



Mate sampling influences the intensity of sexual selection and the evolution of costly sexual ornaments



Danilo G. Muniz^{a,b,*}, Glauco Machado^b

^a Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Brazil

^b LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Brazil

ARTICLE INFO

Article history:

Received 20 October 2017

Revised 30 January 2018

Accepted 19 March 2018

Available online 19 March 2018

Keywords:

Agent-based model

Epigamic trait

In mates

Information filtering

Natural selection

Preference function

Selection gradient

Sexually selected trait

ABSTRACT

Mate choice includes three steps: (1) choosing individual encounters potential mates, (2) assesses and processes information about them, and (3) makes a mate decision. During mate searching females can access only a sample of males in the mating pool and need to choose their mates based on limited information. Thus, mate sampling may influence sexual selection promoted by mate choice because it constrains female choice. Using individual-based simulations, we found that both female choosiness and mate sampling influenced the variance in mating success among males and thus the intensity of sexual selection. So that sexual selection is most intense when females are strongly choosy and can sample many males. Moreover, in evolutionary simulations, the rate of evolutionary change and the final size of male ornament increase with increasing mate sampling. However, under stronger natural selection, evolutionary change is slower and leads to smaller ornaments. Empirical data on the potential for sexual selection (I_s) for several animal species show a positive correlation between the intensity of sexual selection and an index of mate sampling based on behavioral and ecological traits. Based on the results of our simulations, we predict that males of highly mobile species with long-range sexual signal transmission, which allow females to assess many males, will show greater variance in mating success and will be more ornamented than their relatives not exhibiting these features.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

"80% of success is just showing up."

Woody Allen

Sexual selection is an important evolutionary force generated by pre- and post-copulatory processes (reviewed in Eberhard, 2009 and Jones and Ratterman, 2009). Mate choice is a particular type of pre-copulatory process that has long puzzled evolutionary biologists (Jennions and Petrie, 1997; Edward and Chapman, 2011). Many theoretical and empirical studies have been published since Darwin's (1871) original ideas, but both the evolution of mate choice and its consequences to the evolution of sexual ornaments are still subject of intense debate (e.g., Mead and Arnold, 2004; Kokko et al., 2006; Prum, 2010). Despite the controversies, the general pattern generated by mate choice is not disputed: individuals with certain phenotypes acquire more copulations than those with other phenotypes. This pattern is pro-

duced by a sequence of at least three steps: (1) an individual of the choosing sex encounters individuals of the opposite sex, (2) the individual of the choosing sex assesses information about the encountered individuals, and then (3) a mating decision is made. Even though most empirical studies on mate choice have focused only on the last step, i.e. the mating decision, some studies show that mate search and mate assessment (steps 1 and 2) are also essential parts of the mate choice process (see Castellano and Cermelli, 2011 and references therein). Thus, by taking into account all steps involved in the mate choice process, we can achieve a deeper understanding of its evolutionary implications.

Most mathematical models of mate choice make simplifying assumptions about some steps underlying mate choice. Obviously, every theoretical model must make simplifying assumptions because models are, by definition, simplifications of real phenomena (Peck, 2004). However, it is well known that assumptions may also bias conclusions and even lead to wrong qualitative and/or quantitative conclusions (Levins, 1966). For instance, many models of sexual ornament evolution assume that females can assess all males in the population, ignoring the fact that females most certainly encounter only a limited number of the available males during mate search. This mate sampling process generates the so-

* Corresponding author at: Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Brazil.

E-mail address: danielogmuniz@yahoo.com.br (D.G. Muniz).

called *information filtering*, in which mating decisions are made based on limited information (Mossa et al., 2002; Muniz et al., 2017). In fact, empirical studies that estimate the number of males assessed by individual females during mate search show that this number is usually below 10 (average = 4.5 males; see Roff and Fairbairn, 2014). The low number of males sampled by females in nature is probably a consequence of high mate search costs associated with both energy expenditure and predation risk (Kasumovic et al., 2006; Lane et al., 2010). Even in species forming reproductive aggregations, in which many potential mates can be found simultaneously, movement between aggregations can be a limiting factor to how many potential mates an individual can assess (Marsh et al., 2000). Thus, information filtering during mate choice seems to be ubiquitous in natural populations.

Despite the fact that information filtering is likely to be the rule during mate search, the implications of restricted mate sampling for sexual selection and the evolution of sexually-selected ornaments are still poorly explored. Currently, we know that when females can assess only small samples of the male population, the detection of female choosiness is difficult (Benton and Evans, 1998; Muniz et al., 2017). Moreover, mathematical models predict that, when females can sample only a few males in the population, three patterns should be found: (1) the population is less likely to possess ornamented males (Gomulkiewicz, 1991; Kokko et al., 2015), (2) the correlation between female preference and male ornament is weaker (Roff and Fairbairn, 2014), and (3) females show low selectivity and are less polyandrous (Blew et al., 2012). Taken together, these findings suggest that the evolution of male ornaments, as well as the coevolution between female preference/selectivity and male ornament, may be influenced by restricted mate sampling (i.e., when information filtering is intense).

Still, two key questions regarding the consequences of mate sampling have not been addressed so far. The first one is: how does mate sampling influences the intensity of sexual selection as measurable within a single generation? It is reasonable to suppose that in populations where mate sampling is restricted, even males bearing small ornaments could achieve copulations, so that the intensity of sexual selection should be lower than in populations where mate sampling is not restricted. This prediction, however, depends on the degree of female choosiness. Thus, the actual intensity of sexual selection should emerge from the combined action of female choosiness and mate sampling – a subject that has not been explored in theoretical models. Moreover, females may select males performing either comparative or sequential mate choice (Janetos, 1980), and the implications of restricted mate sampling may differ between these two mate choice processes. The second question is: how does mate sampling influence the evolution of ornament size in a population where males already possess a trait subject to female choice? It is reasonable to suppose that in populations where mate sampling is restricted, male ornaments would have slower increase over evolutionary time than in populations where mate sampling is not restricted. However, natural selection may also act against ornament exaggeration (Pomiankowski and Iwasa, 1998), and the combined action of directional sexual selection, stabilizing natural selection, and restricted male sampling on the evolution of male ornaments has not been investigated in theoretical models. Empirically, both questions remain largely unexplored, and the few study cases in the literature are focused on single species (e.g., Marsh et al., 2000; Myhre et al., 2013). To our knowledge, no comprehensive study has been conducted on the effects of mate sampling on the intensity of sexual selection in natural populations.

To answer the two questions raised above and fill the theoretical gaps we pointed out, we used an individual-based model (IBM) approach. We simulated populations where females have unbounded preference for males with large ornaments but have ac-

cess to a limited number of males during mate choice. To address the first question, we followed simulated populations during a single generation, and explored the effects of mate choice process (comparative x sequential), degree of female choosiness, and mate sampling on the intensity of sexual selection. To address the second question, we followed simulated populations through many generations, and explored the effects of mate choice process, intensity of natural selection, and mate sampling on the evolution of male ornament exaggeration. Finally, we contrasted predictions of our simulations with empirical measures of potential for sexual selection (I_s , Arnold and Wade, 1984) taken from natural populations of a wide variety of taxa in which the number of males sampled by females during mate search shows great interspecific variation. By doing so, we sought to test empirically some key predictions derived from our simulations and to demonstrate the broad application of the predictions derived from our simulations.

