UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS

The Role of Spatial Structure in the Process of Mate-Choice Copying

“Documento Definitivo”

Doutoramento em Biodiversidade, Genética e Evolução

Manuel António Pinto Sapage

Tese orientada por:
Professora Doutora Margarida Maria Demony de Carneiro Pacheco de Matos
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Documento especialmente elaborado para a obtenção do grau de doutor

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Nota prévia

A presente tese apresenta artigos científicos já publicados (capítulos 2, 3 e secção 5.2), e outros preparados para serem submetidos (capítulo 4), de acordo com o previsto no n˚2 do artigo 25˚ do Regulamento de Estudos de Pós-Graduação da Universidade de Lisboa, publicado em Diário da República 2ª série – N˚60 – 26 de março de 2018. Uma vez que estes trabalhos foram realizados em colaboração, o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção de dados, análise e discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, Outubro de 2022

Manuel António Pinto Sapage

“Modelling in science remains, partly at least, an art. Some principles do exist, however, to guide the modeller. A first, though at first sight, not very helpful principle, is that all models are wrong; some, though, are more useful than others and we should seek those. At the same time we must recognize that eternal truth is not within our grasp.”

McCullagh, P.; Nelder, J. A. (1989)

Generalized Linear Models, Second Edition, Chapman & Hall, New York

“When I was a doctoral student back in the early 1990s, one of the coolest ideas in animal behavior involved the idea that individuals observed and copied the mate choice decisions of others. […] I wish I could have a few minutes with the late-1990s version of me to marvel with him at this bigger picture and the improvements in the way science works.”

Brooks, R. C. (2020)

The imitation game: a comment on *Davies et al.*
Behavioural Ecology, 31, 1294–1294.

“Dispersal holds a central role for both the dynamics and evolution of spatially structured populations, allowing the genetic cohesion of a species across space, its global persistence despite local extinction, and the tracking of favorable environmental conditions in an ever changing world.”

Ronce, O. (2007)

How Does It Feel to Be Like a Rolling Stone? Ten Questions About Dispersal Evolution.
Annual Review of Ecology, Evolution, and Systematics 2007 38:1, 231-253

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This is what I consider to be the most personal part of the thesis. I imagine that most people skip the acknowledgements while reading a thesis, but I would argue that it has an important role: it forces the candidate to relive the wonderful but arduous journey of making science. Supervisors, colleagues, friends, family, institutions, they all played a role in shaping our scientific identity, to acknowledge them here is to profoundly reflect their role in our lives. This is a reminder of how much I am supported and loved by everyone.

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During the curricular year of my Ph.D. thesis, I was also involved in other scientific work that ended up being published. Although they were not directly related to this topic, they also contributed to enrich my scientific knowledge. I would like to thank all my co-authors of those papers, especially **Luís Borda de Água**, a good friend that taught me a lot.

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Abstract

Mate-choice copying is a type of social learning whereby an individual's mate preference is influenced by the mate choices of conspecifics. This thesis explores the theoretical effects of this behaviour on the evolutionary dynamics of populations. I use individual-based models and focus on spatial structure, as many benefits of copying are predicted to arise under these conditions. The thesis is divided into six chapters. In chapter 1, I give an overview of the field and of the structure of the thesis. Chapter 2 simulates the evolution of copying in a single habitat patch and shows that it can evolve though indirect selection, leading to a higher proportion of adapted males, which increases population fitness. However, this only occurs when female preference does not coevolve with the trait, which is unlikely if we consider only a single habitat. Therefore, chapter 3 simulates the evolution of copying in a heterogenous multi-patch environment with individuals moving between patches. The model shows that copying is especially adaptive to migrating females because it informs them of locally adapted males. This effect promotes greater dispersal but weakens local adaptation, increasing homogeneity between patches. Chapter 4 simulates populations expanding through an environmental gradient, to test whether these effects on dispersal and local adaptation make mate-choice copying less adaptive under these circumstances. The model shows that copying can still be adaptive, increasing the speed of expansion, but depends on the type of preference rules and copying behaviours females use. Chapter 5 is a commentary on two recently published meta-analyses, where I highlight two main avenues for future empirical research. Finally, chapter 6 is a discussion of the thesis main results, of mathematical models' limitations, and of future perspectives, where I highlight the importance of theoretical research for empirical knowledge and vice versa.

Keywords: social learning; sexual selection; dispersal; local adaptation; individual-based simulations.

Resumo

A cópia da escolha de parceiros sexuais (que simplificarei para “cópia”) é um tipo de aprendizagem social onde a preferência sexual de um indivíduo é influenciada pela escolha sexual de conspecíficos. Esta tese explora os efeitos teóricos deste comportamento na dinâmica evolutiva das populações. Para isso exploro modelos baseados em indivíduos focando numa estrutura espacial, pois considero que muitos benefícios da cópia surgem nestas condições. A tese está dividida em seis capítulos. No capítulo 1 faço uma breve introdução ao tema e à estrutura da tese. O capítulo 2 consiste num modelo que simula a evolução da cópia numa única parcela ambiental e mostra que o comportamento pode evoluir por seleção indireta, aumentando a proporção de machos mais adaptados, aumentando a *fitness* da população. Porém, este efeito só ocorre quando a preferência da fêmea não coevolve com a característica do macho, algo improvável numa única parcela. No capítulo 3 simulo a evolução da cópia num ambiente heterogéneo com múltiplas parcelas. Este modelo mostra que a cópia é adaptativa para as fêmeas migrantes, permitindo a escolha de machos mais adaptados localmente. Este efeito aumenta a tendência de dispersão e diminui o grau de adaptação local, aumentando a homogeneidade entre parcelas. O capítulo 4 apresenta um modelo onde populações expandem através de um gradiente ambiental, testando se o efeito da dispersão e da adaptação local tornam a cópia menos adaptativa nestas circunstâncias. O modelo mostra que a cópia pode ser adaptativa, aumentando a velocidade de expansão, dependendo do tipo de preferências e comportamento de cópia usado. No capítulo 5 apresento uma visão crítica de duas meta-análises publicadas por outros autores recentemente, onde saliento dois caminhos para estudos empíricos no tema da cópia. Finalmente, no capítulo 6 apresento uma discussão dos resultados da tese, considerando as limitações dos estudos teóricos e perspetivas futuras.

Palavras-chave: aprendizagem social; seleção sexual; dispersão; adaptação local; simulações baseadas em indivíduos.

Resumo alargado

A escolha de parceiros sexuais é uma das mais importantes decisões na vida de um animal, pois acasalar com um parceiro mal-adaptado pode significar a eliminação da sua descendência. A preferência de um indivíduo por um determinado parceiro pode ser inata, mas também pode ser dependente da escolha dos restantes indivíduos da população. A partir dos finais da década de 1980, observações de campo começaram a reforçar esta ideia e, no início da década de 1990, experiências com guppies (*Poecilia reticulata*) demonstraram que a preferência das fêmeas por um determinado macho pode ser influenciada pela observação da escolha de outras fêmeas. Mais precisamente, a probabilidade de um indivíduo escolher um determinado parceiro sexual pode aumentar ou diminuir após a observação da aceitação ou rejeição desse mesmo parceiro por um conspecífico. Adicionalmente, essa observação pode também influenciar a preferência por parceiros que partilhem características similares. Estes comportamentos constituem aprendizagem social e são denominados de "cópia da escolha de parceiros sexuais" (em inglês 'mate-choice copying', que passo a nomear simplesmente por "cópia"), e que incluem as variantes de "cópia da escolha de parceiros sexuais individual" (que passo a nomear por "cópia individual"), quando o indivíduo focal altera a sua preferência em relação a um parceiro específico, e "generalização da cópia da escolha de parceiros sexuais" (que passo a nomear por "generalização") quando o indivíduo focal altera a sua preferência em relação a todos os parceiros que partilhem características similares. O comportamento de cópia foi posteriormente testado em várias espécies, incluindo aves (e.g. codorniz-japonesa, *Coturnix japonica*) e insetos (e.g. mosca-da-fruta, *Drosophila melanogaster*).

Teoricamente, o comportamento de cópia pode provocar grandes alterações na escolha de parceiros sexuais a nível populacional, pois este comportamento, sobretudo quando envolve generalização, é propício à criação de cascatas de informação, dado que um indivíduo que altera a sua escolha de parceiro após a observação da escolha de outrem pode ser igualmente observado e copiado. Apesar da cópia poder ter um efeito significativo a nível populacional, e inerentemente evolutivo, existe uma grande dificuldade em simular cascatas de informação e em estudar os seus efeitos evolutivos através de experiências empíricas. Devido a isso, os estudos de evolução do

comportamento de cópia e suas consequências são geralmente teóricos, através do uso de modelos matemáticos ou de simulação.

Tradicionalmente, os estudos teóricos do comportamento de cópia tendem a modelar a população desconsiderando o efeito da estrutura espacial do ambiente populacional na escolha de parceiros sexuais dos indivíduos. Porém, a evolução do comportamento de cópia e das suas consequências podem estar interligados com a distribuição espacial dos indivíduos, e.g. indivíduos que dispersam de uma determinada parcela para outra podem beneficiar (ou não) em aprender socialmente com os indivíduos locais na escolha dos seus parceiros, de modo a fazerem escolhas mais adaptadas localmente. A tese aqui apresentada pretende preencher essa lacuna nos estudos teóricos do comportamento de cópia, contribuindo para a compreensão dos efeitos deste comportamento numa população com uma distribuição espacial explícita.

Esta tese está dividida em seis capítulos. No capítulo 1 apresento uma introdução à investigação do comportamento de cópia, incluindo uma breve perspetiva histórica do tema, uma descrição de estudos empíricos e teóricos sobre o tema, os custos e benefícios deste comportamento, o seu enquadramento teórico na teoria da informação e aprendizagem, os seus potenciais efeitos evolutivos e ecológicos, e a sua potencial ligação com o comportamento de dispersão. Apresento também neste capítulo a estrutura da tese e os objetivos de cada um dos restantes capítulos.

Nos capítulos 2 a 4 apresento modelos baseados em indivíduos com os quais exploro vários cenários evolutivos de populações com e sem o comportamento de cópia, considerando diferentes escalas espaciais.

Começando numa escala espacial com uma única parcela, o modelo do capítulo 2 explora a evolução do comportamento de generalização num cenário em que o habitat é homogéneo, e como a sua presença pode afetar a *fitness* de uma população. Este modelo mostra que o comportamento de cópia pode evoluir por seleção indireta caso seja introduzido um macho com uma característica nova e adaptativa na população. Nesta situação, o gene causando o comportamento de cópia pode aumentar de frequência, devido ao sucesso do gene associado à nova característica adaptativa. Isto leva ao aumento da frequência de machos mais adaptados, e assim também da *fitness* da população. Este efeito, porém, apenas acontece quando a preferência inata da fêmea não coevolui com a característica do macho, mantendo-se constante em frequência ao longo das gerações. As condições em que este fenómeno pode acontecer são improváveis considerando um único habitat, mas tornam-se mais plausíveis se considerarmos a distribuição da população em várias parcelas com ambientes distintos, em que as fêmeas tendem a preferir os machos mais adaptados ao seu ambiente local. Nesta situação, a migração das fêmeas entre as várias parcelas poderá assegurar o polimorfismo da preferência.

Por esta razão, no capítulo 3 considerei um modelo em que o ambiente é heterogéneo e a população está distribuída em múltiplas parcelas, com variados graus de autocorrelação espacial. Neste capítulo estudei a evolução do comportamento de generalização e a sua interação com a tendência de dispersão dos indivíduos da população, e a sua capacidade de se adaptarem localmente. Para tal, criei três tipos de populações: (1) populações sem cópia, (2) populações com indivíduos que copiam indiscriminadamente, e (3) populações com indivíduos que copiam apenas quando dispersam para uma nova parcela. Esta última regra foi criada porque se sabe que, em algumas espécies, as fêmeas têm uma maior tendência para copiar a escolha de parceiros sexuais em situações de incerteza, o que pode acontecer quando a fêmea muda para uma parcela com características ambientais distintas. Simulações deste modelo mostram que o comportamento de cópia promove um aumento da tendência de dispersão na população, e este comportamento é especialmente adaptativo quando apenas as fêmeas migrantes copiam, porque estas fêmeas beneficiam de copiar as fêmeas locais, que tendencialmente têm uma preferência por machos mais adaptados à sua parcela. Porém, o aumento da dispersão e do comportamento de cópia diminui o grau de adaptação local das populações, aproximando o valor da característica dos machos entre parcelas.

Tendo em conta o constrangimento observado no capítulo 3, o capítulo 4 considera um modelo em que uma população se expande ao longo de um gradiente ambiental, precisando de se adaptar localmente à medida que vai avançando no gradiente. Será que o comportamento de cópia se mantém adaptativo nestas condições? Para responder a esta pergunta, considerei duas variantes do comportamento de cópia (cópia individual e generalização) e considerei dois tipos de características que podem estar associadas à preferência da fêmea (i.e., regras de preferência): a fêmea pode preferir uma característica de um macho determinada exclusivamente pelo seu genótipo (“independente” da condição ambiental) ou uma característica determinada pela interação entre o seu genótipo e o ambiente (“dependente”, indicador da qualidade do macho). Simulações deste modelo indicam que o comportamento de cópia é adaptativo apenas em determinadas condições: a generalização aumenta a velocidade de expansão no gradiente (e, portanto, a taxa de adaptação) quando a preferência está associada a uma característica independente, enquanto a cópia individual apenas aumenta a velocidade de expansão quando a preferência se associa a uma característica dependente. As duas variantes da cópia também afetam diferentemente a evolução da dispersão, pois a generalização não afeta a mesma, enquanto a cópia individual tende a aumentar a tendência de dispersão da população por aumentar o grau de competição entre indivíduos aparentados. Este resultado realça a importância de se fazer a distinção entre as duas variantes de cópia e as regras de preferência no estudo das consequências deste comportamento na ecologia das populações e na evolução das espécies.

No capítulo 5 apresento uma visão crítica de duas meta-análises publicadas por outros autores recentemente, baseadas em estudos empíricos que exploram os fatores que influenciam o comportamento de cópia. Começo o capítulo com o sumário dos dois estudos em questão, seguido de um comentário mais aprofundado de um deles – que fui convidado a publicar na mesma revista científica. Nesse comentário explorei alguns dos resultados mais significativos da meta-análise, que concluiu que a tendência do comportamento de cópia está associada ao grupo taxonómico e à metodologia utilizada em laboratório para a sua medição. Por essa razão, sugeri dois caminhos complementares que podem ser seguidos por estudos empíricos futuros, nomeadamente o estudo da prevalência deste comportamento no maior número de espécies possível utilizando um protocolo estandardizado, e a exploração do mecanismo de cópia em espécies-modelo. Termino o capítulo com um sumário crítico de outros comentários que foram feitos sobre essa publicação.

Finalmente, no capítulo 6, faço uma síntese dos resultados principais provenientes dos capítulos 2 a 5, seguido de uma discussão geral dos efeitos do comportamento de cópia na dinâmica das populações. Discuto ainda as limitações dos modelos matemáticos utilizados nesta tese e apresento perspetivas futuras para o estudo deste comportamento, onde destaco a importância da investigação teórica para a aquisição de conhecimento empírico e vice-versa.

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Chapter 3: Sapage, M., Varela, S.A.M. & Kokko, H. (2021). Social learning by mate-choice copying increases dispersal and reduces local adaptation. *Functional Ecology*, 35, 705–716.

Chapter 4: Sapage, M., Santos, M., Matos, M., Schlupp, I. & Varela, S.A.M. (2022). The role of mate-choice copying on species range expansion. *Manuscript in preparation to be submitted to Evolution Letters*.

Section 5.2: Sapage, M. & Varela, S.A.M. (2020). Two research avenues for future mate-choice copying studies: a comment on Davies et al. *Behavioural Ecology*, 31, 1291–1292.

Chapter 1

General Introduction

1.1 Going beyond innate preference for individual mate choice

Since Darwin described his theory of sexual selection (Darwin 1871), particularly his idea about females preferring ornamented males, it has remained controversial for almost a century without having due attention. However, when researchers realized, with the first genetic models (Lande 1981; Kirkpatrick 1982), the importance of mate choice in shaping evolutionary dynamics, sexual selection became one of the most important and contemporary topics in biology (Andersson 1994; Andersson & Simmons 2006, Rosenthal 2017). In fact, individuals of many, if not of most animal species do not choose (accept) their mates randomly and being attractive to the opposite sex is an evolutionary advantage. A great textbook example about the power of sexual selection can be found in the evolution of the tailfeathers of many bird species, with those of the peacock (*Pavo cristatus*) perhaps being the most iconic. The length of the peacock's train and its many ornamented eyespots have been suggested by Darwin (1871) and later confirmed (e.g. Petrie et al. 1991) to be sexually selected.

With the advent of genetics in the early 20th century, and the importance it gained in the following years for the understanding of evolution, many early studies of sexual selection have considered female mate preference to be exclusively a genetically determined trait (reviewed in Andersson & Simmons 2006), meaning, among other things that the choice of one female does not affect the choice of others in any meaningful way. This assumption, however, has been shown to be an oversimplification, since animals, despite their genetic (innate) preferences, also learn and, therefore, also rely on their personal experience and on the information provided by others (i.e. social information) during decision-making (reviewed in Verzijden et al. 2012; Varela et al. 2018; Santos & Varela 2021).

