no significant slope in the model). Interestingly, such a system may also help maintain different male sizes in the population, since no directional selection would arise for male size. In fact, the coefficient of variation for male size in our population (CV = 11, 08%) was above the average reported for most animal species in a comprehensive review reported by McKellar and Hendry (2009).

Future studies should also help us understand the evolutionary importance of individual sexual preferences. Some studies conclude that sexual selection alone has the potential to promote speciation (Higashi, Takimoto, & Yamamura, 1999; Turner & Burrows, 1995), and the possibility that distinct female preferences are heritable (Jennions & Petrie, 1997) reinforces this paradigm. The idea that sexual selection plays a large role in speciation is still under debate (Maan & Seehausen, 2011), but we believe that distinct female preferences could potentially facilitate speciation in the long term, since this would maintain the needed genetic variance.

A comparison of population and individual levels of mate preference is an important step towards developing and testing comprehensive hypotheses in sexual selection, since this is a growing field and yet under-represented in the behavioural literature (Ah-King & Gowaty, 2016; Wagner, 1998). Our study also has the advantage of targeting the behaviour of a tropical species, most of which are extremely under-represented in the sexual selection literature (e.g. Macedo, 2010). Because the tropical and temperate regions differ in their selection pressures (e.g. temperature, biodiversity, photoperiod, seasonality, etc.; Willig, Kaufman, & Stevens, 2003), information about tropical species can help us understand the variability and types of adaptations across a larger pool of species, strengthening the conceptual pillars of sexual selection theory.

Our results contribute to the accumulating evidence that mate preference is more labile than previously thought. Actually, mate preference is a flexible behaviour that may vary with environment and the choosy sex genotype, since partner-derived benefits are also expected to be similarly flexible (Candolin, 2003). Interestingly, depending on how individual preference functions are arranged, it may be impossible for a population preference function to be assessed, an important alert for empiricists seeking to describe sexual preferences in a species. In studies in which a population appears to display no sexual preferences, individual preferences might be playing an important role, and such a conclusion can only be assessed when individual preference functions are accounted for. Note, however, that even when a population-level preference is present, individual-level preferences can also play an important role in sexual selection and evolution (e.g. Forstmeier & Birkhead, 2004), and can, at least in principle, help in the process of speciation if such variation is heritable (e.g. Gray & Cade, 2000).

Declaration of Interest

None.

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References

Ah-King, M., & Gowaty, P. A. (2016). A conceptual review of mate choice: Stochastic demography, within-sex phenotypic plasticity, and individual flexibility. *Ecology and Evolution, 6*(14), 4607–4642. https://doi.org/10.1002/ece3.2197.

Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. *Nature, 299*(28), 818–820.

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Baldauf, S. A., Engqvist, L., Ottenheym, T., Bakker, T. C. M., & Thünken, T. (2013). Sex-specific conditional mating preferences in a cichlid fish: Implications for sexual conflict. *Behavioral Ecology and Sociobiology, 67*(7), 1179–1186. https://doi.org/10.1007/s00265-013-1543-4.

Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity, 2*, 349–368.

Bel-Venner, M. C., Dray, S., Allainé, D., Menu, F., & Venner, S. (2008). Unexpected male choosiness for mates in a spider. *Proceedings of the Royal Society B: Biological Sciences, 275*(1630), 77–82. https://doi.org/10.1098/rspb.2007.1278.

Bell, A. (2007). Future directions in behavioral syndromes research. *Proceedings of the Royal Society B: Biological Sciences, 274*, 755–761. https://doi.org/10.1098/rspb.2006.0199.

Bierbach, D., Sommer-Trembo, C., Hanisch, J., Wolf, M., & Plath, M. (2015). Personality affects mate choice: Bolder males show stronger audience effects under high competition. *Behavioral Ecology, 26*(5), 1314–1325. https://doi.org/10.1093/beheco/arv079.

Bulbert, M. W., Hanlon, J. C. O., Zappettini, S., Zhang, S., & Li, D. (2015). Sexually selected UV signals in the tropical ornate jumping spider, *Cosmophasis umbratica* may incur costs from predation. *Ecology and Evolution, 5*(4), 914–920. https://doi.org/10.1002/ece3.1419.

Busso, J., & Rabosky, D. (2016). Disruptive selection on male reproductive polymorphism in a jumping spider, *Maevia inclemens*. *Animal Behaviour, 120*, 1–10. https://doi.org/10.1016/j.anbehav.2016.07.028.

Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews, 78*, 575–595.

Carter, A. J., Goldizen, A. W., & Tromp, S. A. (2010). Agamas exhibit behavioral syndromes: Bolder males bask and feed more but may suffer higher predation. *Behavioral Ecology, 21*(3), 655–661. https://doi.org/10.1093/beheco/arq036.