2. Methods

2.1. Ecological simulations

2.1.1. General description

To investigate the effect of mate sampling on the intensity of sexual selection, we built an IBM, which is a computational simulation in which individuals are explicitly represented (Grimm and Railsback, 2005). This kind of simulation allows for higher realism and facilitate the construction of models including individual variation, complex behavior, and probabilistic events. Our simulation mimics a mating system with conventional sex roles (i.e., choosy females and non-choosy males). Each simulation represents one independent mating season of an entire population, which includes 1000 individuals with an even sex ratio (1:1). The simulation is spatially explicit and space is continuous. Individuals inhabit a squared landscape measuring 3×3 arbitrary units, and individual coordinates are recorded as two values (x, y) between 0 and 3. In the beginning of the simulation, each individual receives random x and y coordinates drawn from a uniform distribution with minimum = 0 and maximum = 3. We adopted rigid boundary conditions, so that individuals at the borders have fewer neighboring individuals, as if they were at the borders of a habitat patch. Males can mate unlimitedly, but each female copulates with a single male chosen among the males available within a radius r from her spatial coordinate. A female will mate with the closest available male if there is no male within r . Males have a sexual ornament z that follows a truncated normal distribution with mean $z_{mean} = 4$, standard deviation $z_{SD} = 2$, and minimum value $z_{min} = 1$. Females have directional preference for males with larger z values.

2.1.2. Mate choice

There are two main ways in which females can evaluate and choose males: *comparatively* or *sequentially*. In a comparative mate choice process, females assess a number of mates and then decide with whom to mate based on the information gathered about all potential mates. The best-of-N process described by Janetos (1980) is an extreme case of comparative mate choice process. Differently, in a sequential mate choice process, females assess males one at a time and, at each assessment, decide whether to mate or not based solely on the traits of that male. In this case, information about previous males does not influence mating decisions. The fixed-threshold process described by Janetos (1980) is a sequential mate choice process.

We ran simulations for both comparative and sequential mate choice processes. In both cases, however, we adopted a probabilistic approach to mate choice, so that in the comparative process, the male with the largest ornament is the most likely to be chosen

but will not necessarily always be chosen. In the sequential process, high ornamentation increases the probability that a male will be accepted by a choosy female. A male with ornamentation below the female preference, however, still has a (low) probability of copulating. Our probabilistic approach accounts for evaluation errors during mate choice, which can be caused by limitations either in female perception or in its ability to process information. The probabilistic approach also allows us to set female choosiness as a model parameter, which we can vary among simulation runs to assess its ecological and evolutionary effects.

In both comparative and sequential processes, females have limited access to males, they can only assess males within a radius r from their own spatial coordinates. This radius is a model parameter, so that higher values of r allow females to sample a higher number of males. During comparative mate choice, females assess the ornaments of all males within radius r . Comparative mate choice probabilities follow a multinomial distribution, so that after assessing the males, the probability P_{ij} that a female i mates with a male j is calculated as:

$$P_{ij} = \frac{z_j^B}{\sum_{k=1}^{M_i} z_k^B}. \quad (1)$$

In Eq. (1), z_j is the ornament value of male j , z_k represents the ornament values of all males assessed by female i , M_i is the total number of males sampled by female i , and B determines preference strength (*sensu* Edward, 2015, see Fig. S1 in the Supplementary content). Therefore, higher values of B make females choosier and increase the probability that each female will mate with the male with the largest ornament among those sampled.

In the sequential process, females encounter the males within radius r sequentially and in random order. At each encounter, the female decides if she will mate with that male based solely on the information about that male. Here, the probability P_{ij} that a female i mates with a male j is:

$$P_{ij} = \text{logit}^{-1}(S \cdot (z_j - T)), \quad (2)$$

where logit^{-1} or inverse logit is a function defined as $f(x)=1/(1+\exp(-x))$, z_j is the ornament of male j , S is the female preference strength, and T is the threshold above which a male has at least 50% probability of copulation (Fig. S1). In this mate choice process, once the female mates, she ceases to sample males. If the female accepts none of the sampled males, she simply mates with the last sampled male. In the sequential mate choice process, mate choosiness is decomposable in two aspects: selectivity and preference (*sensu* Edward, 2015). Therefore, in this process, it is possible to increase female choosiness in two different ways: (1) by increasing the selectivity S , which would increase females' preference strength for males above the threshold T , or (2) by increasing the threshold T , so that males need a larger ornament to attain high copulation probability. In our simulations, we kept S constant and modulated female choice by changing the values of the threshold T .

Under both comparative and sequential processes, the values determining female choice (B , S , and T) are population parameters, so that they do not vary between individuals: all females within each simulation run are equally choosy. Using this ecological simulation, we performed two "simulation experiments" aiming to answer the following question: how does mate sampling limitation influences the intensity of sexual selection as measurable in natural populations? In each of the two simulation experiments, we approached this question from a different perspective. In the first one, female choosiness and mate sampling are independent from each other, whereas in the second, female choosiness and mate sampling are positively correlated. These two approaches will be detailed in the following sections.

2.1.3. Simulation experiment I: female choosiness and mate sampling are independent

Here our goal was to investigate how mate sampling and female choosiness separately influence sexual selection experienced by males. Therefore, in this set of simulations, mate sampling and female choosiness were independent from each other. We ran simulations with all combinations of five values of r (0.1, 0.2, 0.4, 0.8, and 1.5) and four regimens of female choosiness, from random mating to strong choosiness. With $r = 0.1$ females can sample, on average, only two males, representing intense information filtering, whereas with $r = 1.5$ females can sample almost the entire male population. In the comparative mate choice simulations, we explored parameter values corresponding to weak ($B=1$), moderate ($B=2$), and strong ($B=4$) female choosiness plus a scenario of random mating ($B = 0$). In the sequential mate choice simulations, we simulated random mating by making the selectivity S equal to zero. In all other scenarios we kept S equal to 1 and modulated female choice by varying the preference threshold T . We explored values corresponding to weak ($T = 5$), moderate ($T = 6$), and strong ($T = 7$) choosiness. We ran 50 simulations for each combination of parameters, comprising 1000 simulations per mate choice process.

2.1.4. Simulation experiment II: female choosiness and mate sampling are correlated

We ran simulations in which mate sampling and female choosiness are positively correlated because theory posits that when females can sample more males, the evolution of mate choosiness can be facilitated (Bleu et al., 2012; Kokko et al., 2015). In this set of simulations, we used eight values of r (0.1, 0.3, 0.5, 0.7, 0.9, 1.1, 1.3, and 1.5). To maintain the values of female choosiness approximately within the range used in the first set of simulations, we computed the preference strength B in the comparative mate choice simulations as: $B=1+2r$, whereas the threshold in the sequential mate choice simulations was: $T=4+2r$. We ran 50 simulations for each value of r , comprising 400 simulations for each mate choice process.

2.1.5. Measurements of sexual selection

In every ecological simulation run, we measured male reproductive success as its number of mates and calculated the intensity of sexual selection using two metrics: (1) the potential for sexual selection I_s , and (2) the selection gradient on male trait z . The I_s is estimated dividing the variance in male reproductive success in a population by the square of its mean (Arnold and Wade, 1984; Shuster and Wade, 2003). Given that sexual selection on males may be defined as non-random variance in the reproductive success among males produced by differential access to females (Kokko et al., 2006), the I_s metric is a measure of the maximum sexual selection that could operate in a given population (Shuster and Wade, 2003). The selection gradient on a trait is the slope of a linear regression between the standardized trait and individual relative mating success (Lande and Arnold, 1983). Thus, selection gradients measure the intensity of selection on specific traits. We chose to measure sexual selection in these two ways in the simulations because they provide complementary information and are the most commonly used measures of sexual selection in empirical studies.