Researchers started to realize the importance of social information in the sexual selection context when they studied bird species with lek-mating systems. Males of these species aggregate in arenas (leks), where together they perform courtship displays, allowing visiting females to compare their performance and choose their preferred male. What researchers found in these gatherings is that different females tend repeatedly to choose the same males, even when multiple males of similar quality are available as options (Gibson & Höglund 1992). Soon it was hypothesized that females in general (which are considered to be the choosier sex in most species) can learn from each other and change their preference after observing the mate choice of others (Höglund et al. 1990; Gibson et al. 1991). This behaviour was coined "mate-choice copying" by Pruett-Jones (1992), and is a type of "eavesdropping", a term later introduced by McGregor (1993). Eavesdropping refers to the scenarios where social information is gathered by bystander individuals from the outcome of social interactions between senders and receivers. In the case of mate-choice copying (MCC), bystanders are observer females, and senders and receivers are male-female pairs during mating interactions.

In 1992, many studies were published that highlighted MCC as an important mechanism of sexual selection. First, Pruett-Jones (1992) considered that female choice should be defined not only in absolute genetic terms, but in terms of probabilities. Females have an "absolute probability" to choose a given male when they use their own assessment without any social or environmental influences. But females also have a "conditional probability" to choose a given male when they use the choice of other females as mate quality assessment. With these two concepts in mind, "copying occurs when the conditional probability of choice of a given male by a female is either greater or less than the absolute probability of choice depending on whether that male mated previously or was avoided, respectively" (Pruett-Jones 1992). This definition highlights that MCC depends on knowing the choice of other females and that it can be based on negative information (i.e., avoidance) as well. It also raises the need for an important distinction between choice and preference: a female's choice might not necessarily be her preference. Although some authors consider both terms to be synonyms, this is not always the case. More accurately, mate choice is the behavioural pattern manifested by an individual, while preference is the internal representation that predisposes an individual to choose a mate over another (Rosenthal 2017). Therefore, choice is something observable and can be potentially copied by other individuals, while preference is something that can remained hidden within an individual, and has the potential to evolve (Rosenthal 2017).

In that same year, Gibson & Höglund (1992) published the first review describing the evidence of MCC so far, and Dugatkin (1992) published the first study of MCC in a laboratorial setting, using the Trinidadian guppy (*Poecilia reticulata*) as the model species. In a simple experiment, focal female guppies were placed in a tank and allowed to observe through a plexiglass partition one focal male swimming alone, and another focal male close to a model female. The model female was then removed, and the focal female was allowed to choose between the two males. Although the author made sure to alternate the male with the model female in consecutive experiments, focal females chose the model male that they had seen previously with a model female 17 out of 20 times. Being the first empirical study to show female copying, Dugatkin (1992) was cautious in his discussion and did five other experiments to control for multiple alternative explanations, but the results still indicated that female Trinidadian guppies do copy each other. That same year, Dugatkin & Godin (1992) published another study where they reported "the first direct evidence that a female's preference for a particular male can in fact be reversed by social cues". Here, the authors first tested the innate preference of focal females in a binary choice, before allowing the focal females to observe a model female alongside the least preferred male. The authors found that a significant number of females reversed their choice after observing the choice of the model female. Both studies contributed to validate an experimental paradigm to test MCC in the laboratory and made the Trinidadian guppy one of the most used models to study this behaviour (Davies et al. 2020). Moreover, showing MCC in a fish species, with a mating system so different from the birds' lek mating system, helped other researchers to realize that this behaviour might be widespread in nature and, therefore, worthy to be studied.

1.2 Empirical studies of MCC

After the seminal works of Dugatkin (1992) and Dugatkin & Godin (1992), most empirical studies of MCC follow some variation of the experimental paradigm they established, depending on the species and the focus of the study. This paradigm is divided into three steps (Figure 1). First, there is the pre-demonstration step, in which females are allowed to choose between two males, and female preference is usually measured as the time a female takes near each one of the males, which some authors convert to binary choice. Studies have shown that at least in some species, association time is a good predictor of whom females will choose if they were actually allowed to mate (Bischoff et al. 1985; White & Galef 1999; Witte 2006). After this step, a demonstration phase occurs, where the focal female is allowed to observe a demonstrator female placed next to the

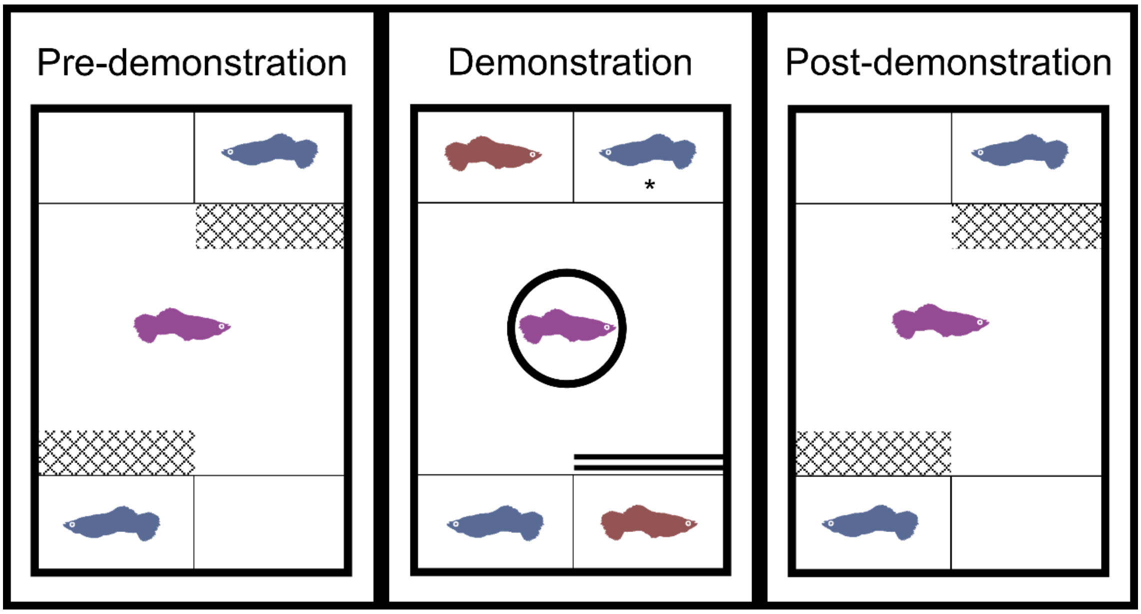

Figure 1. Example of the MCC experimental paradigm applied to fish. The figure indicates the three steps of the protocol, each with the top view of a tank. In the pre-demonstration step, a focal female (purple) can swim freely in the middle section, while males are kept in opposite partitions. Female choice is measured by the time she spends near each male (black grid). In the demonstration step, the focal female is kept in the middle of the tank by a plexiglass cylinder and forced to observe her least preferred male (with an asterisk) with a demonstrator female. In some studies, to control for male behaviour during the demonstration, a pseudo-demonstrator female is placed near the preferred male, but this female is shielded from view of the focal female by an opaque partition (double lines). Finally, the focal female chooses a male again in the post-demonstration step, and MCC is considered to occur if she reverses her choice.

least preferred male, while the preferred male remains alone. This step assumes that the focal female perceives the proximity of the demonstrator female to the least preferred male as a choice, and positive social information about the quality of that male is transmitted back to the focal female. This can positively affect her preference towards that male (and negatively towards the other). Alternatively, researchers can also place a pseudo-demonstrator female near the preferred male (e.g., Schlupp et al. 1994). This female is visually hidden from the focal female (hence the name “pseudo-demonstrator”) to help assuring that the focal female mate choice is not influenced by a difference in male courtship behaviour, but only by the demonstrator female’s choice. After this step, the demonstrator and pseudo-demonstrator females are removed, and the focal female is allowed to choose between the two males again, just like in the pre-demonstration step.

In some experiments (e.g., Dugatkin et al. 2002), the location of the males are switched to make sure that the female is effectively choosing the male and not displaying any preference towards the location where she saw positive social information, and to avoid a side bias of the focal female due to any uncontrolled external effect. Females are considered to have copied the choice of the demonstrator female if they changed their preferred male from the pre-demonstration to the post-demonstration step (i.e., choice reversal).

In some cases, as in Dugatkin (1992), researchers choose to skip the pre-demonstration step and assign the demonstrator female to a pre-determined target male. The focal female choice in the post-demonstration step is then compared with the choice of other control females that did not witness the demonstration. In this case there is not a proper reversal of choice, but the assumption that females from the control and testing groups share the same initial preference. This setup is used, for example, in studies where choice is determined by the observation of an actual mating, such as studies with *Drosophila melanogaster* as described below.

There are two main control experiments that are usually tested along with the MCC experimental paradigm. The shoaling control is commonly used in MCC experiments with fish and consists of substituting both target males of the experiment for females, to guarantee that the reversal in focal female preference is related to mate choice and not just a simple social decision to aggregate with other individuals. Some social species of fish, such as the guppy, tend to form shoals, and the MCC protocol could be mistaking this behaviour with mate choice (Dugatkin 1992). Another common experiment is the consistency control, which is used to test whether females are consistent in their mate choice decision. In this control, females also observe the two males during the demonstration step. This assures that female choice reversal in the MCC treatment is due to the positive information given by the association between the demonstrator female and one of the males, and not by other effects such as random choice, exploration behaviour, or the loss of interest for the preferred male caused by females not being able to physically contact with the males during the pre-demonstration step.

Based on the same experimental paradigm and its controls, researchers found other species with MCC behaviour, such as the sailfin molly (*Poecilia latipinna*) (Schlupp et al. 1994), the Mexican molly (*P. mexicana*) (Heubel et al. 2008), the Amazon molly

(*P. formosa*) (Heubel et al. 2008), and the Japanese quail (*Coturnix coturnix japonica*) (Galef & White 1998). Females are usually used in these studies because they are considered the choosier sex, but copying was also found in males of some species, namely in the sailfin molly (Schlupp & Ryan 1997).

From this point onwards, researchers also began to take an interest in the factors that can affect MCC. For example, in a study with Trinidadian guppies by Dugatkin (1996), the authors found that females tend to copy others when the target males have a similar area of orange patches between them, and tend to ignore the choice of other females and choose the most orange male when they are very dissimilar. Another experiment showed the same effect in sailfin mollies regarding target male size (Witte & Ryan 1998). Other experiments suggest that MCC might also be dependent on the perception of the relative experience of the demonstrator female. Experiments with guppies show that females tend to copy other females that are about the same size or larger than themselves, while ignoring the choice of smaller ones (Amlacher & Dugatkin 2005). Fish size is a good indicator of age in these species, and older fish might be perceived as being more experienced. MCC was also found to be affected by some ecological factors such as atmospheric pressure in the fruit fly *Drosophila melanogaster* (Dagaeff et al. 2016). On the other hand, although MCC is usually thought to have a genetic basis, no correlation has been found between the copying behaviour of female guppies with that of their mothers (Dugatkin & Druen 2007). This is the only empirical study of MCC heritability to date, so more studies are needed to understand the role of genetics on this behaviour (Witte et al. 2015).

Variations in the experimental paradigm have also helped to test specific aspects of the MCC behaviour. For example, most MCC studies have tested the effect of positive social information by demonstrator females (i.e. mate choice) but, theoretically, copying should also occur when individuals decrease their preference towards a mate after receiving negative social information (i.e. rejection) by demonstrator females (Pruett-Jones 1992). Witte & Ueding (2003) demonstrated this effect through video playbacks using sailfin mollies.

Another interesting finding is that, contrary to the original idea that MCC should rely on the observation of demonstrator female choices (Pruett-Jones 1992; Nordell & Valone 1998), the information given by the demonstrator female does not have to be only visual. Galef et al. (2008) found that in Norway rats (*Rattus norvegicus*) the pheromones released from the sexual interaction between a male and a demonstrator female was enough to elicit copying from copier females. So, although demonstrator females were not physically present, copier females still preferred to engage in sexual activity with recently mated males than with non-recently mated ones. Additionally, Kavaliers et al. (2006) found that in mice (*Mus musculus*) female preference can positively change after detecting other females' urine odours mixed with urine odours from a target male. In this case, neither target males nor demonstrator females were physically present. Together, these studies suggest some form of MCC based only on chemical cues.

Some studies have failed, however, to find evidence of MCC. In guppies, for example, all these studies used either store-bought guppies of unknown origin (Lafleur et al. 1997) or individuals originated from feral populations in South Africa (Brooks 1996) or Australia (Brooks 1999), instead of individuals from native populations in Trinidad or their descendants, as tested originally by Dugatkin and colleagues (Dugatkin 1992; Dugatkin & Godin 1992). This suggests that MCC may occur only amongst certain populations within a species, although the reason for this difference in behaviour is still unclear. Nonetheless, the process of guppy domestication (including artificial selection for longer caudal fins and brighter colours) can have significant effects on their brain size (Burns et al. 2009), and the behavioural effects of this process are still unknown (Dugatkin 1998).

MCC is not only found in more 'complex' organisms as fish, birds, and mammals. As mentioned above, MCC can also be found in the fruit fly *D. melanogaster*, a behaviour discovered by Mery et al. (2009). Their study is an important qualitative leap in knowledge, as it provides the first evidence that a complex social behaviour such as MCC can also occur in an invertebrate species. Mery et al. (2009) did two experiments and in both the authors allowed for females to choose between males with very different phenotypes. In the first experiment, females were allowed to choose between large and small males, which are indicators of good and bad growing conditions. In the second experiment, the authors created artificial phenotypes (pink and green) using insect colouring powders and tested both positive information (acceptance) towards one of the phenotypes, and negative information (rejection) towards the other. Females initially preferred larger males, as expected, but after the demonstration phase, both male phenotypes became equally attractive. Also, as expected, there was no initial preference for pink or green males, but after the demonstration phase females learned to prefer the colour of the males that they saw mating before.

In the same year, a second study demonstrated no evidence of MCC in another species of fruit flies, *Drosophila serrata* (Auld et al. 2009). The methods used in the two studies were very different, which may account for the difference in the findings. Auld et al. (2009) tested MCC using siblings as male targets, which the authors could not visually distinguish. The authors needed to colour the males' food and dissect them afterwards to tell them apart. The authors justified this method by citing the study of Dugatkin (1996) where female guppies only copy when males have similar phenotypes. They also did a control by using random males from the stock population, yet still finding no evidence of copying. Other differences between the two studies were that Auld et al. (2009) used heterospecific *Drosophila birchii* females to convey mate rejection (*D. serrata* males still court them but always get rejected), while Mery et al. (2009) used previously mated conspecific females to the same end. Finally, Auld et al. (2009) allowed females to interact immediately with both males after the demonstration phase. This is very different from Mery et al. (2009), where females either were allowed to choose between males different from those of the demonstration phase, but who shared the same phenotype (pink and green) with them, or females were allowed to prospect both large and small males for an entire day while not interacting directly with them. These conditions were determinant because *D. melanogaster* males can have sperm depletion after a mating, and females avoid males that they recently saw mating, which was later demonstrated to impair MCC behaviour in this species (Loyau et al. 2012). Sperm depletion could be the explanation for why Auld et al. (2009) did not find copying behaviour. However, *D. serrata* males are adapted to high sperm competition, as *D. serrata* females have one of the highest incidence of remating within *Drosophila* species (Frentiu & Chenoweth 2008). So, in fact, mate choice in this species should be less relevant and females should be less choosy, thus decreasing the need for MCC (Santos et al. 2014). For these reasons, it is still unknown if the difference in MCC behaviour in both species is real or just an artifact of the different methodologies used. Nonetheless, for *D. melanogaster*, the evidence for MCC has been strengthened with the publication of several additional studies, using various variations of the experimental paradigm that was originally created for the artificial phenotypes (e.g. Dagaeff et al. 2016; Danchin et al. 2018; Nöbel et al. 2018a, b).

Recently, however, Belkina et. al (2021) failed to confirm MCC in their study with *D. melanogaster*, and attributed their discrepant result to differences in experimental set-up, suggesting that MCC might be less robust in this species than previously suggested.

With all these empirical advancements in the study of MCC under laboratory conditions, researchers have returned to the wild, not to perform field observational studies as was done in the beginning with bird lekking species (e.g., Höglund et al. 1995), but to experimentally test whether this behaviour can also happen under natural conditions. With this goal, copying has been demonstrated in the wild for at least three fish species, the sailfin molly (Witte & Ryan 2002), the guppy (Godin & Hair 2009) and the ocellated wrasse (*Symphodus ocellatus*) (Alonzo 2008).

Many of the examples cited so far describe MCC as being a behaviour where an individual changes its choice towards another individual that it previously saw mating (i.e. individual MCC), but, as shown by the experiments with *D. melanogaster* cited above, females can also change their preference towards males that share the same traits with the one they previously saw mating with a demonstrator female. This type of MCC was first demonstrated by White & Galef (2000) with female Japanese quails (*Coturnix coturnix japonica*). In White & Galef (2000) this was demonstrated with two different experiments. In the first one, the authors used artificial red and blue colouring to create conspicuous artificial phenotypes in the tested males, and in the second experiment the authors artificially created ‘pseudomutant’ males by gluing white tail feathers in some of the tested males. These ‘pseudomutants’ simulated a naturally occurring mutation in this species. In both experiments, females significantly increased their preference towards new males that shared the same trait as the male they saw with a female during demonstration, in comparison to control females lacking that information.

This behaviour, coined “MCC generalization”, “generalized MCC”, or “trait copying”, was later found in many different species, including in species where individual MCC has also been found, such as the guppy (Godin et al. 2005) or the sailfin molly (Witte & Noltemeier 2002), and in species like the zebra finch (*Taeniopygia guttata*) (Swaddle et al. 2005; Drullion & Dubois 2008), where MCC had never been documented before. As stated previously, both individual and generalized copying have also been found in the fruit fly (*D. melanogaster*), demonstrated by Mery et al. (2009), where the experiment with large and small males depicts individual MCC and the experiment with the artificial green and pink phenotypes depicts generalization. A list of species with MCC behaviour, including generalization, can be found in a review by Vakirtzis (2011), and a list of empirical MCC studies can be found in two recent meta-analyses (Jones & DuVal 2019; Davies et al. 2020).

