



Original Research Article

A comparison of sexual selection versus random selection with respect to extinction and speciation rates using individual based modeling and machine learning



Sourodeep Bhattacharjee^{*,a}, Brian MacPherson^b, Robin Gras^{a,b}

^a School of Computer Science, University of Windsor, Canada

^b Department of Biology, University of Windsor, Canada

ARTICLE INFO

Keywords:

Individual based modeling
Sexual selection
Machine learning
Speciation
Extinction
Classification
Prediction

ABSTRACT

It is not clear from empirical and simulation studies that populations with females who employ sexual selection have any evolutionary advantages over populations where mates are randomly selected. There is an ongoing debate regarding whether speciation rates and extinction rates differ significantly between sexual selection and random selection. Although there is evidence that sexual selection drives speciation in some animal species, the biological community remains divided regarding this relationship. Similarly, multiple studies point to a possible connection between sexual selection and extinction rates, although there is no clear consensus regarding this connection: Some studies suggest that sexual selection increases the extinction rate whereas others suggest that sexual selection actually shields populations from extinction. Using individual based computer simulations, we found a significant difference between sexual selection and random selection, with respect to speciation rates, extinction rates and species turnover rates: It turned out that speciation rates were significantly higher for random selection, possibly to help offset the higher extinction and turnover rates. Moreover, we used machine learning to generate rules to help predict rates of speciation and extinction both for sexual selection and random selection. Not only were our rules corroborated by empirical studies but they also help to resolve some disputes regarding the role of sexual selection with respect to speciation rates and extinction rates.

1. Introduction

There is a distinction made in the biological literature between sexual selection and random mating (panmixia), sometimes known as the null model. Strictly speaking, random mating as a null model assumes an infinite number of mates for a female, although realistically, there is simulation evidence that random finite mating is possible (Balloux and Lehmann, 2003). Moreover, there is ample evidence from empirical studies that random mating occurs in a number of species: Dannewitz et al. (2005) found that panmixia occurs in the European eel (*Anguilla Anguilla* L.) and likely in other marine species. Using genetic evidence of patterns of differentiation in a migratory species of water-bird (*Pelecanus Erythrorhynchos*), The researches in Reudink et al. (2011) were able to confirm random mating in this species. Further, Roy et al. (2014), using genetic evidence (12 polymorphic microsatellite markers) found that panmixia is likely in a species of halibut (*reinhardtius hippoglossoides*) and White et al. (2011) found evidence of panmixia in a deep sea fish,

Antimora rostrate).

As Hosken and House (2011) observes, sexual selection is a relatively poorly understood concept. They define sexual selection as intra-specific reproductive competition (Hosken and House, 2011). Further, the authors make a distinction between natural selection and sexual selection, where the latter is variance due to mating success whereas the former involves variance with respect to other aspects of fitness (Hosken and House, 2011). An important issue with respect to sexual selection is the so-called good genes hypothesis, which is the idea that females choose males with good genes leading to fit offspring based on the assumption that males manifest evidence of these genes through secondary phenotypic traits such as coloration (Møller and Alatalo, 1999). Møller and Alatalo (1999) performed a meta-analysis where they found a marginally significant correlation between offspring survival and male secondary traits that attract females during mating, indicating that good genes play at least a small role in sexual selection. Byers and Waits (2006) studied the Pronghorn (*Antilopa Americana*) where females engage in selective mating. They concluded that

* Corresponding author.

E-mail addresses: bhattach1@uwindsor.ca (S. Bhattacharjee), macphe4@uwindsor.ca (B. MacPherson), rgras@uwindsor.ca (R. Gras).

secondary male traits may play only a minor role in selection for good genes (Byers and Waits, 2006). At the same time, Byers and Waits (2006) admit that the good genes hypothesis remains an open question.

In our study, using individual-based computer simulations, we compare sexual selection and random mating with respect to speciation rate and extinction rate. One may expect that if sexual selection involves female selection of males with good genes, thereby possibly conferring a fitness advantage on offspring, the extinction rate of species with sexual selection will be lower than for species that mate randomly. However, this question remains unresolved in the literature (Kokko and Brooks, 2003).

Using numerical simulations, the authors of Kokko and Brooks (2003) argue that whether sexual selection leads to lower or higher extinction rates versus random mating depends on whether the female who is responsible for the survival of the species gains the benefits of selective mating without suffering the costs. The authors argue that if the female bears the costs of selective mating without gaining the benefits, the extinction rate will be higher versus random mating whereas if the female gains the benefits of sexual selection while the males bear the costs, then the extinction rate for the species will be lower vs. random mating (Kokko and Brooks, 2003). Jarzebowska and Radwan (2010) provide empirical evidence that sexual selection can actually counteract extinctions of bulb mite populations *Rhizoglyphus robini*. They created 100 small populations of mites, each with 5 males and 5 females, where in 50 populations monogamy was enforced versus 50 populations where sexual selection was allowed (Jarzebowska and Radwan, 2010). They found that the monogamous populations had a significantly higher extinction rate as opposed to the sexual selection populations (Jarzebowska and Radwan, 2010). Along the same lines, Lumley et al. (2015) found that in lineages of the flour beetle (*Tribolium castaneum*) derived from populations with strong sexual selection, fitness persisted despite inbreeding, suggesting that sexual selection serves as protection against extinction. Whereas lineages derived from populations with weak sexual selection or no sexual selection experienced lower fitness and became extinct after 10 generations (Lumley et al., 2015).