2.2. Evolutionary simulations

2.2.1. Simulation description

To evaluate the long-term effects of mate sampling on the evolution of male ornaments, we ran evolutionary simulations in which male ornaments are costly and thus evolve under both natural and sexual selection. The model has discrete non-overlapping generations, and the life cycle of individuals can be summarized

as: (1) natural selection acting on males, (2) mate choice by females, (3) mating, and (4) reproduction. After birth, all females survive to reproduce, whereas males are subject to stabilizing natural selection, which operates as mortality conditional to the size of the sexual ornament. The probability V_j that a male j survives to reproduce is determined by a Gaussian function and is calculated as:

$$V_j = \exp\left(-\frac{(z_j - \mu)^2}{2\sigma^2}\right). \quad (3)$$

In Eq. (3), z_j is the male ornament value, μ is the trait value favored by stabilizing natural selection (i.e., the value that provides survival probability equal to one), and σ determines the intensity of stabilizing natural selection (i.e., how mortality risk increases for z values away from μ). Thus, lower σ values make natural selection more intense on the male ornament (see Fig. S2 in the Supplementary content).

Female mate choice and copulation occur as in the ecological simulations. Again, we ran simulations with both comparative and sequential processes. For each offspring of the new generation, a female from the previous generation was randomly picked (with replacement) to be the mother, and the father was the male chosen by that female (following Raimundo et al., 2014). The procedure was made separately for male and female offspring. This modeling strategy ensures that male reproductive success is proportional to his mating success, and that every female generates on average one male and one female offspring. Therefore, population size and sex ratio at birth are maintained constant through the whole simulation. Each male offspring inherits the z value of his father plus a small Gaussian error (mean \pm SD = 0 \pm 0.1). This simplified way to model the inheritance and evolution of a continuous trait is equivalent to modeling trait size as being influenced by a high number of small-effect alleles, which is akin to what happens in quantitative genetics models (Roff, 1997). Females do not participate in the inheritance of z , and the initial distribution of z was the same as in the ecological simulations.

2.2.2. Simulation experiment III: mate sampling and the evolution of ornament exaggeration

Here, we maintained the optimum for stabilizing natural selection μ as 4 in all simulations and explored two intensities of natural selection: weak ($\sigma = 4$) and strong ($\sigma = 2$). Stabilizing natural selection on a male ornament reproduces a scenario in which the sexual ornament also has a survival related function, as in the classical model of Fisher (1915). In the Supplementary content, we provide results from simulations in which male ornament has no survival function (Fig. S5), so that any ornamentation is detrimental to survival, as in the verbal model by Zahavi (1975).

We ran the evolutionary simulations using a single intensity of female choosiness (moderate mate choice: $B = 2$ for the comparative process, and $T = 6$ for the sequential process) and five different r values ranging from 0.1 to 1.5. We ran 50 simulations for each parameter combination. In preliminary tests, ornament size stabilized by the 30th generation, and evolutionary change was faster during the first 10 generations (Figs. S3 and S4). Thus, we allowed populations to evolve during 50 generations and measured the rate of evolutionary change as the mean change in the mean z of the population up to the 10th generation. We programmed all simulations in the software R 3.2.2 (R Core Team, 2017).

2.3. Analysis of empirical data

To test the effect of mate sampling on the intensity of sexual selection in the wild, we used a subset of the potential for sexual selection (I_s) dataset compiled by Moura and Peixoto (2013). We

included only data from non-manipulative studies conducted under natural conditions (Table S1). We included I_s estimates based on both mating success (i.e., observed copulations) and reproductive success estimated by parentage analysis. We excluded studies in which the data collection protocol prevented the detection of males with no reproductive success because their exclusion underestimates I_s (Shuster and Wade, 2003). In most of the dataset, I_s values estimate to sexual selection acting on males, but we also included in the analysis a few species from the families Syngnathidae (seahorses and pipefish) and Jacanidae (jacana birds) with reversed sex roles, in which I_s represents sexual selection acting on females.

Because the number of potential mates accessed by choosing individuals of different species is rarely available, we developed a mate sampling (MS) index, and used it as predictor variable in the analysis. The MS index is based on six binary variables that could influence mate sampling (Table 1). We calculated the MS index as the mean of all variables scored for each species, so that the index varies between zero and one. Higher values indicate that choosing individuals may sample more potential mates. In the calculation of the MS index, we used the mean, rather than the sum, to make values easily interpretable and to be able to deal with missing data without changing the scale of the index.

To investigate the relationship between I_s and the MS index, we used a customized phylogenetic general linear mixed model (PGLMM, Villemereuil and Nakagawa, 2014). The response variable of the model was the I_s , whereas the predictors were the MS index and the method of reproductive success estimation (mating success or parentage analysis). In the model, we considered that I_s followed a truncated normal distribution in which we modeled both the mean and standard deviation of I_s as function of the predictor variables. We chose truncated normal because this distribution does not assume an *a priori* correlation between mean and variance. We considered the distribution to be truncated at zero because I_s cannot assume negative values. Since the dataset included data from several species, which share different amounts of evolutionary history with each other, we included the phylogenetic relationships between the species as a random effect in the analysis. To do so, we build an ultrametric supertree based on published phylogenies of insects, amphibians, birds, and mammals (Hackett et al., 2008; Pyron and Wiens, 2011; Near et al., 2012; Reis et al., 2012; Bernt et al., 2013; Misof et al., 2014; Selvatti et al., 2015, see topology in Fig. S7 in the Supplementary content). We built the supertree using the software Mesquite (Maddison and Maddison, 2017) and converted the phylogenetic relationships into a covariance matrix using the package ape (Paradis et al., 2004) in the software R. Since the analysis included multiple measures from same species, we also included species identity as an additional random effect.

In the dataset, I_s seemed to increase exponentially with the MS index, thus we adopted an exponential link function for the expected mean value of the model. Including all random effects, the equation for the I_s mean I_{mean} in the PGLMM was:

$$I_{mean} = \exp(\alpha_m + \beta_m \cdot x + \lambda_{phy} \cdot \mathbf{V} \cdot \mathbf{c}_{phy} + \lambda_{sp} \cdot \mathbf{c}_{sp}), \quad (4)$$

where, x represents the MS index. The intercept α_m and the slope β_m were estimated separately according to the method of reproductive success estimation (thus the subscript m). \mathbf{V} is the phylogenetic covariance matrix, \mathbf{c}_{phy} is the vector of phylogenetic random effects, and \mathbf{c}_{sp} is the vector of species identity random effects. Finally, λ_{phy} and λ_{sp} represent the standard deviation of phylogenetic and species identity random effects. Therefore, the λ_{phy} parameter is analogous to the Pagel's λ , as a measure phylogenetic signal on the response variable (Symonds and Blomberg, 2014).

In addition, our ecological simulations predicted an increase in the variation of I_s with increasing mate sampling (see Results).

Table 1

Binary proxies of mate sampling used to calculate the mate sampling index. To each proxy in the dataset we scored 0 or 1, depending on the species. We obtained the mate sampling index as the average of all scores attributed to each species (see also Table S1).

1. Sexual signal transmission: (0) Short-range (tactile, cuticular hydrocarbons); (1) Long-range (acoustic, visual, air-borne pheromones)

Rationale: Long-range sexual signals emitted by the senders (usually males) probably allow individual receptors (usually females) to sample a larger number of partners because the mating signals are transmitted for longer distances.

2. Modality of sexual signals: (0) Unimodal; (1) Multimodal

Rationale: Multimodal communication, in which the same information is emitted using more than one signal with differing transmission properties, may increase the chance that sexual signals will be detected against a background of environmental noise (reviewed in [Hebets and Papaj, 2005](#)). Thus, multimodality may decrease information filtering and increase mate sampling.