Castilho, L. B., Andrade, M. C. B., & Macedo, R. H. (2018). Mating and egg-laying behavior of *Hasarius adansoni* (Araneae: Salticidae) and the influence of sexual selection. *Journal of Arachnology, 46*(3), 398–403. https://doi.org/10.1636/joas16-091.1.

Castilho, L. B., & Macedo, R. F. (2016). Behavioral types and syndromes in the neotropical passarine blue-black grassquit (*Volatinia jacarina*). *Oecologia Australis, 20*(3), 28–36. https://doi.org/10.4257/oeco.2016.2003.04.

Cotton, S., Small, J., & Pomiankowski, A. (2006). Sexual selection and condition-dependent mate choice. *Current Biology, 16*(17), R755–R756. https://doi.org/10.1016/j.cub.2006.08.022.

Dall, S. R., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters, 7*(8), 734–739. https://doi.org/10.1111/j.1461-0248.2004.00618.x.

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London, Series B: Biological Sciences, 270*(1516), 741–747. https://doi.org/10.1098/rspb.2002.2300.

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution, 25*(2), 81–89. https://doi.org/10.1016/j.tree.2009.07.013.

Dingemanse, N., & Réale, D. (2005). Natural selection and animal personality. *Behaviour, 142*, 1159–1184.

Dukas, R. (2005). Learning affects mate choice in female fruit flies. *Behavioral Ecology, 16*(4), 800–804. https://doi.org/10.1093/beheco/ari057.

Edwards, D. L., Melville, J., Joseph, L., & Keogh, S. (2015). Ecological divergence, adaptive diversification, and the evolution of social signaling traits: An empirical study in arid Australian lizards. *American Naturalist, 186*(6), E144–E161. https://doi.org/10.1086/683658.

Elgar, M. A., & Fahey, B. F. (1996). Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae : Araneoidea). *Behavioral Ecology, 7*(2), 195–198.

Elias, D. O., Maddison, W. P., Peckmezian, C., Girard, M. B., & Mason, A. C. (2012). Orchestrating the score: Complex multimodal courtship in the *Habronattus coecatus* group of *Habronattus* jumping spiders (Araneae: Salticidae). *Biological Journal of the Linnean Society, 105*(3), 522–547. https://doi.org/10.1111/j.10958312.2011.01817.x.

Elias, D. O., Mason, A. C., & Hoy, R. R. (2004). The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dossenus* (Araneae: Salticidae). *Journal of Experimental Biology, 207*(23), 4105–4110. https://doi.org/10.1242/jeb.01261.

Fischer, B., Taborsky, B., & Kokko, H. (2011). How to balance the offspring quality quantity tradeoff when environmental cues are unreliable. *Oikos, 120*(2), 258–270. https://doi.org/10.1111/j.1600-0706.2010.18642.x.

Foelix, R. F. (2011). Reproduction. In R. F. Foelix (Ed.), *Biology of spiders* (pp. 218–260). Oxford, U.K.: Oxford University Press.

Forstmeier, W. (2007). Do individual females differ intrinsically in their propensity to engage in extra-pair copulations? *PLoS One, 2*(9). https://doi.org/10.1371/journal.pone.0000952. e952.

Forstmeier, W., & Birkhead, T. (2004). Repeatability of mate choice in the zebra finch: Consistency within and between females. *Animal Behaviour, 68*(5), 1017–1028. https://doi.org/10.1016/j.anbehav.2004.02.007.

Fowler-Finn, K. D., & Rodríguez, R. L. (2011). Experience-mediated plasticity in mate preferences: Mating assurance in a variable environment. *Evolution, 66*(2), 459–468.

Gaskett, A., Herberstein, M., Downes, B., & Elgar, M. (2004). Changes in male mate choice in a sexually cannibalistic orb-web spider (Araneae: Araneidae). *Behaviour, 141*, 1197–1210.

Girard, M., Elias, D., & Kasumovic, M. (2015). Female preference for multimodal courthip: Multiple signals are important for male mating success in a peacock spider. *Proceedings of the Royal Society B: Biological Sciences, 282*(1820), 12–14. https://doi.org/10.1098/rspb.2015.2222.

Godin, J.-G., & Dugatkin, L. A. (1995). Variability and repeatability of female mating preferences in the guppy. *Animal Behaviour, 49*(6), 1427–1433.

Gray, A. D., & Cade, H. W. (2000). Sexual selection and speciation in field crickets. *Proceedings of the National Academy of Sciences of the United States of America, 97*(26), 14449–14454. https://doi.org/10.1073/pnas.97.26.14449.

Hebets, E. A. (2003). Subadult experience influences adult mate choice in an arthropod: Exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences of the United States of America, 100*(23), 13390–13395.