There is also a growing body of studies demonstrating that individual and generalized MCC can occur in humans, both in males and females (Gouda-Vossos et al. 2018). Due to ethical and practical reasons, the method to study this behaviour in humans is usually based on the visualization of photographs of model individuals. Testing subjects are first asked to evaluate the attractiveness of the models, then their attractiveness is manipulated with information about the models' romantic experiences, and their attractiveness is evaluated again (for more information see a meta-analysis on human MCC by Gouda-Vossos et al. 2018).

1.3 The adaptive value of MCC

The adaptive value of MCC (and how to measure it) is not fully understood. However, several hypotheses (methods) have been proposed. Nordell & Valone (1998) developed a conceptual approach where they suggest treating the social information gathered by copier individuals as a resource. Just like any other resource (e.g. food, breeding habitat, or shelter), the information about the quality of potential mates becomes valuable if individuals can choose between several mates. MCC can, therefore, be seen as a way of gathering that information and an alternative to innate choice and individual assessment.

MCC is also thought to help individuals to avoid many costs associated with innate choice and individual assessment, namely a mismatch between genetic adaptations and current environmental conditions (Danchin et al. 2001, 2004), time constraints, potential mate harassment, increase in parasite load, risk of predation, and exposure to sexually transmitted diseases due to a higher mating rate caused by forced matings (Gibson & Höglund 1992; Vakirtzis 2011 and references therein). Additionally, individual MCC can be seen as a type of bet-hedging strategy because individuals guarantee that they do not choose worse than their competitors (Losey et al. 1986; Sirot 2001). These advantages should be particularly significant to experienced individuals when facing unsuccessful reproduction or unknown environmental conditions (Nordell &

Valone 1998; Danchin et al. 2001, 2004; Varela et al. 2018), or to unexperienced ones (e.g. younger females copying older ones but not vice versa Amlacher & Dugatkin 2005, section 1.2).

However, this behaviour might also incur some costs. Individuals that copy the mate choice of others might need complex cognitive abilities associated with learning, and might also be limited by time, as enough time is also needed to prospect and eavesdrop before being able to witness a single mate choice event from conspecifics. As referenced earlier, males chosen by multiple females can also have decreased fertility due to sperm depletion (Gibson & Höglund 1992). Additionally, MCC can also lead to maladaptive choices. This is not as problematic in the case of individual MCC, as the probability of making a wrong choice with social information is not greater than making a wrong choice without social information (Nordell & Valone 1998). But could be more problematic in the case of MCC generalization, where informational cascades can wrongly influence larger numbers of individuals and, therefore, increase the probability of any individual in the population to make a maladaptive choice (Giraldeau et al. 2002; Dubois et al. 2012). Of course, these costs can vary greatly from species to species and even from individual to individual, depending on the context (Davies et al. 2020). Unfortunately, the fitness costs of MCC are difficult to measure, so it has never been estimated (Witte et al. 2015).

1.4 MCC, social learning, and cultural evolution

While empirical studies of MCC are important to understand its prevalence in nature, its adaptive value, and the conditions under which it is most likely to occur, it is also important to conceptualize MCC into a broader framework and understand how it may relate to other biological processes.

MCC is a type of social learning (Witte & Nöbel 2011; Kavaliers et al. 2017; Varela et al. 2018), an associative cognitive process that occurs through direct observation of other animals’ behaviours (usually conspecifics) or, indirectly, through contact with their products, such as tools, scent marks, nests, shelters or other types of constructions (Heyes 1994). Another type of social learning in the sexual selection context is sexual imprinting, a process where continuous exposure to a stimulus during a sensitive period in an animal's life later influences their mating preferences (Immelmann 1975). Examples of this kind of stimuli include the colour patterns, the odour signatures or the vocal repertoires of an individual's parents, kin, or colony mates. In contrast to MCC, however, it occurs very early in life, while copying occurs only when animals gain sexual maturity and start looking for mates (Varela et al. 2018).

While the study of MCC started around 30 years ago, formal research on social learning began sooner, over a century ago (Heyes 1994) and is one of the best known social cognitive mechanisms (Varela et al. 2020). Placing MCC in the framework of social learning allows researchers to better study the neuroscience of MCC. In fact, the study of the neurological mechanisms behind MCC has increased in the last years (e.g. reviewed in Kavaliers et al. 2017).

One important aspect of MCC, being a type of social learning, is the potential for it to become a subject of cultural evolution (Danchin et al. 2004). The main idea behind this phenomenon is that, after observing a mating event, all the individuals that copy will have the tendency to choose the same mates (or similar mates in the case of MCC generalization), and they will also produce social information that might influence the choice of others. This chain reaction that uses social information as a meme, and MCC as a transmission mechanism may ultimately affect biological evolution (Danchin et al. 2004; Danchin et al. 2018; Varela et al. 2018).

Back in 1992, Gibson & Höglund already explored the idea that individual MCC can create short-term fads through informational cascades. With the introduction of the concept of MCC generalization, the possibility of MCC creating long-lasting cultural effects became more plausible. In fact, the ability to generalize the information acquired by social learning is one of the underlying conditions for cultural evolution (Danchin et al. 2004, 2011; Wagner & Danchin 2010). In total, there are four criteria that have been proposed for a behaviour to be culturally transmitted: that it (1) is inherited through social learning, (2) is transmitted across age classes; (3) is maintained long enough to be copied; and (4) can be generalized (Danchin et al. 2004, 2011; Wagner & Danchin 2010). Remarkably, Danchin et al. (2018) published a study where they demonstrated that MCC in *D. melanogaster* possesses all four sufficient conditions to be considered a cultural process, plus a fifth condition: that it possesses repair or reinforcement mechanisms, meaning that individuals tend to copy the most popular choice (conformity). The authors also ran a simulation to show how MCC might evolve as a culture in this species. Their results show that MCC might lead to persistent local traditions. If, however, the traditions are maladaptive, they should tend to persist for shorter periods (Giraldeau et al. 2002; Dubois et al. 2012).

1.5 Theoretical studies of MCC

Empirical studies have shown the widespread occurrence of MCC in nature and conceptual approaches have helped to reflect on its adaptive value and its implications for cultural evolution. The next step is to understand how MCC itself can evolve and its impacts on the direction and strength of sexual selection, something that theoretical studies have been trying to accomplish.

Some of the earliest theoretical models about MCC focused exclusively on species with the lek mating system and were created to understand whether copying others could be a viable strategy (Losey et al. 1986), and to estimate the degree of MCC in natural populations (Wade & Pruett-Jones 1990). From 1992 onwards, when several important studies indicated that MCC was more widespread than initially thought (see section 1.1), theoretical models also became more general. In the seminal paper where Pruett-Jones (1992) defined the concept of MCC, the author also included a simple game-theory model, showing that MCC can be an evolutionary stable strategy (ESS). In this model, Pruett-Jones assumes that females visit males in pairs, and each female can either be a copier or a chooser. Choosers will always sample their males and copiers will copy the mate choice of choosers or choose randomly otherwise. Considering that choosers incur an extra fitness cost k associated to mate sampling (see section 1.4), and the ability for choosers to discriminate allow them to produce offspring that have on average f times more fitness than random choice, the evolutionary stable strategy will then be $p = 1 - (k/f)$, with p being the proportion of choosers in the population. Although the model is very simple, the results indicate that MCC can be an evolutionary stable strategy overall. Note that the term ‘chooser’ used in this model is not the same as the term chooser used in some of the sexual selection literature, where it can be used to contrast with the term ‘courter’ to indicate the behavioural role of individuals during the mate choice process (Rosenthal 2017). Both choosers (non-copiers) and copiers classified by Pruett-Jones (1992) can be classified as choosers in the sense of Rosenthal (2017), while the target individuals can be classified as courters. Here, I will always use the term ‘chooser’ following Pruett-Jones’ (1992) definition.

A few years later, Kirkpatrick & Dugatkin (1994) published a model where they explored the effects of MCC on the evolution of males’ secondary sexual traits. In this model, the authors considered a set of three assumptions that began to be used in future models. The first assumption is that MCC is genetic and populations with MCC can show genetic polymorphism regarding this trait. As a type of learning (Varela et al. 2018), MCC must have a learning genetic basis, but whether there is a specialized genetic mechanism for this behaviour is unknown, although the only study to date that has addressed this topic, failed to find evidence of specialization (Dugatkin & Druen 2007). The second assumption is that younger individuals copy older ones (*i.e.*, oblique transmission). This assumption is based on some empirical evidence with fish (see section 1.2). It allows for the social information to be inherited across time instead of just being transmitted horizontally each generation. However, because it increases the complexity of the simulated system by allowing multiple cohorts to coexist, it has only been considered a few times in other MCC models. The third assumption is about copying rules: females can only copy from another female (“single-mate copying”) or can learn from multiple different mating events (“mass copying”). Because it is unknown how females incorporate the information from multiple events during mass copying, Kirkpatrick & Dugatkin (1994) considered that females copy the average choice of other females, but other authors have considered different rules. Uehara et al. (2005) modelled MCC as a type of Bayesian decision making, suggesting that females have “last choice precedence”, while Danchin et al. (2018) showed that females tend to copy the most popular choice.

Kirkpatrick & Dugatkin's (1994) model revealed that MCC tends to produce positive frequency-dependent selection, meaning that copier females usually increase their preference towards the most common male. This happens because common males are the most likely to be observed mating. The same effect was later found in future studies and can only be broken by introducing further assumptions, such as asymmetry in preference favouring rare males (Agrawal 2001), or when females also take negative information (*i.e.*, information about mating rejections) into account (Santos et al. 2014). The consequence of the positive frequency-dependent selection is that new male traits will not be able to invade a population, unless if the other assumptions are in play (Santos et al. 2014). Together, these studies reveal that MCC has the potential to substantially affect the course of sexual selection, by changing the frequency of male trait alleles or the invasion potential of new alleles.

Regarding the evolution of MCC itself, Servedio & Kirkpatrick (1996) suggest that it can occur in three ways: (1) by directly increasing fitness; (2) by being a by-product of other behaviours selected in other contexts (e.g., an increase in social learning ability in the context of foraging might also increase MCC ability), or (3) through genetic effects. Servedio & Kirkpatrick (1996) explore the latter scenario with a mathematical model, by assuming MCC to be a gene that can evolve through indirect selection by associating with the genes of males with high overall fitness. In this case, if MCC allows females to have a higher chance of breeding with the most successful males, it can evolve even when there is a mild direct cost associated with it (e.g. an energy cost from the learning mechanism).

Other theoretical models have also analysed the adaptive value and evolution of MCC. For example, Stöhr (1998) showed that MCC might evolve in the black grouse (*Tetrao tetrix*) if females have time constraints for mating and younger females can benefit from older ones. Dubois et al. (2012) considered a scenario where non-copier females have an associated cost and can choose erroneously, showing that MCC might lead to maladaptive decisions.

1.6 Evolutionary and ecological effects of MCC

Theoretical models have been showing that MCC can evolve and alter the allele frequency of the target mate traits, thus shaping the course of sexual selection. This gives MCC the potential to be an important driver in major evolutionary processes such as speciation and hybridization (Varela et al. 2018).

One hint of such process in the wild can be found in the Amazon molly (*Poecilia formosa*), a species of fish probably originated from a single crossbreeding event between a sailfin-like male (*P. lattipina*-like) and an Atlantic molly female (*P. mexicana*) (Avise et al. 1991; Schartl et al. 1995; Heubel et al. 2008; Schlupp 2010). The Amazon molly is an all-female species that reproduces through gynogenesis, meaning that females need the sperm of males from one of its parental species to activate embryogenesis, but not to fertilize their eggs. Hence, Amazons create clones of themselves, discarding the genetic information contained in the sperm (Schlupp et al. 1998; Schlupp & Plath 2005). In regions where sailfin and Amazon mollies occur in sympatry, males of sailfin mollies can mate both with conspecific females and with the Amazons. Given that males sailfin mollies have no apparent benefit in mating with the Amazons, researchers started to wonder why they mated with them in the first place. However, it was found that males tend to transfer less sperm when mating with Amazon mollies (Schlupp & Plath 2005), which leads to the question of why males mate with the Amazons. Researchers found that sailfin molly females copy the mate choices of the Amazons, so a male that mates with an Amazon gains the benefit of becoming more attractive to conspecific females (Schlupp et al. 1994). This example suggests that MCC might be helping to maintain a species complex in the wild. Furthermore, researchers also found that only sailfin mollies females originated from populations in sympatry with Amazon mollies copy them, while sailfin mollies originated from allopatric populations do not show signs of heterospecific copying (Heubel et al. 2008).

If sailfin mollies from allopatric populations do not copy Amazon mollies, what will happen if Amazons were to be introduced in those populations? Will sailfin mollies start to familiarize with the Amazon molly and start copying them, creating a system like in other sympatric populations, or will the females refuse to copy Amazons, thus making less beneficial for sailfin males to mate with them? It is still unclear why different populations of sailfin mollies respond differently to heterospecific MCC, so the evolutionary outcome of this scenario is also hard to predict, but different MCC mechanisms can lead to different evolutionary pathways.

This idea can be generalized to other closely related species, populations, or sub-populations, where the way individuals respond to the mate choice of others might lead to convergence or divergence in mate-preference, turning MCC into a force that can aid or hamper the process of speciation or hybridization. Varela et al. (2018) published a critical review where they hypothesize that genotype-by-environment interactions and habitat structure are essential elements to consider while studying the effects of mate choice on evolution. In their conceptual approach, Varela et al. (2018) considered various evolutionary outcomes of speciation and hybridization in scenarios where populations were in micro-allopatry, allopatry, sympatry, or in secondary contact. In all scenarios, the role of MCC was dependent upon (1) the type of MCC (whether there is generalization or not); (2) the frequency of dispersal between habitat patches; (3) the condition of different groups of males (i.e., whether migrant males perform better or worse, or are perceived as of higher or lower quality than local males); (4) the species dispersal ecology (i.e., whether dispersal is sex-biased or not); and (5) the copying rules, that is, the way local and migrant females choose their mates (whether migrant females copy or not, and whether copying females conform to the choice majority of other females, or give more weight to mating interactions with novel males, or to information about male performance).

This conceptual work highlights the importance of understanding how MCC works before extrapolating what role MCC may play in the mechanism of sexual selection and in the evolutionary trajectory of species. It also highlights the interplay between MCC and dispersal on the magnitude of those effects.

1.7 The correlated evolution of MCC and dispersal

As explored above, many possible effects of MCC on ecology and evolution require a spatial setting, through which individuals from different habitat patches only meet with each other through dispersal between patches. It is, therefore, worth exploring how MCC and dispersal may evolve together.

Dispersal is a widespread phenomenon. In many species there are at least some individuals that leave their natal patch to settle elsewhere for breeding. Organisms might disperse passively (e.g., by wind, currents, or carried by other animals), or actively by their own means (Matthysen 2012). The distances they travel are, therefore, related to their passive means of transportation or, when dispersal is active, by their size, type of mobility (flying, swimming, or walking), environmental conditions, resistance, and physical condition (Nathan et al. 2012). The main benefits of dispersal are three: (1) avoiding inbreeding and competition with kin, (2) increasing variance in offspring fitness, and (3) escaping locally unfavourable conditions (Matthysen 2012). However, it can also incur many costs, such as the energy costs associated with movement, the risk of predation during travel, the risk of moving from a familiar to an unfamiliar habitat patch, and reproductive costs (e.g. the cost of losing a breeding season, or of producing maladapted offspring).

Dispersal is often considered a three-stage process, where individuals first leave their current habitat patch (‘departure’ or ‘emigration’ stage), then travel (‘transfer’, ‘transient’, or ‘vagrant’ stage), and finally settle in a new patch (‘settlement’ or ‘immigration’ stage) (Matthysen 2012). Each one of these stages are associated with different characteristics and present different challenges for the individual. In the departure step, individuals need first to decide (or be forced) to disperse, and the causes for dispersal are multifactorial, ranging from genetic, parental (e.g., dispersal decisions made by parents for their offspring), and social (e.g. population density), to abiotic (e.g. temperature and humidity), among others (Fowler 2005; Clobert et al. 2012; Matthysen 2012). During transfer, individuals need to cross an environmental matrix, follow a movement pattern, and choose a new location to settle. This step depends mostly on the environment and on the phenotype of the individual associated with the dispersal mode itself (e.g., wing size, morphology, endurance, etc.) (Benard & McCauley 2008; Matthysen 2012; Zera & Brisson 2012). Finally, during settlement, individuals need to adjust to the new environment.

Individuals that settle after dispersal might find themselves under new environmental conditions, needing to quickly learn how to cope with them and to interact with local unfamiliar conspecifics, if any. While it is possible for individuals to settle in a new environment and learn everything by themselves (i.e., asocial learning), it might be less costly for individuals to learn about their new environment through conspecifics (Danchin et al. 2001). For example, it has been shown that individuals can discover through social learning what food to eat or avoid (Galef & Clark 1971; Hishimura 2000; Danchin et al. 2004; Teles et al. 2015), or what parasitoids to avoid (e.g, Kacsoh et al. 2019). In the dispersal context, it would be theoretically safer for immigrants to follow the behaviour of local individuals, than to risk eating the wrong food or being spotted by a predator due to inappropriate behaviour.