3. Movement: (0) Ambulatory or slow swimmer; (1) Volant or fast swimmers

Rationale: We assume that flying and fast swimmer species are able to perform longer movements, so that choosing individuals (usually females) may sample a larger number of mating partners when compared with ambulatory or slow swimmer species.

4. Mate search: (0) Performed by one sex; (1) Performed by both sexes

Rationale: We assume that if individuals of both sexes perform mate choice, the encounter rate between males and females will be higher, allowing choosing individuals to sample a larger number of individuals from the opposite sex.

5. Reproductive aggregations: (0) Absent; (1) Present (leks, chorus, swarms)

Rationale: When individuals of one sex (usually males) form reproductive aggregations, individuals of the choosing sex (usually females) can sample several partners at once. Populations with high densities during the mating period, which allows individuals to sample many partners, were also considered to form reproductive aggregations.

6. Habitat: (0) Closed (forests, kelp forest, turbid water); (1) Open (savannah, grassland, deserts, shore)

Rationale: In open habitats, sexual signals may travel longer distances, suffering less degradation and attenuation as they travel through the environment. Thus, individual receptors (usually females) may sample a large number of mating partners because the sexual signals may be transmitted for longer distances. Insects living amongst shrubs and low vegetation, as well as other small animals living amongst and below rocks were considered to live in closed habitats.

Thus, we allowed the standard deviation of the model, I_{SD} , to vary as a function of the MS index according to the following equation:

$$I_{SD} = \exp(\gamma_m + \delta_m \cdot x). \quad (5)$$

In Eq. (5), γ is the intercept and δ is the slope in the relationship between I_{SD} and the MS index. As with the mean, the parameters have a subscript m because we fit separate intercepts and slopes according to the method of reproductive success estimation. We adopted an exponential link function for the standard deviation of the model to ensure that values would be positive.

We implemented the customized PGLMM using the *stan* modeling language ([Carpenter et al., 2017](#)) and fit the model using a Bayesian approach via Markov-Chain Monte-Carlo (MCMC) using the package *rstan* ([Stan Development Team, 2016](#)) in the software R 3.2.2 ([R Core Team, 2017](#)). During MCMC optimization, we ran three parallel chains with 20,000 iterations plus 2000 warmup iterations.

3. Results

3.1. Ecological simulations: female choosiness and mate sampling are independent

Under random mating, the potential for sexual selection was minimal ($I_s = 1$), irrespective of the radius r of female mate sampling (Fig. 1A and B). When females were choosy, I_s increased with choosiness and also with the radius r of mate sampling (Fig. 1A and B). The selection gradient followed similar trends, so that it was zero under random mating and increased both with female choosiness and with the radius r of mate sampling (Fig. 1C and D). These results were qualitatively similar under both the comparative and sequential mate choice processes.

3.2. Ecological simulations: female choosiness and mate sampling are correlated

When the intensity of mate choice increased with the radius r of female mate sampling, mean I_s increased exponentially with r , and the standard deviation of I_s also increased with r (Fig. 2A and B). The same pattern emerged in both the comparative and sequential mate choice processes, but it was clearer in the former. Finally, the selection gradient increased steeply between r values

from 0.1 to 0.2, and then increased constantly and linearly until $r = 1.5$ (Fig. 2C and D).

3.3. Evolutionary simulations

Results of evolutionary simulations were qualitatively similar between the sequential and comparative mate choice processes. When the radius of mate sampling r was strongly restrictive ($r = 0.1$), the rate of trait evolution during the first 10 generations was low (Fig. 3A and B), and trait size after 50 generations only slightly deviated from the value favored by natural selection (Fig. 3C and D). The increase in the radius of mate sampling r promoted an increase in the rate of trait evolution (Fig. 3A and B), which resulted in more exaggerated male traits after 50 generations (Fig. 3C and D). Stabilizing natural selection constrained both the rate of evolution and trait size after 50 generations, so that when natural selection was relaxed, male trait became more exaggerated (Fig. 3C and D). Qualitatively similar results were obtained when the optimum ornament value was zero (Fig. S6).

3.4. Analysis of empirical data

We gathered estimates of I_s from 38 studies, and the final dataset included 119 I_s estimates from populations of 33 different species belonging to 18 orders of arthropods, fish, amphibians, lizards, mammals, and birds (Table S1). The MS index varied between 0 and 0.83 (mean \pm SD = 0.38 ± 0.23). The variation in I_s increased with the MS index for both methods of measurement (Fig. 4, Table 2). We observed a positive effect of the MS index on the I_s mean only when it was estimated based on mating success. When estimates were based on parentage analysis, there was no relationship (i.e., the posterior distribution of the slope parameter includes zero, see Table 2). However, because of the truncation in the model distribution, the effect of the MS index on the standard deviation produced a slight increase in the expected mean value I_s for parentage analysis (Fig. 4, orange line). The effect of species identity on I_s was essentially zero, whereas the phylogenetic effect was relatively high and comparable to the effect of the MS index (Table 2).