On the other hand, a study by Morrow and Pitcher (2003) found that sexual selection in 1030 bird species increases the risk of extinction while possibly promoting speciation. Moreover, Morrow and Fricke (2004) found no evidence of a relationship between extinction rate and sexual selection after examining data of body masses of 1007 species of mammals.

Given the conflicting evidence in the empirical literature regarding the relationship between sexual selection and extinction rate, the question appears to remain open. However, a recent individual based modeling study predicts that sexual selection can in some cases increase the probability of extinction while in other cases, it can decrease the probability of extinction (Martínez-Ruiz and Knell, 2017). According to the authors, sexual selection decreases the probability of extinction in larger populations while increasing the probability of extinction in small populations (Martínez-Ruiz and Knell, 2017). We hope that our current simulation study may be able to shed further light on this issue.

A related issue is whether there is a relationship between sexual selection and speciation rate. Similar to the debate regarding the possible connection between sexual selection and extinction rate, there is no clear consensus in the literature regarding the connection between sexual selection and speciation rate. On the pro side, a number of studies do suggest that sexual selection drives speciation. For example, Seddon et al. (2013) studied 84 speciation events in 23 species of passerine birds. They concluded that sexual selection combined with male-male competition hastened the evolution of pre-mating reproductive isolation thereby driving speciation (Seddon et al., 2013). Further, Ellis and Oakley (2016) found that in animals with bioluminescent courtship displays (suggesting sexual selection), there was a high rate of speciation. Additionally, the author of Boughman (2001)

found that sexual selection generated by sensory drive contributes to reproductive isolation and hence drives speciation in threespine sticklebacks (*Gasterosteus* spp.). Closer to the con side of the debate, Kraaijeveld et al. (2011) conducted a meta-analysis to determine the effect size of any possible correlation between sexual selection and speciation rate. The authors found a small albeit significant positive correlation between sexual selection and speciation rates (Kraaijeveld et al., 2011). Morrow et al. (2003) argued that there is no evidence that sexual selection drives speciation in birds. They employed data for 1030 bird species across 467 genera to compare speciation rates between species with strong sexual selection with species with random mating (Morrow et al., 2003). They found that although species richness varied across the genera, there was no correlation between species richness and sexual selection (Morrow et al., 2003).

In an individual based modeling study, Thilbert-Plante and Hendry (2009) found that sexual selection reduced reproduction in immigrants thereby reducing speciation by hybridization. Assuming that hybridization is a contributing mechanism for speciation, intra-specific sexual preferences would appear to reduce species divergence. Further, Thilbert-Plante and Hendry (2009) suggest that sexual selection alone is not sufficient to promote speciation. On the other hand, computer simulations employed by Uyeda et al. (2009) showed that genetic drift can work in conjunction with sexual selection to promote speciation. Moreover, van Doorn et al. (2009), using individual based computer simulations, found that sexual selection acts in concert with natural selection to promote reproductive isolation and eventual speciation. However, Rafał (2018), using agent based modeling computer simulations of sexual selection found that sexual selection by itself can initiate speciation as well as contribute to population diversity. Thus, even in terms of the simulation literature, there is a measure of disagreement regarding the role of sexual selection in speciation. Using our individual based modeling computer simulations, we hope to shed additional light on the possible connection between speciation rate and sexual selection.

Concepts closely related to extinction and speciation rates are the notions of species turnover and species diversification rates respectively. Turnover rates can be defined as the interplay between species extinction and the advent of new species either through speciation or through immigration, so that speciation tempers extinction (Brown and Kodric-Brown, 1977; Doherty et al., 2003; Hanski, 1998). Doherty et al. (2003) report that dichromatic species of birds with higher rates of sexual selection due to color displays have a 23% higher local extinction rate and a 25% higher turnover rate than monochromatic (only black and white vision) bird species, which is consistent with the findings of Morrow and Pitcher (2003). Diversification rate can be defined as the difference between speciation rate and extinction rate as outlined in Magallon and Sanderson (2001) and in De Vos et al. (2015). Similar to Seddon et al. (2013), Ellis and Oakley (2016) and Boughman (2001) regarding the relationship between sexual selection and speciation rate, Kazancıoğlu et al. (2009) report that sexual selection (as evidenced by dichromatism) accelerates diversification rates in parrotfishes (Scaridae). Moreover, Janicke et al. (2018) collected empirical data from a wide range of animal taxa employing sexual selection. The authors found that taxonomic families with strong sexual selection on males demonstrate higher levels of species richness as opposed to taxa without strong sexual selection on males (Janicke et al., 2018). On the other hand, Day et al. (2008) found no significant difference in diversification rates between dichromatic species of cichlid fish and monochromatic species of cichlid fish in Lake Tanganyika.

Further, in an individual based modeling simulation study employing a genetic algorithm, Todd and Miller (1997) report that sexual selection initiates speciation along with biodiversity by creating new fitness peaks. Also, it was found in a combined phylogenetic and computer simulation study that sexual selection increases genetic diversity within populations of jumping spiders (*Habronattus pugillis*)

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