An example of the link between social learning and dispersal can be found at the origin of coloniality in birds, where researchers found that the density of birds in colonies cannot simply be explained by the amount of available habitat (i.e., ‘ideal free distribution’) (Fretwell & Lucas 1969; Křivan et al. 2008). Because of this, it was first thought that birds aggregate as a defence mechanism against predation via dilution effects, group vigilance, and communal defence (Wittenberger & Hunt 1985; Brown & Brown 2001), but coloniality also makes individuals more prone to be found by predators (Wittenberger & Hunt 1985; Brown & Brown 2001). A study compared both hypotheses through phylogenetic analysis and found that colonies do make birds more vulnerable to predation (Varela et al. 2007). To move away from the cost-benefit impasse, Danchin & Wagner (1997) suggested that coloniality might have appeared through ‘commodity selection’, meaning that birds choose their breeding site by observing the reproductive success of others, leading them to aggregate in the same favourable places, with the costs and benefits of aggregation arising as by-products. While individuals might choose their breeding sites by assessing all the potential costs and benefits by themselves, it is easier to evaluate the quality of a breeding site by observing the breeding success of others, as this requires less time, probably less complex cognitive abilities and it summarizes all the information about the breeding location (Danchin & Wagner 1997; Danchin et al. 2001).

There are many studies that show how animals use social information to choose their breeding site. In a 17-year study of the black-legged kittiwake (*Rissa tridactyla*), Danchin et al. (1998) showed that individuals prospect other nests to find their own breeding location, and the decision to disperse does not depend on their own breeding success but on the success of others. In the collared flycatcher (*Ficedula albicollis*), it has been shown that both immigration and emigration rates depend on the breeding success of conspecifics, however immigrants only take into account the mean number of offspring per nest in a patch (“quantity”), while local individuals also take into account their condition (“quality”) when deciding to emigrate (Doligez et al. 2002). In these studies, individuals use conspecific cues as a shortcut to habitat choice, a process similar to when individuals use conspecific information to choose their mates in MCC.

Social learning through eavesdropping on the breeding success of others for habitat copying has been found to be most useful when the environment is relatively stable from breeding season to breeding season (within the lifetime of an individual), but still showing larger fluctuations in the long run (between generations). When the environment changes locally, individuals may feel the need to disperse to new patches of higher quality. So temporal changes may lead to dispersal. The short-term environmental autocorrelation assures that the environment is predictable enough that individuals can still benefit from the information they have learned in the previous breeding season, but not static enough that other less costly strategies – such as prospecting for the presence of conspecifics or philopatry – can be equally good predictors (Danchin et al. 2001; Doligez et al. 2003). The larger temporal fluctuations also mean that new information about habitat quality needs to be learned from generation to generation. This limited environmental predictability is in fact part of a model for the evolution of learning, called the Stephen's model (Hollis & Guillette 2015).

Although immigrants can benefit from social learning, local individuals might also use social information obtained from immigrants to some extent. In the common lizard (*Lacerta vivipara*), Cote & Clobert (2007) found that local individuals can use immigrants as a source of information to extrapolate the density of the surrounding populations, and subsequently use that information to decide whether to disperse or not.

The above examples show how individuals can use social information during the dispersal process, mostly to find a location to breed. However, once arrived in the new patch, the challenge of how to choose a mate in the new location has never been tackled before. That is a relevant problem because choosing mates correctly should substantially reduce the reproductive costs associated with dispersal. Innate preferences are not the best help because they are not adapted to the new environment after dispersal, and individual assessment of mate quality can add substantially more time to the one already invested in dispersal. Therefore it is reasonable to assume that MCC can be a valuable strategy when individuals try to breed in a new location. This idea is also in accordance with the notion that females tend to copy when they perceive others as being more experienced, or when they lack information (Nordell & Valone 1998) and migrant females are the ones who most need information. By learning from local females which local males are the best to mate with or the more popular, migrant females' offspring will be better locally adapted, or in better competitive conditions, than if migrant females had mated with migrant males or with local males of inferior quality or less popular.

Within this framework, by reducing the reproductive costs of dispersal, MCC has the potential to promote the evolution of dispersal itself. By doing so, we can also predict that MCC can affect population dynamics by promoting mate choice convergence between individuals from different patches (similarly to what has been explored in Varela et al. 2018). This should lead to higher allele transfer between patches, thus reducing local adaptation rates. Finally, the same process should also interfere with a species ability to not only disperse within the species typical range distribution but also to expand it, probably by accelerating the process.

Therefore, given the accumulated knowledge so far, with all the theoretical, empirical, and conceptual studies about MCC, it must be advantageous for individuals to use this behaviour when they disperse and settle in a new location. When they do, the effects of MCC on population dynamics should be significant, particularly when the environment is patchy, when its quality is heterogeneous across patches, and when there is some degree of environmental autocorrelation (closer habitat patches are more similar to each other than more distant ones). However, there is a lack of studies that links dispersal ecology with MCC, and this thesis is an effort to cover this gap. For this purpose, I used mathematical models to study the effects of MCC on population dynamics, simulating from the simplest scenario with only one patch and no dispersal, to scenarios with multiple patches, dispersal, and range expansion.

1.8 Aims and Structure of the Thesis

In this thesis, I used individual-based models to explore the benefits and consequences of MCC in population dynamics using different spatial structures, and I explored how dispersal, sexual selection strength, type of MCC (individual or generalization), MCC conditions, and preference rules (which phenotypic traits females use to evaluate their mates) affected the outcome of the simulations. I found that MCC can have significant influence in the evolutionary fate of populations, namely their degree of dispersal, of local adaptation, and speed of range expansion. The influence of this social learning behaviour can also depend on factors like the type of copying, MCC conditions, or preference rules, which should be considered in future empirical studies.

In chapter 2, I[1] start on a small scale, that of a single habitat patch. I present an individual-based model where the environment is homogeneous. My goal was to understand the evolution of MCC itself and how it can affect, at this scale, a population's average fitness. Here, I used similar assumptions and compared my model with Servedio

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[1] Although I use the first person singular here to keep the writing style congruent, I would like to point out that in this chapter I was the second author. In the other chapters, I was always the first author.

& Kirkpatrick (1996), where they found that MCC, determined genetically, might evolve through indirect selection by hitchhiking a male trait that is adaptive. In their model, the authors considered only a case where female innate preference do not coevolve with the male trait and in my model, I additionally considered a case where coevolution occurs. I hypothesized that the evolution of MCC through indirect selection should not occur if preference coevolves with the male trait, because it will be harder for copiers to hitchhike the adaptive male trait. If that is the case, MCC might be more likely to evolve if multiple patches are considered (which are the scenarios that I developed in chapters 3 and 4), because migration can help to maintain genetic variation for preference.

A second objective of the model in chapter 2 was to validate the approach of studying MCC with individual-based models. In MCC research, most theoretical models are created using a set of mathematical equations that are solved in respect to specific parameters, either algebraically or through simulations (e.g., Pruett-Jones 1992; Kirkpatrick & Dugatkin 1994; Servedio & Kirkpatrick 1996; Stöhr 1998; Agrawal 2001; Uehara et al. 2005; Brennan et al. 2008; Dubois et al. 2012). This approach contrasts with individual-based (or agent-based) models where, through computer simulations, researchers explicitly simulate the behaviour of individuals through an algorithm (a set of instructions) and sample the desired variables (e.g, Sirot 2001; Santos et al. 2014; Danchin et al. 2018) . Although models created using explicit mathematical equations can more easily understand the behaviour of specific parameters, this might not be possible when the model itself is too complicated. In those cases, individual-based models are an excellent alternative approach (Kokko 2007). My model in chapter 2 is individual-based and considers non-overlapping generations, while Servedio & Kirkpatrick's (1996) model uses a set of recursion equations (equations that describe the difference in allele frequencies of the population during each iteration) and considers overlapping generations. I, therefore, directly compared my results with those of Servedio & Kirkpatrick (1996) and confirmed the robustness of these types of models for studying MCC. This validation allowed using the same model structure in chapters 3 and 4.

In chapter 3, I switch to a scale of many habitat patches. I present an individual-based model, where the environment is heterogeneous but autocorrelated between patches. I study the evolution of MCC, as well as the interplay between copying, dispersal, and local adaptation. I introduce variation on the type of copying rule females can use either only when they disperse (as this is the situation in which females most lack information about local male quality), or both when they disperse and stay in their natal patch. In this model, I wanted to test the hypothesis that the cost of migration can be reduced if migrant females copy the choices of local females. Thus, the existence of MCC in a population should increase the tendency of individuals to disperse, and this effect should be even stronger if copying is conditional to a female being a migrant, which in turn should also increase the proportion of copying individuals in the population. Additionally, if MCC increases dispersal, I predict that it will indirectly reduce levels of local adaptation due to increased migration flow.

Chapter 4 takes the concept of chapter 3 further and uses individual-based models to simulate a scenario where individuals are expanding their distribution range through an environmental gradient. Again, I study the evolution of MCC, as well as the interplay between copying and dispersal, plus their joint effect on the speed of expansion. This time, I used hard selection since individuals leave their original habitat range (in contrast with chapter 3, where I used soft selection) and introduced variation on the type of MCC females can perform (individual or generalized MCC), and on preference rules females can use (whether the male trait of female preference is condition dependent or condition independent on the environment). As in chapter 3, I predict dispersal to evolve, along with an increase in the proportion of copying individuals. However, individual and generalized MCC may be differently adaptive under the condition dependent and condition independent rules. Because generalization can lead to greater deviations between the trait that was learned, and the traits present in the males chosen by copier females, I predict that it is less adaptive than individual MCC during an invasion process when copying is condition dependent. On the other hand, when copying is condition independent, I predict that generalization should be more adaptive than individual MCC. In these scenarios non-copier females are less accurate in their choices, so deviations from the learned choice caused by generalization may be less costly, or even advantageous, because copying females are more likely to end up mating with better-adapted males than non-copiers.

Chapter 5 centres around an Invited Commentary on a published meta-analysis study about factors that influence MCC (Davies et al. 2020). This is one of two studies published recently about the topic, the other being Jones & DuVal (2019), and it summarizes the state of empirical research in MCC. I start this chapter by giving a description of both studies, followed by the published commentary itself, where I suggest a framework for future empirical research of MCC. After this section, I give an overview of other published commentaries in the study and the reply of the original authors. Finally, I give a critical overview of all the commentaries, referring to the importance of empirical studies to the development of more accurate theoretical models, something that I explore in more detail in the general discussion.

Chapter 6 is the general discussion of the thesis, where I highlight the key findings of my work and discuss why I chose specific model assumptions in chapters 2 to 4, and how they might affect the outcome of these models. I also suggest future perspectives on how to study the effects of MCC on ecology and evolution and what I consider to be the main questions left unanswered for this topic, focusing both on empirical and theoretical research, and how they should work in synergy.

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Chapter 2

Mate-choice copying: A fitness-enhancing behavior that evolves by indirect selection

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All figures, tables, and other sections denominated with the letter "S" can be found in Appendix I.

2.1 Abstract

A spatially explicit, individual-based simulation model is used to study the spread of an allele for mate-choice copying (MCC) through horizontal cultural transmission when female innate preferences do or do not coevolve with a male viability-increasing trait. Evolution of MCC is unlikely when innate female preferences coevolve with the trait, as copier females cannot express a higher preference than noncopier females for high-fitness males. However, if a genetic polymorphism for innate preference persists in the population, MCC can evolve by indirect selection through hitchhiking: the copying allele hitchhikes on the male trait. MCC can be an adaptive behavior—that is, a behavior that increases a population's average fitness relative to populations without MCC—even though the copying allele itself may be neutral or mildly deleterious.

Keywords: Indirect selection, individual-based simulations, mate-choice copying, sexual selection, social information.

2.2 Introduction

Many animals acquire new patterns of behavior by witnessing what others are doing, a process known as social learning (Heyes and Galef 1996; Galef and Laland 2005). Mate-choice copying (hereafter referred to as MCC) is one form of social learning based on inadvertent social information (also known as public information; Danchin et al. 2004; but see Wagner and Danchin 2010) where mating decisions (usually by females) are influenced by observation of the mating preferences of others (Pruett-Jones 1992; Dugatkin 1996a). The first theoretical models of MCC (Bradbury and Gibson 1983; Bradbury et al. 1985; Losey et al. 1986; Wade and Pruett-Jones 1990; Dugatkin and Hoglund 1995; Stöhr 1998) sought to explain the high variance observed in male mating success in avian leks (Wiley 1991), in which males aggregate and females' survey potential partners for copulation. These models assumed that noncopier females assessed male quality independently (though not flawlessly; Ryan et al. 2007), whereas copier females assessment depended on male mating success. Generally, if sampling costs associated with active mate choice are assumed, models predict that MCC is an advantageous short-cut strategy to identify high-quality mates (Pomiankowski 1990).

Despite the initial focus on lekking species, the first experimental evidence for female copying (Dugatkin 1992; Dugatkin and Godin 1992) came from guppies (*Poecilia* *reticulata*), a species where males actively pursuit mates. Similarly, in the fruit fly *Drosophila melanogaster*, where males display courtship behavior, Mery et al. (2009) showed that females copied mating preferences for arbitrary (in terms of potential mate quality) phenotypic traits. Mery et al. (2009) artificially generated two male phenotypes by dusting flies with green or pink powder. A prospector female witnessed a, for example, green male copulating with a model female and second a, for example, pink male that did not copulate because the model female was nonreceptive. After this double demonstration, two new colored males were presented to the prospector female. Females preferably mated with the male dusted with the color associated with active copulation.

Bayesian decision theory suggests that a female should perform MCC only when her own perception does not indicate much difference between two males (Uehara et al. 2005; see also Brooks 1996; Nordell and Valone 1998). Results from guppies and sailfin mollies (*Poecilia latipinna*) show that females rely on personal information when males are substantially different (Dugatkin 1996b; Witte and Ryan 1998), supporting this hypothesis. Contrarily to this, however, Mery et al. (2009) also showed that prospector females used social information even after observing model females mated with poor condition males. In *Drosophila*, juvenile performance is positively correlated between the sexes but adult performance is negatively correlated. Thus, there is no net intersexual correlation for total fitness (Chippindale et al. 2001). Owing to this intersexual conflict, a female choosing to mate with a “good” quality male will produce average adult daughters. It may, thus, be that there are nonadaptive reasons for the expression of MCC behavior in *Drosophila*, and perhaps in other species (Dugatkin and Godin 1995): how and why is this behavior maintained, and why did it evolve?

Indirect mate choice population genetics models provide an alternative approach to the study of evolutionary dynamics and consequences of MCC. A standard example of indirect selection is Fisher’s (1958, pp. 151–152) runaway coevolution, in which (innate) female preference evolves as a correlated response to the selection of male traits, which female preference itself induces, creating a self-sustaining feedback loop. The body of theory that developed around Fisher’s proposal originally assumed that females assess males independently of what other females are doing (Lande 1981; Kirkpatrick 1982; Pomiankowski 1988; but see Bailey and Moore 2012). However, later models that explicitly addressed the coevolution of learned female preferences and male traits have shown that a process akin to Fisherian runaway selection can occur (Kirkpatrick and Dugatkin 1994; Laland 1994; Ihara et al. 2003). Servedio and Kirkpatrick (1996) were the first to address the important question of how MCC can initially arise through indirect selection. They showed that when copier females mate with males that have higher total lifetime fitness, MCC may spread by hitchhiking on the male trait even if the copying gene is mildly deleterious. Once MCC is established, it creates a strong positive frequency-dependent bias that eliminates novel or rare male traits, irrespective of their fitness (Laland 1994; Kirkpatrick and Dugatkin 1994; but see Agrawal 2001). The potentially maladaptive consequences of MCC can be somewhat alleviated by including negative social information (i.e., when females can reverse their choice after having observed a previously attractive male being rejected by another female) in the models (Santos et al. 2014).

Kirkpatrick and Dugatkin (1994) and Servedio and Kirkpatrick (1996) models make different assumptions about female innate preferences. Although there is no genetic variation for preference in either model, Kirkpatrick and Dugatkin (1994) assume females have an innate preference for the more common, unfit males; whereas Servedio and Kirkpatrick (1996) assume both copier and noncopier females are born with an innate preference for high-fitness (combination of natural and sexual selection) males. In Servedio and Kirkpatrick (1996), preference and copying are jointly controlled by a single locus and preference changes only through cultural evolution. Thus, female innate preference is overridden after observing mate choices of an older female cohort. Yet, there is abundant evidence for genetic variation in female innate preference (Bakker and Pomiankowski 1995; Chenoweth and Blows 2006; Fowler-Finn and Rodríguez 2016), which is a requirement in Fisherian runaway models (Lande 1981; Kirkpatrick 1982; Tomlinson and O’Donald 1996; Kokko et al. 2002; Mead and Arnold 2004). Furthermore, genetic preference can also (co)evolve by indirect selection when natural selection favors a correlated trait that increases other fitness components such as fecundity (Kokko et al. 2003). To include genetic evolution of innate preference in studies of MCC will thus require modeling the evolution of at least three characters/genes: a gene/trait for innate female preference for a given male trait, a gene/trait acting in females that determines whether they rely on inadvertent social information or choose based on innate preference (the “copying” gene), and the gene/trait of males. The focus of this article is to explore such a scenario numerically using a “major-gene” approach. We therefore let female innate preferences and copying tendencies coevolve with a male trait, and assume that a female copying tendency is evolutionarily linked to her innate preference. This serves to avoid the criticism that copying and innate preference are independent and go against each other (Vakirtzis 2011). Results are compared to the situation where females vary in fixed innate preferences, rendering coevolution with the male trait impossible, as in Servedio and Kirkpatrick (1996).