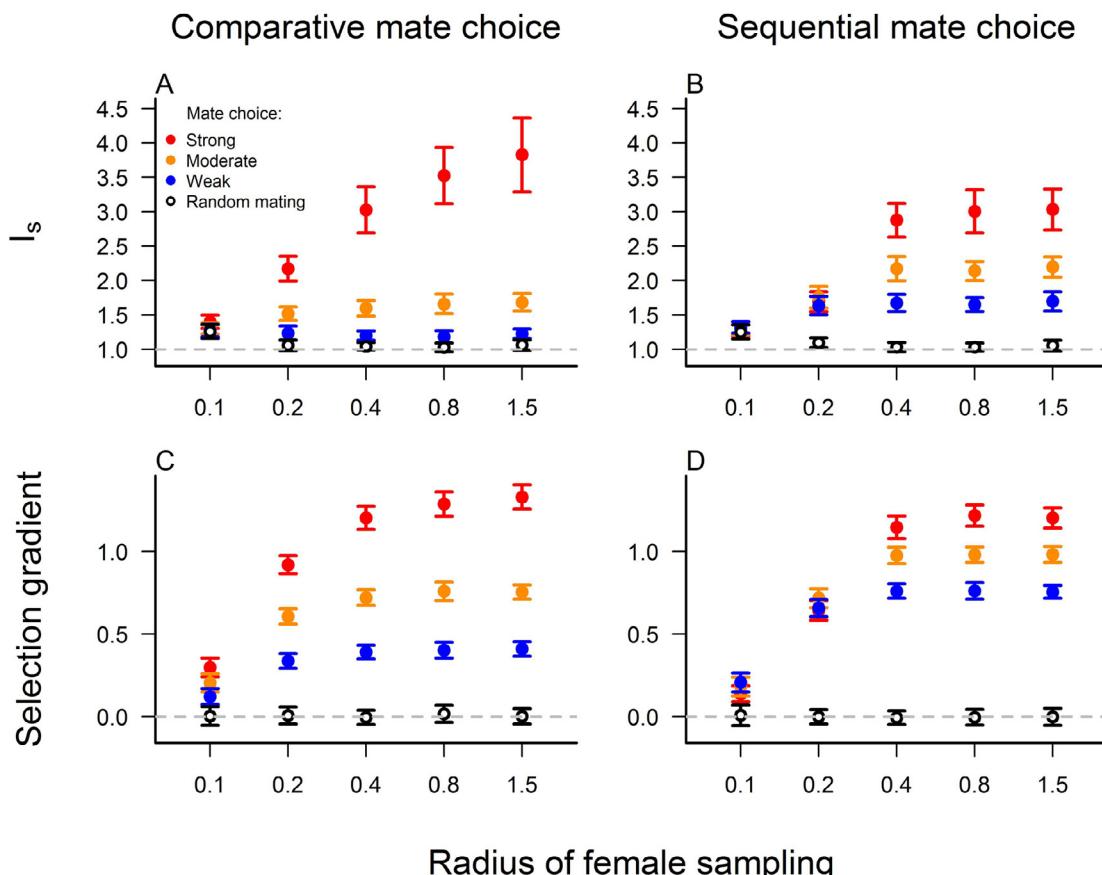


Fig. 1. Results of the ecological simulations in which female choosiness and the radius (r) of mate sampling vary independently from each other. Points and bars represent mean \pm SD of 50 simulated populations, and the dashed lines indicate theoretical expectation under random mating. Colors represent simulations with different intensities of female choice (red: strong, orange: moderate, blue: weak, black: random mating, see text for details). (A and B) Potential for sexual selection I_s . (C and D) Selection gradient on male ornament. (A and C) Simulations with comparative mate choice. (B and D) Simulations with sequential mate choice. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2

Summary of the customized phylogenetic general linear mixed model relating the potential for sexual selection I_s and the mate sampling (MS) index in natural populations. In the model, both the mean and standard deviation of I_s were allowed to vary as a function of the MS index, and separate intercepts and slopes were estimated for I_s measured via mating success or parentage analysis. We present the median and 95% credible intervals (CI) of the posterior distribution of all parameters. The 0.00 values in the table represent values below 10^{-30} .

Model parameter	Posterior median	95% CI
I_s mean		
Intercept (α)		
Mating success	-4.72	-14.74 to 5.76
Parentage analysis	-1.33	-11.86 to 9.36
Slope (β)		
Mating success	9.59	7.11–12.96
Parentage analysis	6.02	-2.27 to 15.58
I_s standard deviation		
Intercept (γ)		
Mating success	-0.89	-1.27 to -0.38
Parentage analysis	-1.25	-2.47 to 0.10
Slope (δ)		
Mating success	2.84	2.11–3.51
Parentage analysis	2.70	0.30–4.79
Random effects standard deviation (λ)		
Phylogeny	6.26	3.49–13.87
Species identity	0.00	0.00–0.07

4. Discussion

Our study adds new predictions and insights on the effects of mate sampling on sexual selection and its evolutionary effects. (1) When female choosiness and mate sampling are independent from each other, the intensity of sexual selection (measured by both I_s and selection gradient on male ornament) increases asymptotically with increasing mate sampling. According to our simulations, sexual selection is expected to be intense only when female choosiness is high and females have access to many males. (2) When female choosiness and mate sampling are positively correlated, the joint action of both factors promotes an exponential increase in I_s and a linear increase in the selection gradient on male ornament. In both predictions (1) and (2), variation in I_s increases with its mean, a result that could not be anticipated. Moreover, predictions (1) and (2) are qualitatively similar under the comparative and sequential mate choice processes. (3) The rate of evolutionary change and the final size of male ornament increase with increasing mate sampling. (4) Under stronger natural selection, evolutionary change is slower and leads to smaller ornaments. Here predictions (3) and (4) are both qualitatively and quantitatively similar under the comparative and sequential processes. Finally, in the analysis of empirical data, I_s increases with mate sampling, and its variation is higher among species with higher mate sampling. This pattern, which is similar to that found in our simulations, holds only I_s is estimated from mating success, but not from parentage analysis.

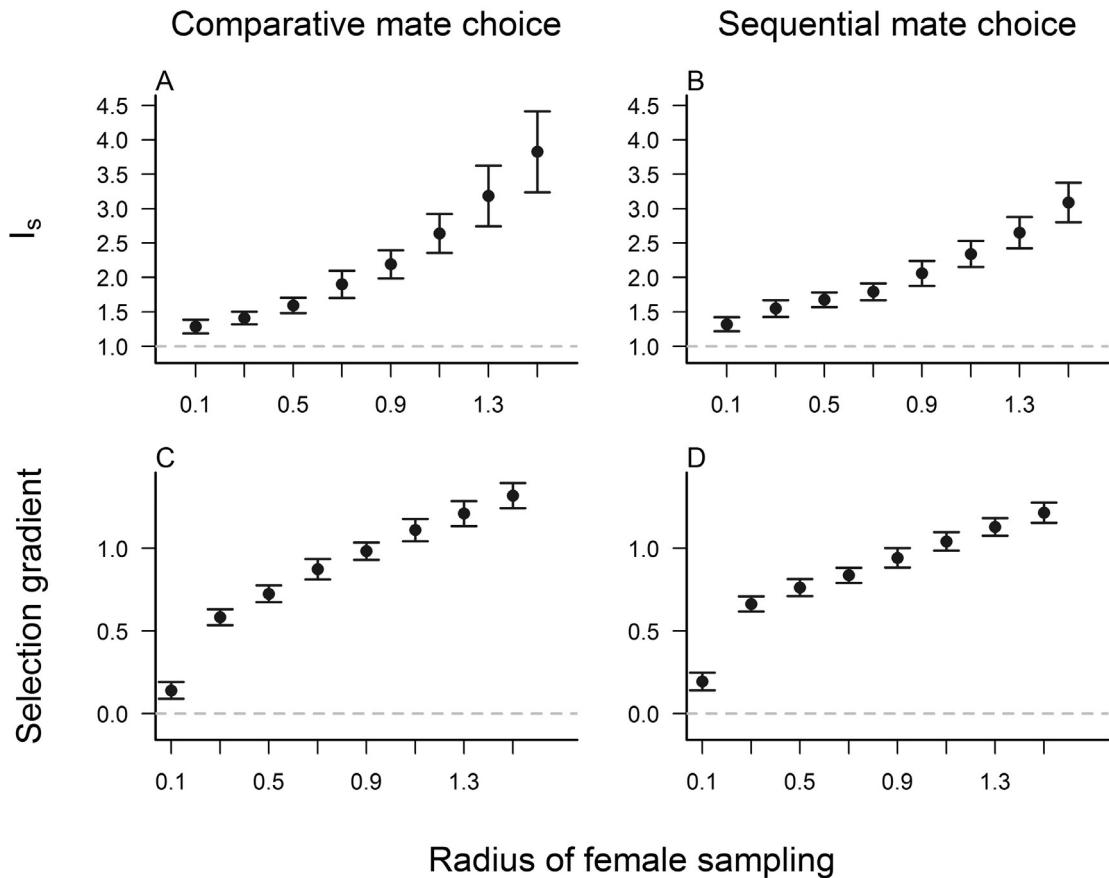


Fig. 2. Results of the ecological simulations in which female choosiness and the radius (r) of female sampling were positively correlated. Points and bars represent mean \pm SD of 50 simulated populations and the dashed lines indicate theoretical expectation under random mating. (A and B) Potential for sexual selection I_s . (C and D) Selection gradient on male ornament. (A and C) Simulations with comparative mate choice. (B and D) Simulations with sequential mate choice.