Higashi, M., Takimoto, G., & Yamamura, N. (1999). Sympatric speciation by sexual selection. *Nature, 402*, 523–526.

Hoefler, C. D., Persons, M. H., & Rypstra, A. L. (2008). Evolutionarily costly courtship displays in a wolf spider: A test of viability indicator theory. *Behavioral Ecology, 19*(5), 974–979. https://doi.org/10.1093/beheco/arn055.

Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology, 28*(4), 948–952. https://doi.org/10.1093/beheco/arx023.

Jakob, E., Marshall, S., & Uetz, G. (1996). Estimating fitness: A comparison of body condition indicies. *Oikos, 77*(1), 61–67.

Jennions, M., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society, 72*, 283–327.

Jia, F., & Greenfield, M. D. (1997). When are good genes good? Variable outcomes of female choice in wax moths. *Proceedings of the Royal Society of London - Series B: Biological Sciences, 264*(1384), 1057–1063. https://doi.org/10.1098/rspb.1997.0146.

Johnson, J. B., & Basolo, A. L. (2003). Predator exposure alters female mate choide in the green swordtail. *Behavioral Ecology, 14*(5), 619–625. https://doi.org/10.1093/beheco/arg046.

Kasumovic, M. M., & Andrade, M. C. B. (2006). Male development tracks rapidly shifting sexual versus natural selection pressures. *Current Biology, 16*(7), R242–R243. https://doi.org/10.1016/j.cub.2006.03.017.

Kasumovic, M. M., Brooks, R. C., & Andrade, M. C. B. (2009). Body condition but not dietary restriction prolongs lifespan in a semelparous capital breeder. *Biology Letters, 5*(5), 636–638. https://doi.org/10.1098/rsbl.2009.0335.

Keiser, C. N., Lichtenstein, J. L., Wright, C. M., Chism, G. T., & Pruitt, J. N. (2018). Personality and behavioral syndromes in insects and spiders. In A. Córdoba-Aguilar, D. González-Tokman, & I. González-Santoyo (Eds.), *Insect behavior: From mechanisms to ecological and evolutionary consequences* (pp. 236–256). Oxford, U.K.: Oxford University Press.

Kelly, C. D. (2018). The causes and evolutionary consequences of variation in female mate choice in insects: The effects of individual state, genotypes and environments. *Current Opinion in Insect Science, 27*, 1–8. https://doi.org/10.1016/j.cois.2018.01.010.

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. *Evolution, 36*(1), 1–12.

Kokko, H., Jennions, M., & Brooks, R. (2006). Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution and Systematics, 37*(1), 43–66. https://doi.org/10.1146/annurev.ecolsys.37.091305.110259.

Kralj-Fišer, S., Schneider, J., & Kuntner, M. (2013). Challenging the aggressive spill-over hypothesis: Is pre-copulatory sexual cannibalism a part of a behavioural syndrome? *Ethology, 119*(8), 615–623. https://doi.org/10.1111/eth.12111.

Landry, C., Garant, D., Duchesne, P., & Bernatchez, L. (2001). 'Good genes as heterozygosity': The major histocompatibility complex and mate choice in Atlantic salmon (*Salmo salar*). *Proceedings of the Royal Society of London, Series B: Biological Sciences, 268*(1473), 1279–1285. https://doi.org/10.1098/rspb.2001.1659.

Maan, M. E., & Seehausen, O. (2011). Ecology, sexual selection and speciation. *Ecology Letters, 14*, 591–602.

Macedo, R. (2010). *Behavioral ecology of tropical animals* (1st ed., Vol. 42). London, U.K.: Academic Press.

McKellar, A. E., & Hendry, A. P. (2009). How humans differ from other animals in their levels of morphological variation. *PLoS One, 4*(9), 1–5.

Møller, A. P. (2010). Interspecific variation in fear responses predicts urbanization in birds. *Behavioral Ecology, 21*(2), 365–371. https://doi.org/10.1093/beheco/arp199.

Møller, A. P., & Alatalo, R. V. (1999). Good-genes effects in sexual selection. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 266*, 85–91.

Place, S. S., Todd, P. M., Penke, L., & Asendorpf, J. B. (2010). Humans show mate copying after observing real mate choices. *Evolution and Human Behavior, 31*(5), 1–6. https://doi.org/10.1016/j.evolhumbehav.2010.02.001.

Pogány, Á., Vincze, E., Szurovecz, Z., Kosztolányi, A., Barta, Z., Székely, T., et al. (2018). Personality assortative female mating preferences in a songbird. *Behaviour, 155*, 481–503.

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rabaneda-Bueno, R., Aguado, S., Fernández-Montraveta, C., & Moya-Laraño, J. (2014). Does female personality determine mate choice through sexual cannibalism? *Ethology, 120*(3), 238–248. https://doi.org/10.1111/eth.12197.