Many species exhibit a patchy population structure, with individuals distributed in spatially scattered aggregates (see Santos et al. 2014). We used a discrete, spatially explicit individual-based simulation model where MCC occurs through horizontal cultural transmission (in *Drosophila* and in other taxa learning within a single generation has been documented; Servedio and Dukas 2013, and references therein). Females and males are associated with a location in a two-dimensional lattice and interactions happen locally. That is, female and male local groups are within signaling and receiving distance during courtship and mating activities. The focus is centered on females rather than on males because MCC appears to be more frequent in females (Dugatkin 1996a; Westneat et al. 2000), although MCC by males is also known to happen (Auld and Godin 2015). Furthermore, it is assumed that females learn to copy preference for phenotypic traits (Kirkpatrick and Dugatkin 1994; White and Galef 2000; Agrawal 2001; Swaddle et al. 2005; Mery et al. 2009), which remains to be demonstrated in males (Witte et al. 2015).

Results show that Fisherian sexual selection, where innate female preference coevolves with the male trait, makes the evolution of MCC unlikely. However, the spread of the copying allele by indirect selection can reinforce the invasion of a new, high-fitness male trait once a genetic polymorphism for innate female preference is allowed to persist. This novel finding suggests that under these circumstances, MCC is an adaptive strategy, because it helps the invasion of an overall fitter trait that results in average fitness of MCC populations to be higher than average fitness of populations without MCC.

2.3 The Model

2.3.1 Spatial Setting and Genomes

For the sake of simplicity, we assumed a sexual population of chromosomes (the "organisms") living in a two-dimensional regular lattice of linear length, $L = 30$, with approximately $0.90L^2$ randomly distributed nonempty entries (population size $N \approx 800$ individuals with average $1{:}\,1$ sex ratio) and periodic boundary conditions (i.e., a torus).

Each chromosome has three sex-limited loci. Locus one $(pref)$ is expressed in females, and codes for a preference gene with two alleles: allele 0 indicates that the female has an innate preference for males with trait x; allele 1 indicates the preference is for males with trait y. The second biallele locus (soc) is also expressed in females and codes for a "social" gene: allele 0 indicates that (noncopier) females will mate according to their innate preference dictated by the allele at locus one $(pref)$, whereas allele 1 specifies that (copier) females rely on socially acquired information that prevails over the fixed genetic preference (see, e.g., Vakirtzis 2011). Neither loci affect female survival or fecundity (but see below). Finally, the third locus $(trait)$ affects male survival and specifies the male trait: type x has allele 0; type y has allele 1.

2.3.2 Life Cycle and Mating Decisions

Generations are discrete and nonoverlapping. At the start of each generation, each cell in the lattice is randomly occupied by a female, by a male, or remains empty. The initial population at generation t_0 is seeded with frequencies $p_{pref}^{t_0}$, $p_{soc}^{t_0}$ and $p_{trait}^{t_0}$ for allele 1 at each locus. Only Moore neighborhood sexual interactions are allowed, with eight cells surrounding a central cell on the square lattice (Fig. S1).

At each time step, we pick a random position in the lattice occupied by a virgin (target) female and define its Moore neighborhood. A neighbor male courts the female and she can accept or reject mating based on her preference. Noncopying females rely on their innate preference and always act as demonstrator females. Naïve-copying females ("observers") mate and act as demonstrator females only after acquiring social information (see Fig. S2). When the target female is a demonstrator female, she will accept mating if courted by a male whose phenotype matches her innate (noncopier) or learned (copier) preference. If, on the other hand, there is a conflict between the female preference and the male trait, she can eventually mate according to her cost of choice relative to random mating (Pomiankowski 1987). Note that any female might encounter a biased sample of males in her neighborhood, which can result in her choosing nonpreferred males. Therefore, female preference (i.e., the sensory and behavioral components that influence females to mate differentially with certain male phenotypes; Heisler et al. 1987) should be distinguished from mate choice (i.e., the outcome of interactions among individuals resulting in the a posteriori deviation from random mating; see Appendix S1—Matting pattern). A choosy female shows unequal preferences and mates with the nonpreferred male with probability $P = 1 -$ "choice cost". Thus, choosiness increases linearly with cost and is maximum when ("choice cost"$= 1$, whereas if "choice cost" $= 0$, the female shows an equal preference for any male type. We assumed this cost to be the same for copier and noncopier females. We also assumed that females do not incur in viability or fecundity costs for being too discriminant (e.g., "choice cost" > 0.5).

At the end of each time step, the target female can either mate or remain unmated. If she mates, naïve-copying females in the Moore neighborhood imprint on her choice. Two processes of cultural transmission are assumed (Mesoudi 2011, table 3.1): "one-to-many" where the decision taken by the mating female influences all others naïve-copying females in the Moore neighborhood; "one-to-one" where only one randomly chosen naïve-copying female in the Moore neighborhood is influenced. Therefore, like both Kirkpatrick and Dugatkin (1994), and Servedio and Kirkpatrick (1996), we assumed only positive social information. The routine repeats itself through different random sites in the lattice until 85% of females have mated. This decision rule was made for simulation convenience: it allows for a relatively fast cycling through the lattice while at the same time keeping a high proportion of mated females at each generation. The assumption of horizontal cultural transmission, where at the beginning of each generation noncopiers are the only demonstrator females, puts some limitations in the model because the frequency of the copying allele cannot reach 100% (the first "social" female that later acts as a demonstrator female necessarily needs to observe the mate choice of at least one noncopier female). A stop criterion in the algorithm was $p_{soc} \geq 0.95$. Females mate only once, but any male can potentially mate with more than one female.

2.3.3 Offspring Generation

After mating, recombination occurs in the diploid stage followed by mutation. With probability r, the crossover operation picks one point m ($m = 1, 2$) at random from each parental chromosome to form one offspring chromosome by taking all alleles from the first parent up to the crossover point, and all alleles from the second parent beyond the crossover point. All mating pairs produce the same number of progeny, and a new generation starts by randomly allocating the offspring in the lattice (keeping $N \approx 800$). Each haploid individual is assigned to be a female or a male with equal probability. Mutations happen at any locus at rates μ_{pref}, μ_{soc}, and μ_{trait}.

Natural selection was incorporated in the form of viability, with selection coefficients $0 \leq s_x$, $s_y < 1$ for a type $x(y)$ male, respectively. Viability selection $1 - s_x\left(1 - s_y\right)$ was introduced as hard selection (Christiansen 1975). Namely, we assumed that after migration to a random cell in the grid a male's probability of survival before reproduction equals its viability. We usually assume that common resident males in the population have trait x. Furthermore, we generally assumed that there is no direct fitness cost to the learned preference (so the copying allele is neutral), but we also considered some cases when copier females pay a slight viability cost $1 - s_c$ relative to that of noncopier females (making the copying allele mildly deleterious). This might be a likely scenario because there are costs associated to the capacity of learning (Mery and Kawecki 2003, 2004; Barnard et al. 2006; Burger et al. 2008).

Simulation programs were implemented in MATLAB (version R 2015) algebra environment using tools supplied by the Statistics Toolbox (MATLAB and statistics toolbox Release 2015). Routines used to run the analyses are provided in the Supporting Information.

2.4 Results and Discussion

2.4.1 Case 1: Evolution of MCC with fixed innate preferences

To facilitate comparisons with Servedio and Kirkpatrick (1996), we first suppose that innate female preference does not evolve. To define preference strength in the population, we proceeded as follows. Allele 1 at the *pref* locus starts with frequency $p_{pref}^{t_0}$ (i.e., a fraction $1 - p_{pref}^{t_0}$ of noncopier females would favor mating with resident x males) and no mutation ($\mu_{pref} = 0$). To avoid evolution at this locus when $0 < p_{pref}^{t_0} < 1$, we reset allele frequencies in each offspring generation by randomly filling this locus with both alleles according to their initial frequencies. This also avoids the building up of linkage disequilibrium with the $pref$ locus.

To check spreading conditions for trait *y* and the copying allele, extensive computer simulations were performed using a wide range of parameter values for all combinations of innate preference ($p_{pref}^{t_0} = 0.1, 0.2, \dots, 0.9$), selection coefficients against the resident male ($s_x = 0, 0.05, \dots, 0.35$), and cost of choice (“choice cost” $= 0.3, 0.5, 0.7$). Table S1 (one-to-many horizontal cultural transmission) and Table S2 (one-to-one horizontal cultural transmission) summarize these results. Conditions for invasion of the copying allele are the same under either cultural transmission rules, but the one-to-one rule results in a lower equilibrium frequency for the copying allele (Fig. S3). In what follows, we focus on results for the one-to-many rule.

The parameter “choice cost” plays an important role in the evolutionary fate of the copying allele. If female choosiness is weak (“choice cost” $= 0.3$), the copying allele never spreads. With intermediate choosiness (“choice cost”$= 0.5$), the copying allele may spread if $p_{pref}^{t_0} \leq 0.6$ and natural selection against the resident male x is relatively strong (Figure 1A). Finally, at strong choosiness (“choice cost”$= 0.7$), the copying allele spreads if selection against the resident male x is strong enough and innate preference ranges between $0.3 \leq p_{pref}^{t_0} \leq 0.8$ (Fig. 1B and C). Our model also confirms (not shown) that the copying allele spreads even when there is mild direct selection against it (i.e., $s_c \approx 0.01 - 0.001$; see Servedio and Kirkpatrick 1996). In Tables S1 and S2, we

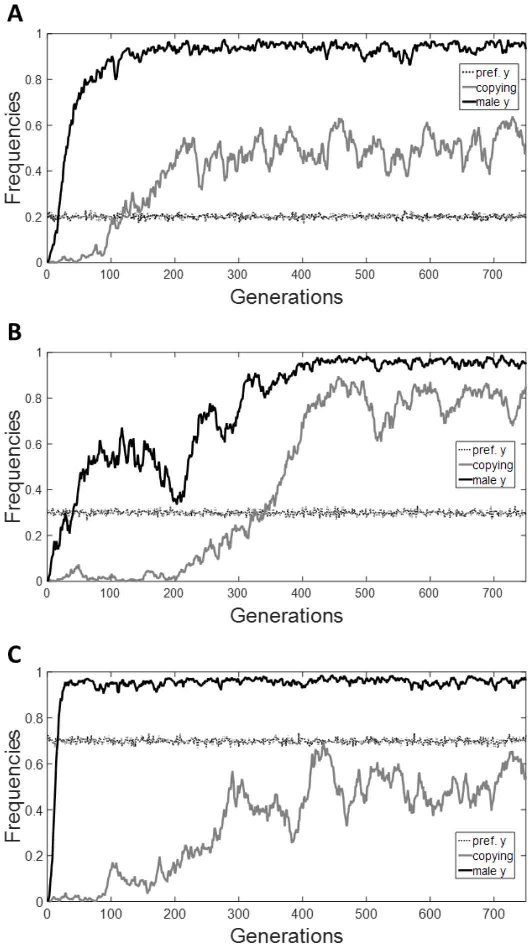

Figure 1. Evolutionary fate of the fitter trait (male y) when the copying allele can coevolve but innate preference (pref. y) remains fixed throughout generations. In all cases, the initial frequencies and mutation rates were $p_{trait}^{t_0} = 0$ and $\mu_{trait} = 0.01$ (trait y), $p_{soc}^{t_0} = 0$ and $\mu_{soc} = 0.001$ (copying allele), and recombination rate, $r = 0.05$. A plots a sample simulation where 80% of the noncopier females prefer the common unfit resident male x (i.e., $p_{pref}^{t_0} = 0.20$, $\mu_{pref} = 0$, $s_x = 0.35$ and $s_y = 0$) and "choice cost" $= 0.5$. B plots a case where $p_{pref}^{t_0} = 0.30$ and $\mu_{pref} = 0$, $s_x = 0.30$, $s_y = 0$ and "choice cost" $= 0.7$. Parameter values for C were $p_{pref}^{t_0} = 0.70$ and $\mu_{pref} = 0$, $s_x = 0.20$, $s_y = 0$ and "choice cost" $= 0.7$.

assumed $r = 0.05$, but increasing the recombination rate does not substantially change the results (not shown).

In those cases where the copying allele spreads, the equilibrium frequency of the copying allele decreases with increases in the frequency of the fixed innate preference for the novel trait (Fig. S3). The behavior of the system (Fig. 1) matches Servedio and

Kirkpatrick (1996), that is, the system evolves at two timescales: the trait evolves first, and is followed by a slower evolution of the copying allele. Most importantly, the time lag between timescales varies according to parameter values. When noncopier females tend to prefer resident males ($p_{pref}^{t_0} < 0.5$), the new trait and the copying allele increase in frequency in parallel (Fig. 1A and B), whereas when noncopier females prefer introduced males ($p_{pref}^{t_0} > 0.5$), the copying allele spreads only once the new trait has invaded (Fig. 1C). This suggests that MCC might reinforce invasion by a novel trait when natural selection (viability) against resident males opposes sexual selection (innate preference of noncopier females). To verify this, we ran simulations that purposefully avoided the evolution of the copying allele (i.e., $p_{soc}^{t_0} = 0$, $\mu_{soc} = 0$) under those conditions where the allele spread when coevolving with the introduced trait (Table S1). See Figures 2–3 for some numerical examples. As predicted, the equilibrium frequency of the trait ($\hat{p}_{trait}$) was lower without MCC when noncopier females prefer the resident male (cf., Figs. 2A–C and B–D). On the other hand, there was little change in $\hat{p}_{trait}$ when innate preference of noncopier females tends to favor the novel male trait (cf., Figs. 3A–C and B–D).

It appears, therefore, that MCC is adaptive (i.e., a strategy that leads the population to a higher relative fitness) because it helps the invasion of an overall fitter trait when innate preference goes against its invasion. Note, however, that the copying allele spreads through indirect selection and does not increase the likelihood of invasion by the new trait. This is the case because copier females copy both types of choices from the noncopiers: the choice of the novel male and the choice of the resident male. It is only the stronger (learned) preference of copier females toward the high-fitness males that increases the equilibrium frequency of the novel trait (Appendix S1).

A potential caveat of the previous conclusion is that the situation could be reversed when innate preference tended to favor a novel trait that has lower viability. For instance, we can envisage a situation where populations are locally adapted to different environments (Kawecki and Ebert 2004) and immigrant males entering a given population have a lower viability, but females might favor mating with these males (Bárbaro et al. 2015). Setting “choice cost” = 0.7, we ran simulations assuming

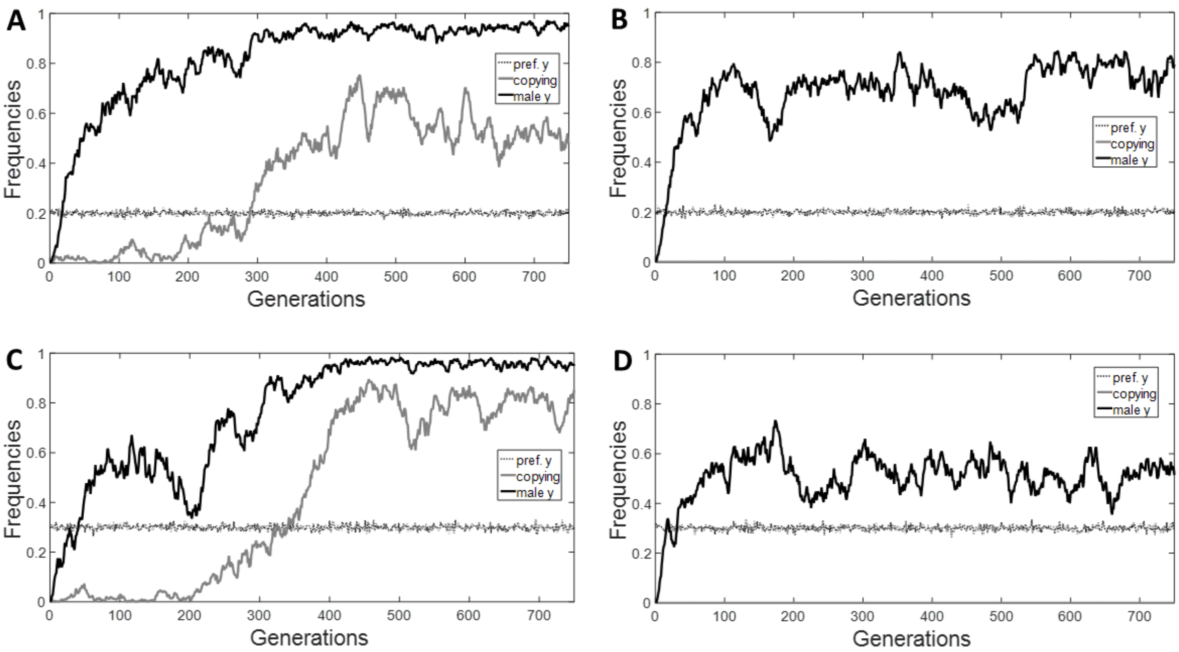

Figure 2. Evolutionary fate of the fitter trait (male y) with (panels A, C) and without (panels B, D) coevolution of the copying allele when noncopier females have a fixed innate preference (pref. y) favoring the common resident male x. In all cases, the new trait was introduced with $p_{trait}^{t_0} = 0$ and $\mu_{trait} = 0.01$, and recombination rate was $r = 0.05$. The copying allele was introduced with $p_{soc}^{t_0} = 0$ and allowed to mutate ($\mu_{soc} = 0.001$) or not ($\mu_{soc} = 0$). A plots a sample simulation with $\mu_{soc} = 0.001$ where 80% of the noncopier females prefer trait x (i.e., $p_{pref}^{t_0} = 0.20$, $\mu_{pref} = 0$, $s_x = 0.30$, and $s_y = 0$) and "choice cost" = 0.5. B is the same as A, but $\mu_{soc} = 0$. Parameter values in C were $\mu_{soc} = 0.001$, $p_{pref}^{t_0} = 0.30$, $\mu_{pref} = 0$, $s_x = 0.30$, and $s_y = 0$, and "choice cost" = 0.7. D is the same as C, but $\mu_{soc} = 0$.