In our simulations, we limited mate sampling by varying the size of the area where females could find males, which is analogous to changing female perception capability or her mate search effort. However, mate sampling under natural conditions is also influenced by other features. For example, many bird and frog species emit acoustic signals that allow females to access information about males' presence and quality from long distances (Bradbury and Vehrencamp, 1998), and that may also increase the number of sampled partners. Males of many insect species, in turn, are evaluated based on cuticular hydrocarbons, sensed only upon contact (Provost et al., 2008), which may decrease the number of sampled partners if the population is not spatially aggregated. Given that our simulations indicate that mate sampling influences both the intensity of sexual selection and the evolution of male ornaments, we predict that males of highly mobile species with long-range sexual signal transmission will show greater variance in mating success and will also be more ornamented than their relatives not exhibiting these features. These are new ideas derived from our simulations that can be tested in the future using comparative methods. These ideas may also provide insights on the evolution of sexually-selected ornaments in a great variety of animal groups, including both invertebrates and vertebrates.

In the last 10 years, many empirical studies with different animal groups have explored the effect of sampling experience on female choosiness. For instance, females of some cricket species change their selectivity depending on the quality of the males they listened during development (e.g., Bailey and Zuk, 2008). Additionally, female sticklebacks evaluate and rate a male's brightness according to the males they have previously sampled (Bakker and

Milinski, 1991). A scenario in which females become more selective as they have access to more males is similar to our simulation experiment II, in which female choosiness is correlated with mate sampling. Therefore, in species in which there is socially-cued phenotypic plasticity on female mate choice (Kasumovic and Brooks, 2011) we would expect a very strong relationship between female mate sampling and the intensity of sexual selection on males (as in Fig. 2). This prediction can be empirically tested using populations of the same species showing great variance in an ecological factor that influences female mate sampling, such as individual density.

Previous empirical studies have shown that environmental conditions can influence the number of mates sampled by the choosing sex. In the tungara frog, for instance, sexual selection is more intense when chorus ponds are spatially aggregated, because pond aggregation allows females to visit multiple choruses and sample more males (Marsh et al., 2000). Moreover, sexual selection in the two-spotted goby is less intense in structurally complex habitats where females' perception is limited (Myhre et al., 2013). In this study, we present the first multi-taxon analysis on the effect of mate sampling on the intensity of sexual selection. The exponential increase in the mean I_s with increasing potential for mate sampling found in the analysis of empirical data is remarkably similar to the prediction of our ecological simulation in which female choosiness was correlated with mate sampling area. However, we the relationship between mean I_s and mate sampling was found only when I_s was estimated based on mating success (not on parentage analysis). Additionally, the highest I_s values were found when I_s was estimated from mating success. Thus, either parentage studies

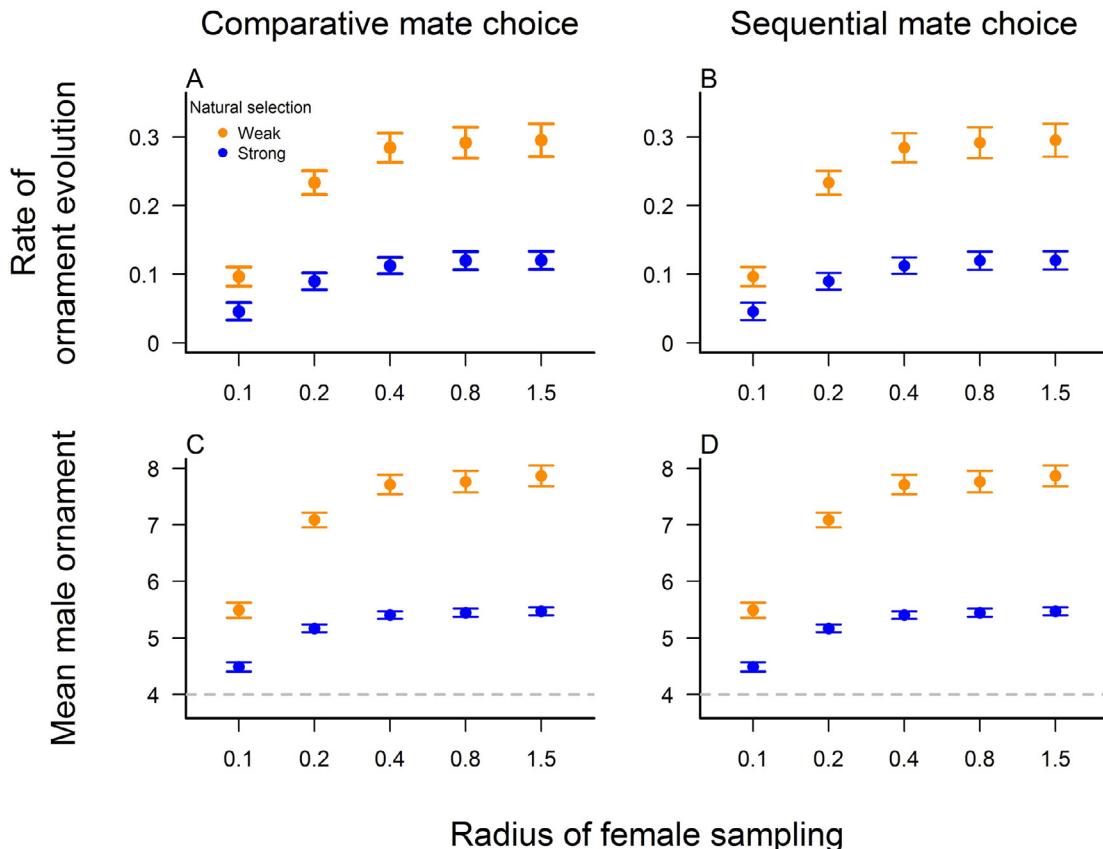


Fig. 3. Results of the evolutionary simulations. In each simulation, female choosiness was kept constant through time and male ornament could evolve. Points and bars represent mean \pm SD of 50 simulated populations and the dashed lines indicate the ornament value favored by natural selection. Colors represent simulations with different intensities of natural selection against male ornament exaggeration (blue = strong, orange = weak). (A and B) Rate of ornament evolution during the first 10 generations. (C and D) Mean male ornament after 50 generations. (A and C) Simulations with comparative mate choice. (B and D) Simulations with sequential mate choice. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

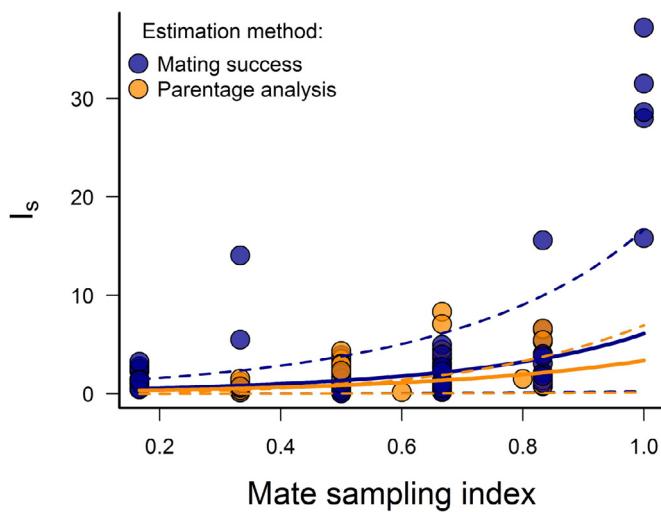


Fig. 4. Relationship between the potential for sexual selection (I_s) and the mate sampling index in natural populations. Higher values of the index indicate that choosing individuals may sample more mates. The continuous line represents the mean I_s expected by the fitted model, and dashed lines delimit the 95% prediction interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

are biased towards populations where sexual selection is weak, or post-copulatory processes (sperm competition and cryptic female choice) decrease the effect of mate sampling on the intensity of

sexual selection. If females are more likely to accept multiple partners when they have access to more males (Bleu et al., 2012), populations where females access many males will also be those in which post-copulatory processes are more important. Thus, sexual selection should be weakened because post-copulatory processes can promote lower variance in reproductive success among males (Kvarnemo and Simmons, 2013).