Réale, D., Reader, S., Sol, D., McDougall, P., & Dingemanse, N. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*, 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x.

Richman, D. B., & Jackson, R. R. (1992). A review of the ethology of jumping spiders (Araneae, Salticidae). *Bulletin of the British Arachnological Society, 9*(2), 33–37.

Ronald, K., Ensminger, A., Shawkey, M., Lucas, J., & Fernández-Juricic, E. (2017). Testing a key assumption in aninal communication: Between-individual variation in female visual systems alters perception of male signals. *Biology Open, 6*, 1771–1783. https://doi.org/10.1242/bio.028282.

Ronald, K. L., Fernández-Juricic, E., & Lucas, J. R. (2012). Taking the sensory approach: How individual differences in sensory perception can influence mate choice. *Animal Behaviour, 84*(6), 1283–1294.

Ronald, K., Fernández-Juricic, E., & Lucas, J. (2018). Mate choice in the eye and ear of the beholder? Female multimodal sensory configuration influences her preferences. *Proceedings of the Royal Society B: Biological Sciences, 285*(1878), 1–10.

Rundus, A., Biemuller, R., DeLong, K., Fitzgerald, T., & Nyandwi, S. (2015). Age-related plasticity in male mate choice decisions by *Schizocosa retrorsa* wolf spiders. *Animal Behaviour, 107*, 233–238.

Santangelo, N. (2015). Female breeding experience affects parental care strategies of both parents in a monogamous cichlid fish. *Animal Behaviour, 104*, 31–37. https://doi.org/10.1016/j.anbehav.2015.03.004.

von Schantz, T., Bensch, S., Grahn, M., Hasselquist, D., & Wittzell, H. (1999). Good genes, oxidative stress and condition-dependent sexual signals. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 266*, 1–12.

Schilte-Hostedde, A., Zinner, B., Millar, J. S., & Hickling, G. (2005). Restitution of mass–size residuals: Validating body condition indices. *Ecology, 86*(1), 155–163.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. *Nature Methods, 9*(7), 671–675.

Schuett, W., Tregenza, T., & Dall, S. R. X. (2010). Sexual selection and animal personality. *Biological Reviews of the Cambridge Philosophical Society, 85*(2), 217–246. https://doi.org/10.1111/j.1469-185X.2009.00101.x.

Sih, A., Bell, A. M., & Johnson, C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution, 19*(7), 372–378.

Sih, A., Bell, A. M., Johnson, C., & Ziemba, R. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology, 79*(3), 241–277.

Sinervo, B., Svensson, E., & Comendant, T. (2000). Density cycles and an offspring quantity and quality game driven by natural selection. *Nature, 406*(6799), 985–988. https://doi.org/10.1038/35023149.

Smith, B. R., & Blumstein, D. T. (2010). Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). *Behavioral Ecology, 21*(5), 919–926. https://doi.org/10.1093/beheco/arq084.

Stamps, J., & Groothuis, T. (2010). Developmental perspectives on personality: Implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 365*(1560), 4029–4041. https://doi.org/10.1098/rstb.2010.0218.

Swaddle, J. P., Cathey, M. G., Correll, M., & Hodkinson, B. P. (2005). Socially transmitted mate preferences in a monogamous bird: A non-genetic mechanism of sexual selection. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 272*(1567), 1053–1058. https://doi.org/10.1098/rspb.2005.3054.

Tregenza, T., & Wedell, N. (2000). Genetic compatibility, mate choice and patterns of parentage: Invited review. *Molecular Ecology, 9*(8), 1013–1027. https://doi.org/10.1046/j.1365-294x.2000.00964.x.

Turner, G. F., & Burrows, M. T. (1995). A model of sympatric speciation by sexual selection. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 260*, 287–292. https://doi.org/10.1098/rspb.1995.0093.

Wagner, W. E. (1998). Measuring female mating preferences. *Animal Behaviour, 55*, 1029–1042.

Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics, 34*, 273–309.

Wolf, M., & Wessing, F. (2010). An explanatory framework for adaptive personality differences. *Philosophial Transactions of the Royal Society B, 365*(1560), 3959–3968. https://doi.org/10.1098/rstb.2010.0215.

Zhao, Q. S., Hu, Y. B., Liu, P. F., Chen, L. J., & Sun, Y. H. (2016). Nest site choice: A potential pathway linking personality and reproductive success. *Animal Behaviour, 118*, 97–103. https://doi.org/10.1016/j.anbehav.2016.05.017.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Things are not always linear; Additive modeling. In A. F. Zuur, E. N. Ieno, N. J. Walker, A. A. Saveliev, & G. M. Smith (Eds.), *Mixed effects models and extensions in ecology with R* (pp. 35–69). New York, NY: Springer.