$p_{pref}^{t_0} > 0.5$ with $s_x = 0$ and $s_y > 0$ to see whether coevolution of the copying allele and the "invading" trait could increase equilibrium frequency of the latter. In some situations, the copying allele spread to frequency $\hat{p}_{soc} \approx 0.30$, but the equilibrium frequency of the novel trait remained essentially the same with and without MCC (results not shown). Therefore, the former conclusion that MCC is adaptive under some scenarios seems to be sound.

Once established in the population, MCC can cause a strong positive frequency-dependent advantage toward resident males, making it difficult for a fitter male to invade (Kirkpatrick and Dugatkin 1994; but see Agrawal 2001; Santos et al. 2014). We tested this for those conditions in Table S1 where the copying allele spreads, but now assumed different initial frequencies ($p_{soc}^{t_0} = 0.2, 0.4, 0.6, 0.8$). Usually, the frequency of the

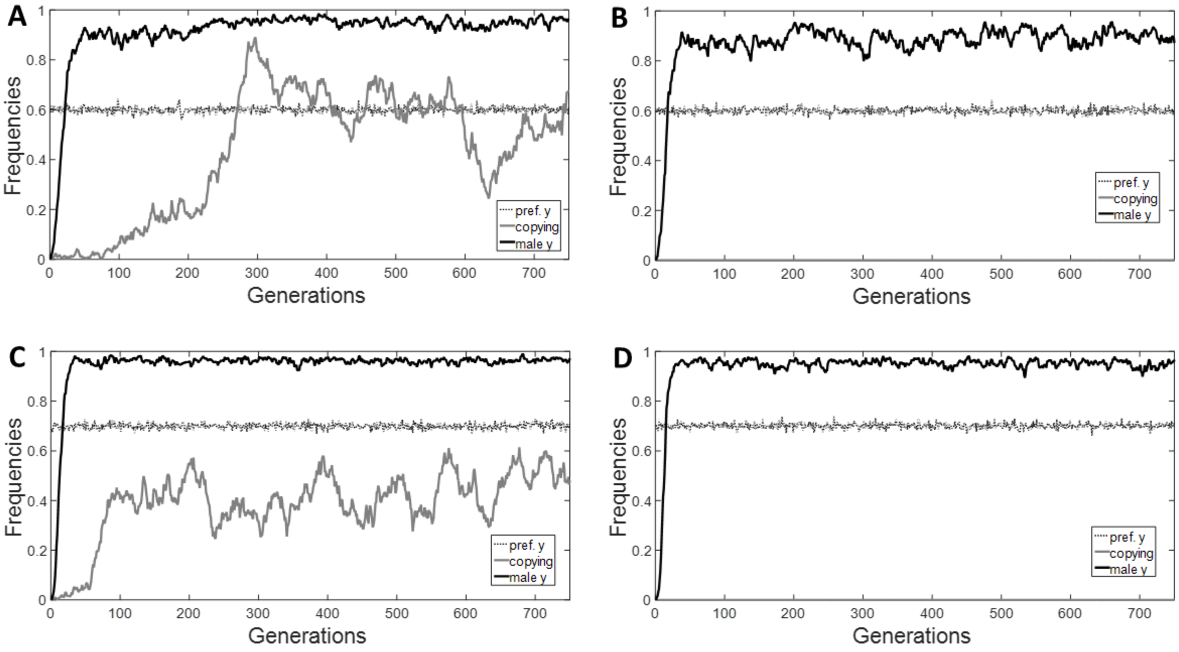

Figure 3. Evolutionary fate of the fitter trait (male y) with (panels A, C) and without (panels B and D) coevolution of the copying allele when noncopier females have a fixed innate preference (pref. y) favoring the introduced male y. In all cases, the new trait was introduced with $p_{trait}^{t_0} = 0$ and $\mu_{trait} = 0.01$, and recombination rate was $r = 0.05$. The copying allele was introduced with $p_{soc}^{t_0} = 0$ and allowed to mutate ($\mu_{soc} = 0.001$) or not ($\mu_{soc} = 0$). A plots a sample simulation with $\mu_{soc} = 0.001$ where 40% of the noncopier females prefer trait x (i.e., $p_{pref}^{t_0} = 0.60$, $\mu_{pref} = 0$, $s_x = 0.15$, and $s_y = 0$) and 'choice cost' $= 0.7$. B is the same as A, but $\mu_{soc} = 0$. Parameter values in C were $\mu_{soc} = 0.001$, $p_{pref}^{t_0} = 0.70$, $\mu_{pref} = 0$, $s_x = 0.25$, and $s_y = 0$, and “choice cost” $= 0.7$. D is the same as C, but $\mu_{soc} = 0$.

copying allele drops at early generations and then rises in frequency following (and helping; see above) the spread of the new trait (Figure S4). Therefore, our results do not support the idea that MCC hampers the establishment of a novel trait in the population. The same result is obtained if the frequency of the copying allele is kept constant through time.

2.4.2 Case 2: Evolution of Both MCC and Innate Preference

A general result from our model is that Fisherian sexual selection, where innate female preference coevolves with the novel male trait, makes the invasion of the copying allele very unlikely (Table S3). This happens because (i) innate preference for the novel trait quickly drops in frequency ($p_{pref} \rightarrow 0$) making the invasion of the trait more difficult and, hence, the copying allele cannot hitchhike with the new trait allele (Fig. S5); or because (ii) viability selection can overcome the initially strong sexual selection against the novel trait, and its invasion produces a concomitant coevolution of innate preference toward y males ($p_{pref} \to 1$; Appendix S1). These findings agree with previous results that assumed fixed preferences: a strong innate preference toward resident males x, or toward the novel trait y, make it very difficult for the copying allele to spread (Tables S1 and S2; see also Fig. S3).

2.5 Concluding Remarks

In the model by Servedio and Kirkpatrick (1996), where female innate preferences do not evolve but are biased toward the high-fitness male trait, the copying allele spreads by hitchhiking with the male trait allele. This raises the question of why we do not observe the spread of the copying allele once the novel trait has invaded and innate preferences are highly biased toward this trait. The reason probably is that the strength of preferences is modeled differently in both cases. Servedio and Kirkpatrick (1996; see also Kirkpatrick and Dugatkin 1994) model preferences by quantifying how much more likely a female is to mate with a given male, and are (in theory) upper unbounded: copier females replace their innate preference by an effective preference due to the proportion of matings observed (eq. 2 in Servedio and Kirkpatrick 1996), and can express a preference toward the high-fitness trait that is higher than that of noncopier females. In our model, however, preferences are bounded and depend on allele frequencies: when coevolving with the spread of the novel male trait, female innate preference hitchhikes to its maximum frequency $p_{pref} \approx 1$ (barring mutation), and the proportion of mating with high-fitness males is larger for noncopier than copier females (see Appendix S1). Therefore, if MCC evolves by indirect selection we have to add additional assumptions (complications) to our model to understand how genetic variation in female preferences is maintained. An obvious choice is to assume a higher mutation rate at the *pref* locus (i.e., $\mu_{pref} \gg \mu_{soc}$) — which does not seem to be very realistic — as this would keep the innate preference toward the novel male trait segregating at intermediate levels (Fig. S6).

In an influential review, Kirkpatrick and Ryan (1991) suggested that there was considerable circumstantial evidence showing that innate preferences evolve because of their direct effects on female fitness rather than the genetic effects on offspring resulting from mate choice. Our assumption that innate preferences do not alter female survival or fecundity and might coevolve with the male traits violates this conclusion. Nevertheless, a recent review by Fowler-Finn & Rodríguez (2016) comprising 43 studies on trait — preference covariance, identified a substantial number of papers (27) that detected such covariance, and presence of genetic variation in innate mate preferences was the main predictor (but see also Greenfield et al. 2014). This suggests that Fisherian sexual selection might be widespread, and also that there might be a long-term balance between the loss of genetic variation and other forces such as mutation, migration, and changes in the direction of selection that maintain genetic variation for preference (Bakker and Pomiankowski 1995; Greenfield et al. 2014). This variation is a critical condition for the evolution of MCC in our model.

Along with MCC, two other mechanisms may allow females to change innate mate preferences: sexual imprinting and personal experience (Verzijden et al. 2012). Through sexual imprinting, females acquire a mate preference usually from their father or mother at an early age. Later in life, personal experience allows females to learn from direct evaluation of the male’s courtship performance. Both mechanisms may override female innate preference with consequences to sexual selection (Verzijden et al. 2005; Dukas 2013; Servedio and Dukas 2013), but they do not create informational cascades. Informational cascades, the sequential transfer of information in a network of individuals, can only be generated in species where females learn from observing the choices made by others using MCC (Gibson and Hoglund, 1992; Giraldeau et al., 2002; Kendal et al., 2005; Rieucau and Giraldeau, 2011). MCC could lead to small or large informational cascades, depending on the proportion of copier females in the population, which is an interesting regulatory system for the population.

In conclusion, if genetic variation in innate preference persists in the population and females do not incur high viability or fecundity costs for being too discriminant, the spread of the copying allele is easier when innate preference is biased toward the low fitness, more abundant resident males. In this case, MCC can be an adaptive behavior even if the copying allele itself is neutral or mildly deleterious.

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Chapter 3

Social learning by mate-choice copying increases dispersal and reduces local adaptation

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Author contributions: All authors helped to conceive the problem and contributed to the design of the study. MS wrote the code to the mathematical model, ran the simulations, analysed the data, and wrote the first draft of the manuscript. All authors contributed substantially to the writing.

All figures, tables, and other sections denominated with the letter "S" can be found in Appendix II.

3.1 Abstract

1. In heterogeneous environments, dispersal may be hampered not only by direct costs, but also because immigrants may be locally maladapted. While maladaptation affects both sexes, this cost may be modulated in females if they express mate preferences that are either adaptive or maladaptive in the new local population.

2. Dispersal costs under local adaptation may be mitigated if it is possible to switch to expressing traits of locally adapted residents. In a sexual selection context, immigrant females may learn to mate with locally favoured males. Mate-choice copying is a type of social learning, where individuals, usually females, update their mating preferences after observing others mate. If it allows immigrant females to switch from maladapted to locally adapted preferences, their dispersal costs are mitigated as mate choice helps them create locally adapted offspring.

3. To study if copying can promote the evolution of dispersal, we created an individual-based model to simulate the coevolution of four traits: copying, dispersal, a trait relevant for local adaptation, and female preference. We contrast two scenarios with copying — either unconditional or conditional such that only dispersers copy — with a control scenario that lacks any copying.

4. We show copying to lead to higher dispersal, especially if copying is conditionally expressed. This leads to an increase in gene flow between patches and, consequently, a decrease in local adaptation and trait-preference correlations.

5. While our study is phrased with female preference as the learned trait, one may generally expect social learning to mitigate dispersal costs, with consequent feedback effects on the spatial dynamics of adaptation.

Keywords: Dispersal, individual-based simulations, lek paradox, local adaptation, mate-choice copying, sexual selection, spatial dynamics.

3.2 Introduction

Mate-choice decisions may be based on innate preferences, individual experience or on the observed choices of others. The last of these, mate-choice copying, is a type of social learning that involves updating mate preferences after observing others' choices (Dugatkin, 1992, 1996; Pruett-Jones, 1992; Wade & Pruett-Jones, 1990). Females may prefer either the successful males themselves (Bowers et al., 2012) or generalize their preferences to males with similar phenotypes (‘trait copying’ or ‘mate-choice copying generalization’; Bowers et al., 2012; Brooks, 1998; Drullion & Dubois, 2008; Godin et al., 2005; Mery et al., 2009; Swaddle et al., 2005; White & Galef Jr., 2000; Witte & Noltemeier, 2002).

Mate-choice copying (synonymous with ‘mate copying’; Danchin et al., 2020) is documented in many taxa (Davies et al., 2020; Jones & DuVal, 2019), e.g. birds (Kniel et al., 2017; Swaddle et al., 2005), fish (Dugatkin & Godin, 1992; Heubel et al., 2008; Schlupp & Ryan, 1997; Witte & Ryan, 1998), mammals (Galef et al., 2008; Kavaliers et al., 2017), insects (Dagaeff et al., 2016; Germain et al., 2016; Mery et al., 2009; Monier et al., 2018) and spiders (Fowler-Finn et al., 2015). Empirical studies typically test whether copying occurs in a species or aim to evaluate conditions that make copying favoured over innate preferences. Theoretical studies have complemented the picture by exploring when copying is expected to invade and spread (Dubois et al., 2012; Losey et al., 1986; Pruett-Jones, 1992; Santos et al., 2017; Servedio & Kirkpatrick, 1996; Stöhr, 1998) and how copying affects the direction and strength of sexual selection (Agrawal, 2001; Kirkpatrick, 1982; Santos et al., 2014)

Mate-choice copying is argued to be adaptive because it allows the female to mate with higher quality mates (Gibson & Höglund, 1992; Nordell & Valone, 1998; Valone & Templeton, 2002; Danchin et al., 2004; Dugatkin, 2005; Uehara et al., 2005; Wagner & Danchin, 2010; reviews Vakirtzis & Roberts, 2012, Varela et al., 2018). But this yields another question: why is copying needed to achieve a good outcome, i.e. why should any female not already possess preferences for best traits? If temporal changes are fast, i.e. the best mate for a given female varies through time (Ingleby et al., 2010), females might need updated information regarding better adapted (Getty, 2014; Wade, 2014) and/or more popular males (Kokko et al., 2007). Theoretical work that focuses on the ‘informedness’ of individuals has, indeed, considered age effects. Young females are conceivably inexperienced, and although they may possess innate preferences, observing and copying experienced females' behaviour can be of benefit; still, it is not always clear why informedness should increase with age, i.e. why innate preferences are insufficient.

Older and experienced females may also opt for mate-choice copying if, for example, their previous breeding attempt failed (Amlacher & Dugatkin, 2005; Danchin et al., 2008; Hill & Ryan, 2006). In both cases, the probability of copying is argued to increase with the difficulty of the discrimination task (Nordell & Valone, 1998).

Irrespective of age and experience, some individuals may be poorly informed in settings where spatial variation in environmental demands combines with local adaptation and gene flow (Holman & Kokko, 2014). Here, immigrant females may be uninformed of locally best traits. We show that this creates population-level feedback where mate-choice copying may facilitate the evolution of dispersal itself.

The reasoning is the following. Migrants experience an additional cost of dispersal when there is spatial variation in the environment (Berdahl et al., 2015; Blanquart & Gandon, 2014), because their traits are shaped by past selection in their natal environment, with unknown (and likely worse) performance in the environment they disperse to. For females, an additional complication is that their mate preferences—if genetically determined—may be similarly shaped by past selection. If preferences (and not just traits) are locally adapted, immigrant females may mate suboptimally. This problem can be minimized through copying, assuming that dispersal is not so strong that immigrants swamp locally adapted females, which would lead to uninformed immigrants copying each other's choices. Copying thus allows immigrant-origin lineages gain locally adapted alleles and reduces the costs of dispersal. As shown below, it also ultimately reduces the degree of local adaptation via improved gene flow (reduction of genetic differentiation between different habitats).

3.3 Material and Methods

We model obligately sexual, haploid populations (which allows us to model one allele per locus, as our focus is not on effects of genetic dominance; see Kokko, 2007), initialized in a locally adapted state with only short-distance dispersal (a negative exponential dispersal kernel with a low mean). We thereafter allow the dispersal kernel to evolve in populations with or without a mate-choice copying locus. This locus, if present, has two alleles c (for innate preference) and C (for copying), only expressed in females. We contrast three scenarios. In the unconditional scenario, females with the C allele copy the mate choice of others at every copying opportunity; in the conditional scenario, they only do so if they have emigrated from their natal patch. In the control scenario, females only express innate preferences (no mate-choice copying evolves), while dispersal still evolves.

The population inhabits a toroid world (a doughnut-shaped continuous surface, each side having length 1). The benefit of using a toroid world is to avoid the need to specify what happens if individuals encounter the edge of the modelled world; under toroid assumptions, they can always continue moving in any direction even if the world is finite. The world is divided into 25^2 patches with environmental heterogeneity that translates into a spatially varying and positively autocorrelated optimum for individuals' trait values (note that we include spatial but not temporal variation of the environment). Positive spatial autocorrelation ensures that neighbouring patches do not differ very strongly from each other (details described in step 1 below); in other words, it allows the scale of environmental variation to be broader than a single patch. This is of benefit since broadly similar conditions across several patches, combined with finite dispersal distances, allow local adaptation to proceed and overcome the effects of drift—even if local patches (demes) themselves are kept small for the sake of realistic mate choice (females do not evaluate very many males before mating; Roff & Fairbairn, 2014).

We model genotypes with five different loci (S, T, P, C, D), some of which have sex-limited expression. The S locus determines sex, with alleles 0 (for females) and 1 (for males). The T locus (T stands for trait) has a pleiotropic effect. In both males and females, its value (real number between 0 and 1) relative to an environmental (spatially varying) optimum determines viability; in males, it additionally codes for a phenotype directly observable to females. The P locus likewise takes allelic values between 0 and 1 but is only expressed in females; it specifies a preference for specific phenotypes of males. Females prefer males whose trait locus matches the female's preference locus, which allows females to show local adaptation for locally adapted male traits. The C locus, with 2 alleles c and C, is likewise only expressed in females and controls female copying behaviour. Finally, the D locus, expressed in all individuals, determines the mean of the individual's dispersal kernel, with values between 0 and 1 (where 1 would imply a mean distance equal to the length of the entire world)

Each run of the simulation proceeds as follows: (1) creation of the patch-specific environmental values, (2) population initialization, (3) survival, (4) dispersal, (5) mate choice by females and (6) reproduction. The simulation starts following steps 1 through 6, thereafter repeating steps 3 through 6 for each generation. Note that the order of the events dictates that viability selection is applied at the natal patch. Generations are non-overlapping.