Some I_s values in the empirical dataset are high above the predictions of the fitted model (Fig. 4). These are observations from populations of the lizard *Anolis garmani* ($I_s = 5.5$, MS index = 0.33), the amphipod *Gammarus minus* ($I_s = 14.04$, MS index = 0.33) and the lekking bird *Chiroxiphia linearis* ($I_s > 25$, MS index = 1). Males of the first two species engage in some form of male-male competition: *A. garmani* males defend mating territories on tree trunks (Trivers, 1976), whereas *G. minus* males guard virgin females prior to their sexual maturation (Culver et al., 1994). Therefore, the deviation from the expected by the fitted model may be an effect of intense sexual selection produced by male-male interactions, and not by female choice alone. In the case of *C. linearis*, the lekking behavior represents an extreme case of mate sampling, in which females have access to a large number of potential mates during the mate choice process (McDonald, 1989). Still, the I_s estimate for *C. linearis* was much higher than other species with similar MS index, which we suppose is an effect of strong female choosiness in this bird species.

Strong natural selection and restricted mate sampling constrained the rate of evolutionary change and the final size of male ornament in our simulations. In nature, selection may act against the exaggeration of male ornaments in two not mutually exclu-

sive ways. First, males that invest more in ornaments may compromise other fitness-related activities, such as immunocompetence (e.g., Folstad and Karter, 1992). Second, exaggerated ornaments may make males slower and/or more conspicuous, increasing their chance of being singled out by predators (e.g., Godin and McDonough, 2003). Exposure to predation may also influence mate sampling by increasing mate search costs (e.g., Polis et al., 1998). The higher the cost of mate search, the more advantageous it is to mate with neighboring available individuals (Forsgren, 1997; Wikelski et al., 2001; Beckers and Wagner, 2011). Even when the searching individuals are not the ones performing choice (e.g., Glaudas and Rodríguez-Robles, 2011), lower mate search may decrease encounter rates between the sexes and thus reduce mate sampling. Consequently, natural selection may have a *direct* effect on the evolution of male ornaments by decreasing survival probability of highly ornamented individuals, and an *indirect* effect by increasing the costs of mate search and reducing mate sampling.

In conclusion, we provide evidence that mate sampling may have marked effects on sexual selection, both within a generation and in evolutionary time. Therefore, classical models of sexual selection in which females are assumed to have access to unlimited males (e.g., Fisher, 1915; Grafen, 1990) represent extreme scenarios in which sexual selection is at maximum intensity. By weakening sexual selection, limited mate sampling may have additional evolutionary effects. For instance, in some theoretical models, ornament exaggeration can reach such extreme values that populations may go extinct (Houle and Kondrashov, 2002), or mate choice may no longer be advantageous, generating continuous cycles of variation in both preference and ornament size (Iwasa and Pomiąkowski, 1995). By preventing extreme exaggeration, limited mate sampling may restrict the conditions under which such extraordinary events occur. Thus, we argue that mate sampling is an important part of the mate choice process, and that factors influencing the number of potential mates sampled by individuals should be considered in the study of mate choice both by theoreticians and empiricists.

Acknowledgments

We thank Paulo E. C. Peixoto for providing the empirical dataset used here and for suggestions on the manuscript, Rafael L. G. Raimundo, Regina H. Macedo, Gustavo S. Requena, and two anonymous reviewers for comments on earlier versions of the manuscript, and Eduardo S. A. Santos for helping with the phylogenetic analysis. This work was supported by São Paulo Research Foundation (FAPESP grants 2011/12675-2, 2012/50229-1, 2012/20468-4, and 2013/13632-5) and National Council for Scientific and Technological Development (CNPq grant 483041/2012-3).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jtbi.2018.03.026.

References

- Arnold, S., Wade, W., 1984. On the measurement of natural and sexual selection: applications. *Evolution* 38, 720–734.
- Bailey, N.W., Zuk, M., 2008. Acoustic experience shapes female mate choice in field crickets. *Proc. R. Soc. Lond. B* 275, 2645–2650.
- Bakker, T.C.M., Milinski, M., 1991. Sequential female choice and the previous male effect in sticklebacks. *Behav. Ecol. Sociobiol.* 29, 205–210.
- Beckers, O.M., Wagner, W.E., 2011. Mate sampling strategy in a field cricket: evidence for a fixed threshold strategy with last chance option. *Anim. Behav.* 81, 519–527.
- Benton, T.G., Evans, M.R., 1998. Measuring mate choice using correlation: the effect of female sampling behaviour. *Behav. Ecol. Sociobiol.* 44, 91–98.
- Brent, M., Bleidorn, C., Braband, A., Dambach, J., Donath, A., Fritzsch, G., Golombek, A., Hadrys, H., Jühling, F., Meusemann, K., Middendorf, M., Misof, B., Perseke, M., Podsiadlowski, L., Reumont, B., Schierwater, B., Schlegel, M., Schrödl, M., Simon, S., Stadler, P.F., Stöger, I., Struck, T.H., 2013. A comprehensive analysis of bilaterian mitochondrial genomes and phylogeny. *Mol. Phylog. Evol.* 69, 352–364.
- Blew, J., Bessa-Gomes, C., Laloï, D., 2012. Evolution of female choosiness and mating frequency: effects of mating cost, density and sex ratio. *Anim. Behav.* 83, 131–136.
- Bradbury, J.W., Vehrencamp, S.L., 1998. Principles of Animal Communication. Sinauer Associates, Sunderland.
- Carpenter, B., Gelman, A., Hoffman, M., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M.A., Li, P., Riddell, A., 2017. Stan: a probabilistic programming language. *J. Stat. Softw.* 76, 1–32.
- Castellano, S., Cermelli, P., 2011. Sampling and assessment accuracy in mate choice: a random-walk model of information processing in mating decision. *J. Theor. Biol.* 274, 161–169.
- Culver, D.C., Jernigan, R.W., O'Connell, J., Kane, T.C., 1994. The geometry of natural selection in cave and spring populations of the amphipod *Gammarus minus Say* (Crustacea: Amphipoda). *Biol. J. Linn. Soc.* 52, 49–67.
- Darwin, C., 1871. The Descent of Man and Selection in Relation to Sex. John Murray, London.
- Eberhard, W.G., 2009. Postcopulatory sexual selection: Darwin's omission and its consequences. *Proc. Nat. Acad. Sci. USA* 106 (S1), 10025–10032.
- Edward, D.A., 2015. The description of mate choice. *Behav. Ecol.* 26, 301–310.
- Edward, D.A., Chapman, T., 2011. The evolution and significance of male mate choice. *Trends Ecol. Evol.* 26, 647–654.
- Fisher, R.A., 1915. The evolution of sexual preference. *Eugen. Rev.* 7, 184–192.
- Folstad, I., Karter, A.J., 1992. Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* 137, 603–622.
- Forsgren, E., 1997. Mate sampling in a population of sand gobies. *Anim. Behav.* 53, 267–276.
- Glaudas, X., Rodríguez-Robles, J.A., 2011. Vagabond males and sedentary females: Spatial ecology and mating system of the speckled rattlesnake (*Crotalus mitchelli*). *Biol. J. Linn. Soc.* 103, 681–695.
- Godin, J.G.J., McDonough, H.E., 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behav. Ecol.* 14, 194–200.
- Gomulkiewicz, R., 1991. Limited female choice and the evolution of secondary sexual characters. *Am. Nat.* 138, 1396–1407.
- Grafen, A., 1990. Sexual selection unhandicapped by the Fisher process. *J. Theor. Biol.* 144, 473–516.
- Grimm, V., Railsback, S.F., 2005. Individual Based Modeling and Ecology. Princeton University Press, Princeton.
- Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., Yuri, T., 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 320, 1763–1768.
- Hebets, E.A., Papaj, D.R., 2005. Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.* 57, 197–214.
- Houle, D., Kondrashov, A.S., 2002. Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. R. Soc. Lond. B* 269, 97–104.
- Iwasa, Y., Pomiąkowski, A., 1995. Continual change in mate preferences. *Nature* 377, 420–422.
- Janetos, A.C., 1980. Strategies of female mate choice: a theoretical analysis. *Behav. Ecol. Sociobiol.* 12, 107–112.
- Jennions, D., Petrie, M., 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* 72, 283–327.
- Jones, A.G., Ratterman, N.L., 2009. Mate choice and sexual selection: what have we learned since Darwin? *Proc. Nat. Acad. Sci. USA* 106 (S1), 10001–10008.
- Kasumovic, M.M., Bruce, M.J., Herberstein, M.E., Andrade, M.C.B., 2006. Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). *Behav. Ecol.* 18, 189–195.
- Kasumovic, M.M., Brooks, R.C., 2011. It's all who you know: the evolution of socially cued anticipatory plasticity as a mating strategy. *Q. Rev. Biol.* 86, 181–197.
- Kokko, H., Jennions, M.D., Brooks, R., 2006. Unifying and testing models of sexual selection. *Annu. Rev. Ecol. Evol. Syst.* 37, 43–66.
- Kokko, H., Booksmythe, I., Jennions, M.D., 2015. Mate-sampling costs and sexy sons. *J. Evol. Biol.* 28, 259–266.
- Kvarnemo, C., Simmons, L.W., 2013. Polyandry as a mediator of sexual selection before and after mating. *Proc. R. Soc. Lond. B* 368, 20120042.
- Lande, R., Arnold, S.J., 1983. The measurement of selection on correlated characters. *Evolution* 37, 1210–1226.
- Lane, J.E., Boutin, S., Speakman, J.R., Humphries, M.M., 2010. Energetic costs of male reproduction in a scramble competition mating system. *J. Anim. Ecol.* 79, 27–34.
- Levins, R., 1966. The strategy of model building in population biology. *Am. Sci.* 54, 421–431.
- Maddison, W.P., Maddison, D.R. Mesquite: a modular system for evolutionary analysis Version 3.31. Available at: <http://mesquiteproject.org>, 2017.
- Marsh, D.M., Rand, A.S., Ryan, M.J., 2000. Effects of inter-pond distance on the breeding ecology of tungara frogs. *Oecologia* 122, 505–513.
- McDonald, D.B., 1989. Cooperation under sexual selection: age-graded changes in a lekking bird. *Am. Nat.* 134, 709–730.
- Mead, L.S., Arnold, S.J., 2004. Quantitative genetic models of sexual selection. *Trends Ecol. Evol.* 19, 264–271.

- Misof, B., Liu, S., Meusemann, K., Peters, R.S., Flouri, T., Beutel, R.G., Niehuis, O., Petersen, M., 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346, 763–768.
- Mossa, S., Barthélémy, M., Stanley, H.E., Amaral, L.N., 2002. Truncation of power law behavior in “scale-free” network models due to information filtering. *Phys. Rev. Lett.* 88, 138701.
- Moura, R.R., Peixoto, P.E.C., 2013. The effect of operational sex ratio on the opportunity for sexual selection: a meta-analysis. *Anim. Behav.* 86, 675–683.
- Muniz, D.G., Santos, E.S.A., Guimarães, P.R., Nakagawa, S., Machado, G., 2017. A multinomial network method for the analysis of mate choice and assortative mating in spatially structured populations. *Methods Ecol. Evol.* 38, 42–49.
- Myhre, L.C., Forsgren, E., Amundsen, T., 2013. Effects of habitat complexity on mating behavior and mating success in a marine fish. *Behav. Ecol.* 24, 553–563.
- Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P., Wainwright, P.C., Friedman, M., Smith, W.L., 2012. Resolution of ray-finned fish phylogeny and timing of diversification. *Proc. Nat. Acad. Sci. USA* 109, 13699–13703.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Peck, S.L., 2004. Simulation as experiment: a philosophical reassessment for biological modeling. *Trends Ecol. Evol.* 19, 530–534.
- Polis, G.A., Barnes, J.D., Seely, M.K., Henschel, J.R., Enders, M.M., 1998. Predation as a major cost of reproduction in namib desert tenebrionid beetles. *Ecology* 79, 2560–2566.
- Pomiankowski, A., Iwasa, Y., 1998. Runaway ornament diversity caused by Fisherian sexual selection. *Proc. Nat. Acad. Sci. USA* 95, 5106–5111.
- Provost, E., Blight, O., Tirard, A., Renucci, M., 2008. Hydrocarbons and insects' social physiology. In: Maes, R.P. (Ed.), *Insect Physiology: New Research*. Nova Science Publishers, New York, pp. 19–72.
- Prum, R.O., 2010. The Lande-Kirkpatrick mechanism is the null model of evolution by intersexual selection: Implications for meaning, honesty, and design in intersexual signals. *Evolution* 64, 3085–3100.
- Pyron, R.A., Wiens, J.J., 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Mol. Phylogenet. Evol.* 61, 543–583.
- R Core Team, 2017. R: A Language and Environment For Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria Available at: <https://www.R-project.org/>.
- Raimundo, R.L.G., Gibert, J.P., Hembry, D.H., Guimarães Jr., P.R., 2014. Conflicting selection in the course of adaptive diversification: the interplay between mutualism and intraspecific competition. *Am. Nat.* 183, 363–375.
- Reis, M., Inoue, J., Hasegawa, M., Asher, R.J., Donoghue, P.C.J., Yang, Z., 2012. Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proc. R. Soc. Lond. B* 279, 3491–3500.
- Roff, D.A., 1997. *Evolutionary Quantitative Genetics*. Springer, Dordrecht.
- Roff, D.A., Fairbairn, D.J., 2014. The evolution of phenotypes and genetic parameters under preferential mating. *Ecol. Evol.* 4, 2759–2776.
- Selvatti, A.P., Gonzaga, L.P., Russo, C.A.M., 2015. A Paleogene origin for crown passerines and the diversification of the Oscines in the new world. *Mol. Phylogenet. Evol.* 88, 1–15.
- Shuster, S.M., Wade, M.J., 2003. *Mating Systems and Strategies*. Princeton University Press, Princeton.
- Stan Development Team. RStan: the R interface to Stan R package version 2.14.1. Available at: <http://mc-stan.org/>, 2016.
- Symonds, M.R.E., Blomberg, S.P., 2014. A primer on phylogenetic generalised least squares. In: Garamszegi, L.Z. (Ed.), *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. Springer, Heidelberg, pp. 105–130.
- Trivers, R.L., 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. *Evolution* 30, 253–269.
- Villemereuil, P., Nakagawa, S., 2014. General quantitative genetic methods for comparative biology. In: Garamszegi, L.Z. (Ed.), *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. Springer, Heidelberg, pp. 287–303.
- Wikelski, M., Carbone, C., Bednekoff, P.A., Choudhury, S., Tebbich, S., 2001. Why is female choice not unanimous? insights from costly mate sampling in marine iguanas. *Ethology* 107, 623–638.
- Zahavi, A., 1975. Mate selection: a selection for a handicap. *J. Theor. Biol.* 53, 205–214.