In step 1, to simulate environmental heterogeneity, an environmental value is attributed to each patch using the algorithm described in Holman and Kokko (2014) that creates a matrix of environmental values with an adjustable spatial autocorrelation. The algorithm first generates a random value between 0 and 1 for each patch, then, for $25^2 \times 100$ iterations (a large enough number so that each patch, on average, experiences 100 impacts), it updates a randomly chosen patch p by setting its environmental value E_p to $\mu_p + r\,(1 - \beta)$, where μ_p is the mean environmental value of the eight patches surrounding patch p. These successive iterations bring the autocorrelation between neighbouring patches to a level that is controlled by the parameter β ($0 \leq \beta < 1$). $\beta = 0$ implies there is no spatial autocorrelation, and when $\beta \approx 1$, neighbouring patches are very similar to each other. After all iterations, the resulting matrices were rescaled to have mean environmental value 0.5 and standard deviation 0.2 (see Figure S1 in Supporting Information for examples)

In step 2, we give 20,000 young individuals random coordinates $0 \leq x,y < 1$. The sex of each individual is randomly chosen (S locus is randomized to be 0 or 1), and we assume initial local adaptation with the following procedure. Values for T and P alleles are drawn randomly from a Gaussian distribution with mean E_p (where p is the patch that the individual's coordinates imply it resides in) and standard deviation 0.05. Values that fall below 0 or exceed 1 are given a value of 0 or 1 respectively. Mate-choice copying is initially absent, i.e. all individuals are initialized with the c allele at the copying locus; C alleles are introduced later via mutation (see below). For the dispersal-determining D locus, individuals are initialized with random values drawn from a uniform distribution ranging between 0 and 0.005.

Viability selection (step 3) is applied in a density-dependent manner. At most 16 individuals survive in each patch. The value is chosen to allow each female to observe a low number of males and females (we expect patches to contain close to 8 females and 8 males; in nature, examples of more than 10 males sampled before mating appear rare; Roff & Fairbairn, 2014), and also to produce a global population of maximally 10,000 adults. No viability selection occurs in patches containing up to 16 individuals. In patches with more than 16 individuals, we first compute an adaptedness value for each individual i in patch p:

$$v_{\mathrm{A}i} = e^{-S_{\mathrm{N}}\left(a_{\mathrm{T}i} - E_p\right)^2}, \tag{1}$$

where $S_{\mathrm{N}} > 0$ scales the strength of natural selection and $a_{\mathrm{T}i}$ is the allele value of individual i at the T locus. This expression is close to 1 when the difference between $a_{\mathrm{T}i}$ and E_p is small, indicating little mismatch between the phenotype and the environment, and declines at a rate controlled by S_{N} as the mismatch increases. Actual survival probability depends on $v_{\mathrm{A}i}$ relative to competitors, and to generate stochasticity that allows mild differences in individual $v_{\mathrm{A}i}$ to translate to different rank orders when competing for the 16 survival ‘slots’, we compute the relative success $v_{\mathrm{A}i}*$ for individual i by drawing from an exponential distribution with mean $v_{\mathrm{A}i}$. At each generation, the 16 individuals with the highest $v_{\mathrm{A}}*$ of each patch are retained, while the others die.

In step 4, dispersal distances are drawn for each individual from a negative exponential distribution with a mean equal to the allelic value at the D locus. The direction of dispersal is random. The toroid arrangement of the patches ensures that the dispersal kernel can be applied even if dispersal distances exceed 1, the width of the world. More importantly (given that very long-distance dispersal is unlikely), short dispersal distances may mean not leaving the natal patch; coordinates are still updated, but the environmental value that the individual experiences does not change. We apply dispersal mortality of 0.05 to each individual whose new coordinates bring it outside its natal patch.

In step 5 (mate choice), females only perceive males who reside in the same patch as potential mates. Females only mate once; males may mate multiply. While we impose no restrictions on male mating capacity, their realized success is limited by the fact that males can only be chosen by females residing in the same patch. Within each patch, non-copier females mate first, after which copier females choose mates based on observations of all non-copier females' matings. There are three categories of non-copiers: (a) all females with the c allele, (b) females with a C allele who have not left their natal patch in the conditional scenario and (c) females who attempt to copy but their patch offers no non-copier female whose behaviour they could observe. Non-copier females (of any category) observe all the males in their patch and preferentially mate with a male whose value at the T locus is close to the female's value at her P locus. Specifically, each non-copier female *f* assigns a preference value $v_{\mathrm{P}fm}$ for each male m according to the equation:

$$v_{\mathrm{P}fm} = e^{-S_{\mathrm{S}}(a_{\mathrm{P}f} - a_{\mathrm{T}m})^2}, \tag{2}$$

where $S_{\mathrm{S}} \geq 0$ scales the strength of sexual selection that female choice can impose on males, $a_{\mathrm{P}f}$ is the female's allelic value at the P locus and $a_{\mathrm{T}m}$ is the male's allelic value at the T locus. The expression reaches its highest possible value, 1, when the male trait perfectly matches the female's preference, and declines towards zero for increasing levels of mismatch. The probability that female f chooses male m^* in the presence of other competitors is

$$Prob(f, m^*) = \frac{v_{\mathrm{P}fm^*}}{\sum_{m=1}^{M_p}(v_{\mathrm{P}fm})}, \tag{3}$$

where M_p is the number of males in patch *p*.

A higher value of S_{S} means that females are choosier, i.e. realized matings more closely match their innate preferences. Values at the P locus do not modulate the strength of preferences, but instead indicate which phenotypes of males are preferred by each female. If $S_{\mathrm{S}} = 0$, mating is random, i.e. values at the P locus do not impact realized mate choice.

While non-copier females choose, copier females observe. We assume trait-based mate-choice copying (Danchin et al., 2018), i.e., copying females update their preferences for certain phenotypes rather than specific males (thus a male with zero success so far can become favoured should he be phenotypically similar to a male observed to mate). If choices made by non-copier females yield a single winner among the males, copier females replace, phenotypically, their innate preferences with a value that equals the T of this winner: $a^*_{\mathrm{P}f} = a_{\mathrm{T}m^{**}}$, where m^{**} is the identity of the winner. In case of a tie, one of the males is randomly chosen to be the winner, independently so for each of the copier females.

A copier female *f* then assigns the value $v_{\mathrm{P}fm}$ to each male *m* analogously to the non-copier case above,

$$v_{\mathrm{P}fm} = e^{-S_{\mathrm{S}}\left(a^{*}_{\mathrm{P}f} - a_{\mathrm{T}m}\right)^{2}}, \tag{4}$$

and the actual choice of a mate follows Equation 3 above.

In step 6, reproduction occurs in all patches with at least one male and one female. These patches produce 32 offspring each. Each offspring has a mother and a father. The mother is chosen randomly (as we assume no fecundity differences among females), and the sire is the mother's chosen mate as determined above. Breeding is density dependent with these assumptions: a female breeding in patch with a total of F_p females present will produce, on average, $32/F_p$ offspring. The expected number of offspring produced by a focal male is $32/F_p$ times the number of females who chose this male. Density dependence is relevant as it causes selection for dispersal to avoid competing with kin (Hamilton & May, 1977; Li & Kokko, 2019). Offspring are initially placed at in the same coordinates as their mothers.

For each locus, offspring inherit one allele, randomly chosen from either parent, without any linkage between loci. The T, P and D loci have a mutation probability of 0.01. Mutation is implemented by adding, to the original allelic value, a random value drawn from a Gaussian distribution with mean 0 and standard deviation 0.05, 0.05 or 0.005 for T, P and D loci respectively. Post-mutation allelic values below 0 or above 1 are assigned the value of 0 or 1 respectively. For the biallelic mate-choice copying allele, a mutation changes the value of the allele from c to C and vice versa, and the mutation probability was time-dependent: it was first set to zero for a burn-in period of 7,500 generations (such that C individuals remain absent), and to 0.001 thereafter, except for the control scenario (which never permits mate-choice copying). The ‘burning in’ phase of 7,500 generations allows for all other loci to evolve to equilibrium values, and for dispersal specifically to show a balance between avoidance of kin competition on the one hand and avoidance of dispersal costs (direct and indirect) on the other.

After breeding, all adults die, and the offspring experience viability selection as described above. Each simulation was run for 15,000 generations, 20 times for each parameter value of S_{S} (taking the values of 0, 25, 50, 75 and 100) and for each scenario (control, unconditional and conditional). From generation 7,500 onwards, we recorded the genotype and coordinates of all individuals every 2,500 generations. This census was performed after the dispersal step and its associated mortality.

To understand the impact of mate-choice copying on local adaptation, we created a local adaptation score (L) for each population. This measure quantifies the degree to which trait values, $a_{\mathrm{T}p}$, align with the environmental value in the E_p in the breeding patch:

$$L = -\frac{\sum_p \left(a_{\mathrm{T}p} - E_p\right)^2}{N}, \tag{5}$$

where N is the global number of surviving adults after dispersal. The negative sign in Equation 5 implies that high L corresponds to better local adaptation.

We compared mean allelic D values, C allele proportions, the local adaptation score L and trait-preference correlation coefficients across scenarios using one-way ANOVA tests (among all three scenarios) or Welch two samples t tests (between the conditional and unconditional scenarios). Pairwise t tests were used for comparisons of two different time points within populations. Significant differences were followed by a post hoc Tukey's honest significance test. To account for multiple testing, we applied Bonferroni corrections so that the corrected p-value = min $\{n \times p,\ 1\}$, where p is the original p-value and n is the number of hypothesis being tested. This may lead to a higher number of false negatives than other methods (McDonald, 2014), thus our conservative approach should provide a strong argument for all significant cases that we find and discuss.

The Shapiro–Wilk test of normality revealed that some of our data deviate significantly from normality. Although the tests we employed are robust against deviations from normality, as a precaution, we repeated all the analyses for the significantly non-normal data using nonparametric statistical tests. Since the results were similar, we only report parametric results.

The code for the mathematical model (programmed in C, using the GNU Scientific Library, version 2.3; Galassi et al., 2009) have been deposited in the Dryad Digital Repository (Sapage et al., 2020). The statistical analyses were done with R, version 3.6.1 (R Core Team, 2019).

3.4 Results

3.4.1 Presence of mate-choice copying increases dispersal

Scenarios did not differ with respect to dispersal at generation 7,500 (all corrected $p > 0.05$ for differences in mean D allele values; Table S1), an expected outcome since copying was not yet present in any of the scenarios. The control scenario that continued to lack mate-choice copying in subsequent generations did not show any significant difference in dispersal tendency between generations 7,500 and 15,000 (all corrected $p > 0.05$; Table S2). In scenarios where the C allele was introduced by allowing mutations to occur from generation 7,500 onwards, dispersal experienced a new evolutionary boost followed by reaching a new equilibrium (Figure 1), as evidenced by no significant difference when contrasting mean D allele values between generations 12,500 and 15,000 (all corrected $p > 0.05$; Table S2).

We only expect differences in dispersal across scenarios if $S_S > 0$: non-random mating is required for copying to mitigate the costs of dispersal that we envisage. Indeed, $S_S = 0$ yielded no diferences across scenarios (corrected $p > 0.05$; Table S1) for allelic values of D at generation 15,000, while differences emerged when $S_S > 0$: most populations with copying evolved significantly higher mean values of D than control populations (Figure 1). The exception, which we attribute to a type II error, was the comparison between the conditional and the control scenarios at $S_S = 25$, where the p-value remained marginally above significance (Tukey HSD $p = 0.05006$).

3.4.2 If sexual selection is strong, conditional copying increases dispersal more strongly than unconditional copying

Significant differences in the mean D allelic value at generation 15,000 arose between the conditional and the unconditional copying scenarios, when $S_S \geq 75$ (Figure 1). Here, conditional scenarios consistently produced more dispersal.

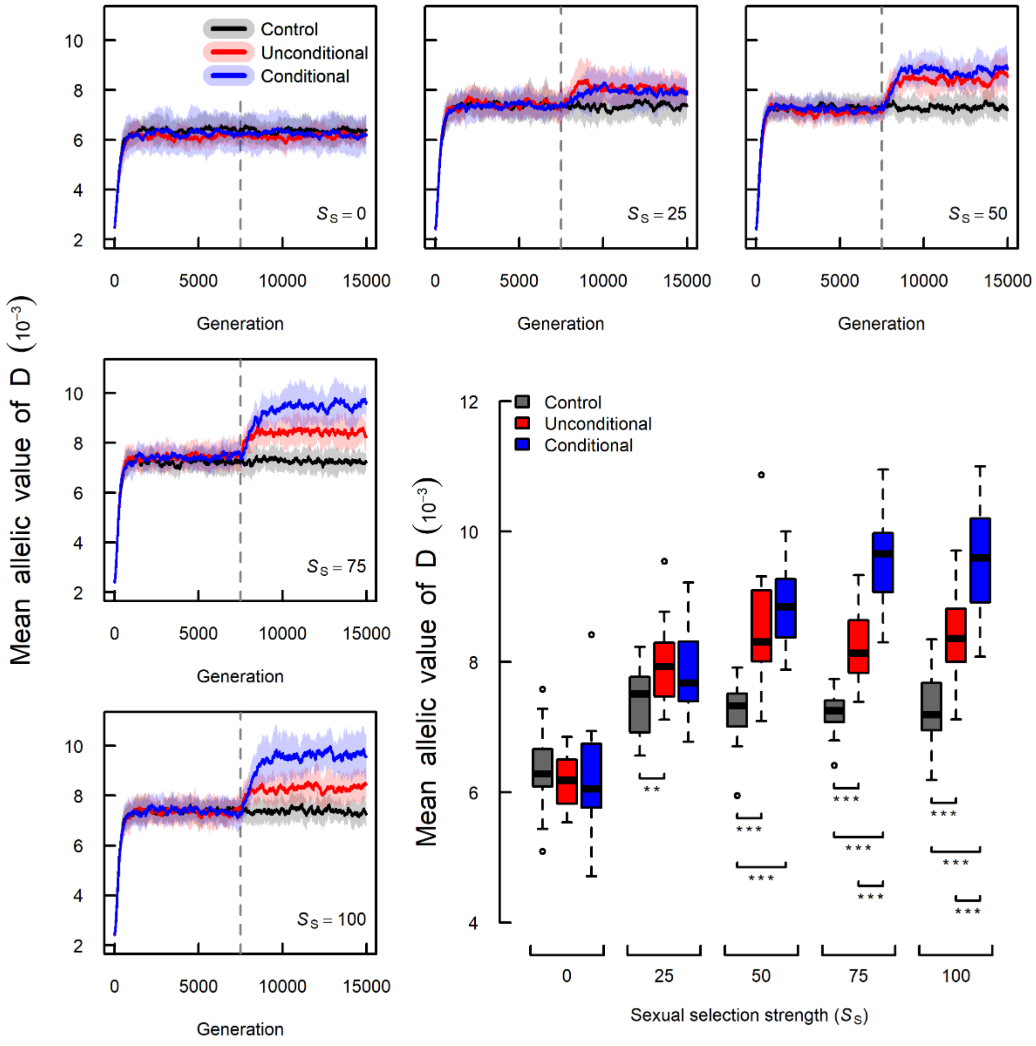

Figure 1. Mate-choice copying selects for higher dispersal. Line plots: evolution of D for each sexual selection strength (S_S) as indicated in the plot and mate-choice copying scenario (‘control’, ‘unconditional’ and ‘conditional’ as indicated by colour). Lines depict the means (across 20 simulation runs) of (population-wide) D and the standard deviations of the means (shading); the vertical line denotes the generation at which mutation towards copying is introduced, and the coevolution with dispersal begins. Box plot: distribution of D at generation 15,000. Thick lines depict the medians of the distribution of each population's mean D; box, the 25% and 75% interquartile range; vertical dashed lines, the most extreme values within 1.5 of the interquartile range; opened circles, extreme values outside of this range. Stars indicate pairwise differences between populations within each case (Tukey HSD test for cases where the ANOVA test with the Bonferroni correction was significant, see Section 2). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Other parameters: $\beta = 0.99$, $S_N = 50$.

3.4.3 Associations of the C allele and high dispersal within a population remain weak

Are the above results driven by (a) C individuals (potential copiers) themselves dispersing at higher rate than individuals with the allele c or (b) the presence of C in a population elevating dispersal for everyone? At generation 15,000, there was a tendency for C individuals to disperse more than c individuals (in both scenarios where C alleles existed), but the difference was usually too small to be significant (Figure 2). Thus, any evidence for a statistical association between C and the allelic value for D remains too weak to favour the first interpretation.

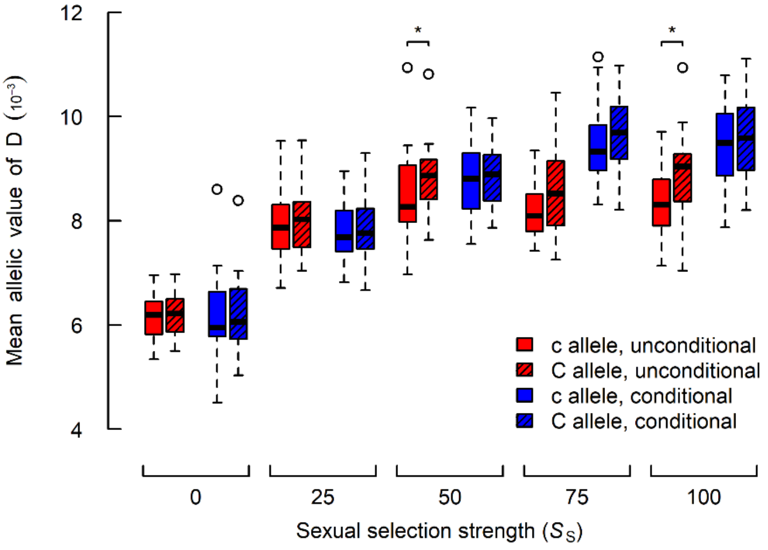

Figure 2. Overall, individuals with c and C alleles show no significant differences in dispersal across a wide range of values for the strength of sexual selection. The distribution of the mean allelic value of D at generation 15,000 over 20 simulations for each set of parameters, graphed as in Figure 1, but separately for individuals with the c or C allele. Significance was calculated using a pairwise t test: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Parameters as in Figure 1.

3.4.4 Unconditional copying only evolves if sexual selection is suitably weak; conditional copying does so across a range of strengths of sexual selection

The frequency of the C allele remained constant (did not change significantly) between generations 12,500 and 15,000 (all corrected $p > 0.05$; Table S3), thus the proportion of copiers had reached an equilibrium by generation 12,500. In conditional as well as unconditional scenarios, random mating ($S_S = 0$) should make the C allele neutral, and with sufficient time its frequency should reach 0.5. This prediction was supported: the frequency of the C allele does not differ significantly from 0.5 at generation 15,000 (Figure 3). Under nonrandom mating ($S_S > 0$), both scenarios deviated significantly from the neutral expectation, but the effect depended on the strength of sexual selection. At a low value of S_S ($S_S = 25$), the frequency of the copier allele C was elevated more in the unconditional than in the conditional scenario and exceeded 0.5 in both cases. This conclusion reversed for $S_S \geq 50$, where unconditional copying led to a significantly lower frequency of the C allele than the conditional scenario, with the former frequencies falling significantly below the neutral expectation 0.5 (Figure 3).

3.4.5 Mate-choice copying weakens local adaptation and trait-preference correlations

The local adaptation score *L* showed no significant differences between scenarios in generation 7,500 (all corrected $p > 0.05$, Table S4). As expected, control scenarios without copying also yielded no significant differences in *L* between generations 7,500 and 15,000 (all corrected $p > 0.05$; Table S5), and L also did not differ between scenarios in generation 15,000 under random mating ($S_S = 0$, $p > 0.05$). Differences emerged when mating was non-random, and they became significant once sexual selection was strong: when $S_S \geq 75$, scenarios with copying showed significantly less local adaptation than the control scenario (Figure 4a). Whether mate-choice copying operated conditionally or unconditionally did not significantly impact the local adaptation score.

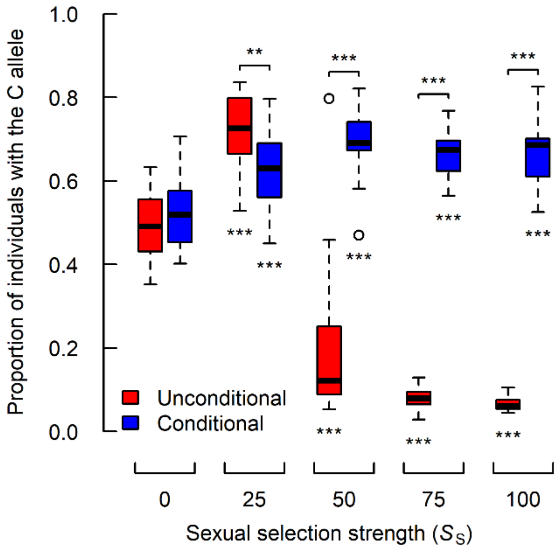

Figure 3. Unconditional copying evolves when sexual selection is weak; conditional copying evolves across a wide range of values for the strength of sexual selection. Box plot design follows the conventions of Figures 1 and 2, with data now giving the proportion of individuals with the C allele at generation 15,000 over 20 simulations for each set of parameters. Stars below each box represent significant differences from 0.5 (one-sample t test); stars above give significance for differences between populations with 'unconditional' and 'conditional' mate-choice copying for identical values of S_S (Welch two-sample t test); for both tests,*p < 0.05, **p < 0.01, ***p < 0.001. Parameters as in Figure 1.

To understand the impact of mate-choice copying on the correlation between male traits and female preferences, we calculated Pearson's correlation coefficients for the corresponding alleles. They were not significantly different between scenarios in generation 7,500 (all corrected $p > 0.05$; Table S6), control scenarios did not show any significant difference in the correlation coefficient between generations 7,500 and 15,000 (all corrected $p > 0.05$; Table S7), and the correlation coefficient did not differ between scenarios in generation 15,000 when mating was random ($S_S = 0$, corrected $p > 0.05$). Introducing sexual selection ($S_S > 0$) increased these correlations, but the magnitude of this response was scenario-dependent: at generation 15,000, control populations showed a significantly higher correlation coefficient than either scenario with mate-choice copying. This was true across all positive values of S_S (Figure 4b). The conditional scenario showed a significantly higher correlation coefficient than the unconditional one when sexual selection was weak ($S_S = 25$), but this result was reversed as S_S increased, and the reversed finding became significant for $S_S = 75$ or higher (Figure 4b).

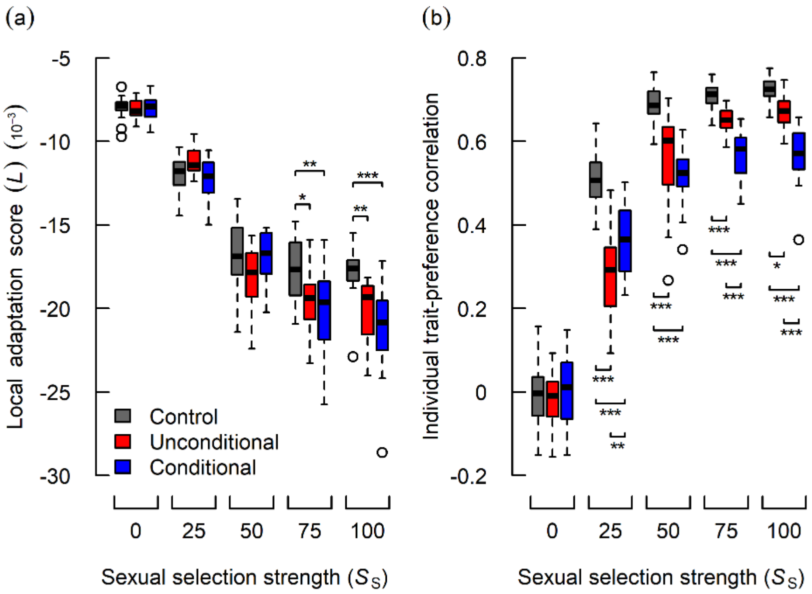

Figure 4. Mate-choice copying (a) reduces local adaptation when sexual selection is high, and (b) weakens trait-preference correlations. The box plots (design as in Figures 1–3) are complemented with stars that indicate statistical significance (*$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) of pairwise differences between scenarios at generation 15000 over 20 simulations for each set of parameters (Tuckey HSD test, calculated for cases where the ANOVA test with the Bonferroni correction was significant, see details in see details in methods). Parameters as in figure 1.

3.4.6 Sexual selection increases the effect of mate-choice copying on dispersal

To investigate whether stronger sexual selection (high S_S) can amplify the effect of mate-choice copying on dispersal, we created a linear model where the response variable was the mean D value at generation 15,000 and the predictors were S_S, the scenario, and their interaction. The control scenario was used as the baseline. We also tested a linear model with the explanatory variable S_S transformed to $\log(S_S + 1)$, because of the nonlinearity in Equation 4; the model with the transformation fitted the data better (AIC calculated by the 'extractAIC' function from the R statistical software [Venables & Ripley, 2002], without transformation: –4312; with transformation: –4393). Diagnostic plots did not show any major deviation from model assumptions. According to this model, when $\log(S_S + 1) = 0$ (i.e. $S_S = 0$), mean dispersal did not differ between control populations and unconditionally copying populations (allelic values for D; difference estimate:

-2.40×10^{-4}; $t = -1.12$; $p = 0.233$), but both were significantly higher than dispersal in conditionally copying populations (difference estimate: -4.24×10^{-4}; $t = -2.11$; $p = 0.035$). Given that all populations should evolve identically under random mating, and the previous results showed no significant difference between populations in this case (Figure 1), we regarded this particular result as an artefact of a model fit that is predominantly impacted by the evolutionary responses to higher values of S_S.

The linear model shows S_S to increase dispersal in all scenarios. An increase of one $\log(S_S + 1)$ unit creates a significant increase of 1.96×10^{-4} in the mean allelic value of D in control populations lacking copying ($t = 5.02$; $p < 0.001$), with an additional significant increase of 3.14×10^{-4} in the unconditional copying scenario ($t = 5.677$; $p < 0.001$) and an additional significant increase of 5.38×10^{-4} in the conditional copying scenario ($t = 9.756$; $p < 0.001$). Overall, the dispersal-enhancing effect of sexual selection is significantly strengthened by mate-choice copying, and it reaches its maximum effect if copying is conditional on dispersal.

3.5 Discussion

Results show that mate-choice copying increases dispersal, especially when females are choosier (sexual selection is stronger). Dispersal, in turn, has knock-on effects on gene flow and local adaptation. Gene flow becomes stronger, and local adaptation becomes weaker, when immigrant females can compensate for lack of local knowledge by copying the choices of others. Mate-choice copying also decreased the correlation between the male trait and the female preference alleles. These phenomena, taken together, counteract the depletion of male trait genetic variation by persistent innate female preferences.

The evolution of mate-choice copying can be hampered when innate female preferences coevolve with the male trait (Santos et al., 2017; Servedio & Kirkpatrick, 1996), raising the question of how sufficient variation in preferences can be maintained for a female to have any reason to switch from her innate to an observed preference (in the absence of variation, a switch should never be worthwhile). In their population-genetic models, Servedio and Kirkpatrick (1996) maintained the polymorphism in preferences by mutation, while Santos et al. (2017) did so by randomly distributing the preference locus each generation. In our case, environmental heterogeneity was the responsible factor. Our finding that mate-choice copying can spread, but that it can also make local populations less well adapted, is a novel twist on the idea that local adaptation of both traits and preferences, combined with dispersal, can maintain a persistent supply of locally acting selection gradients (thus helping to make the so-called lek paradox disappear; Holman & Kokko, 2014).

Sexual selection can be switched off in our model by assuming random mating. Dispersal evolves to be low in such a setting. Complete philopatry still does not evolve as it would make individuals compete for breeding resources (females) or matings (males) with close kin (Li & Kokko, 2019), but dispersal mortality, as well as the risk of being maladapted to faraway parts of the landscape, keeps dispersal rates low. Sexual selection can make this latter cost smaller, but this only works if dispersing females subsequently mate with locally adapted males (and not, e.g., with males who are themselves maladapted immigrants). Dispersal readily responds to this cost reduction, and evolves to be higher, when the option of mate-choice copying is available. Copying allows choosy females to express a different phenotype than her P locus would dictate. An immigrant female's offspring will therefore, all else being equal, be better locally adapted than in the absence of mate-choice copying. However, we also show that all else is not equal: when the evolutionary process with mate-choice copying involves higher dispersal, this also improves gene flow and reduces local adaptation in the global population as a whole.

Dispersal was particularly enhanced if mate-choice copying was conditionally expressed by females who had dispersed, confirming the intuitive prediction that copying is best performed in unfamiliar surroundings. For philopatric females, copying may lead to counterproductive updating of preferences to those of immigrants, whose preferences have been shaped by selection elsewhere; expressing one's own innate preferences may then be favoured. Conditional copying, then, appears the superior way to alleviate the local adaptation cost of dispersal; it accordingly produces a more robust feedback between copying and dispersal across different strengths of sexual selection, compared with unconditional copying. This result is in line with earlier findings that indiscriminate copying can be maladaptive (Dubois et al., 2012; see also Kendal et al., 2018). We are unaware of empirical studies documenting differences in copying behaviour between immigrants and philopatric females; such plasticity appears worth looking for.

Our results do not rely on assortative mating or other processes (e.g. physical linkage) creating a statistical association between the C allele (copying) and the D allele (dispersal). While, in principle, only high-D individuals ‘need’ the C allele (assuming philopatric individuals should not copy), such associations remain weak at the genetic level. This does not strictly exclude any possibility for linkage disequilibria: an immigrant non-copier would presumably mate non-ideally and thus high-D combined with c would be selected against at the stage when her offspring viabilities are tested. But as her choices are blind with respect to the dispersal status or (unexpressed) C locus of the sire, any effects here remain weak. Instead, it appears that a high frequency of C in a population facilitates high D mainly via (a) an overall expectation that preference updating is frequently an option for individuals in a lineage (all female offspring who have inherited C from the mother or from the father can do so) and (b) a reduction of the overall importance of local adaptation. The latter is a general finding in the literature on local adaptation and dispersal: once dispersal is relatively frequent, the costs of settling in a new location are reduced, because recurrent gene flow prevents strong local adaptation in the first place (Berdahl et al., 2015; Blanquart & Gandon, 2011). Our contribution is to show that mate-choice copying can amplify this effect quite substantially.

Note that the C allele in our model only experienced indirect selection, via its effects on the identity of a female's chosen mate. Earlier population genetic work has investigated both direct and indirect selection on copying (Santos et al., 2017; Servedio & Kirkpatrick, 1996). Direct selection, which we ignore, could either favour or disfavour copying: copying might help reduce the time and energy costs of assessing male quality, or there may be mild costs inherent in the copying process itself (e.g. costs of learning) or pleiotropic effects (Servedio & Kirkpatrick, 1996). While our chosen focus on the coevolution of copying and dispersal (via local adaptation) made us leave direct costs outside our study, it is intuitively clear that copying may reach higher frequencies than reported by us if it also helps to avoid direct costs.

Our contrasts between different scenarios were run in parallel, without the conditional strategy directly competing with the unconditional one. Even so, it is still useful to reflect whether the differences in the evolved frequencies of the C allele are a measure of ‘success’ of a certain kind of copying strategy. Usually, high frequencies of C associate with conditional expression, but an exception is found at weak sexual selection (S_S = 25), potentially explicable as a result of the quite variable realized matings at low value of S_S (Box 1). Matings are in this case impacted by stochasticity, irrespective of whether the choices follow innate preferences or updated (copied) ones; the net effect is that non-copier females may lose to copier females (in terms of mate quality). Given that females with a C allele are much more likely to be copiers in the unconditional scenario than in the conditional one, the situation described by Box 1 arises more often in the unconditional scenario. This provides new insight into the debate (Giraldeau et al., 2002; Kendal et al., 2018; Nordell & Valone, 1998; Vakirtzis, 2011; Varela et al., 2018; Witte et al., 2015) regarding the conditions under which mate-choice copying can be adaptive.

Note that although the model has many parameters, it simultaneously presents a simplified view of dispersal and mate-choice copying in a heterogeneous environment. For example, we modelled dispersal as a simple exponential kernel, ignoring e.g. sex-biased dispersal (Li & Kokko, 2019), dispersal kernels with flexibilities offered by more than one variable (Bonte et al., 2010; Chapman et al., 2007; Nathan et al., 2012; Poethke et al., 2011; Tung et al., 2017) or any decision-making during dispersal (which can have a strong impact on the kernel in settings with two sexes; Shaw & Kokko, 2014). Also, to avoid having to specify effects of genetic dominance on several traits, we also chose to investigate haploidy. Dominance relationships between two alleles at a diploid locus can take very many forms when fitness effects also depend on spatial location; we ignored these real-life complications to focus on a minimal genetic set-up that permits all the intended feedbacks between mate-choice copying, dispersal and local adaptation to occur. This obviously leaves avenues for further study.

More generally, mate-choice copying is just one example of social learning, which happens to be expressed in a sexual selection context (Kendal et al., 2018; Verzijden et al., 2012). If there is a need to locally adapt to new conditions after dispersal, and social learning offers a way to acquire a new set of behaviours (Varela et al., 2020), then our model's conclusions should generalize to situations where behaviours other than mate choice are learned. The prediction that social learning enhances dispersal appears quite generally applicable—as does its flipside, i.e. local adaptation may become less strong in the long term due to homogenization of traits over the spatial range of a species when learning and dispersal together promote strong gene flow (Varela et al., 2018). This finding, should it generalize, could be of importance in cultural evolution as a whole.

Box 1. Example of the effect of S_S on mate-choice copying

Consider a case where the environmental value $E_p = 0.5$, and there are three males M_A, M_B, M_C with trait values 0.4, 0.5 and 0.6 respectively.

First, assume strong sexual selection, $S_S = 100$, and assume that there is a locally adapted female with a value of 0.5 at the P locus. Following Equations 2 and 3, she will choose a male with probability $Prob(F_A,M_A) = Prob(F_A,M_C) \approx 0.212$ and $Prob(F_A,M_B) \approx 0.576$. A copier female F_B ignores her innate preferences and updates her preferences to 0.4 if F_A chose M_A, to 0.5 if F_A chose M_B and to 0.6 if F_A chose M_C. The actual probabilities of mating, conditional on F_A having chosen M_A, are $Prob(F_B,M_A \mid F_A,M_A) \approx 0.721$, $Prob(F_B,M_B \mid F_A,M_A) \approx 0.265$, $Prob(F_B,M_C \mid F_A,M_A) \approx 0.013$. The probabilities are similarly calculated for all other choices of female F_A. In the end, the probability of female F_B choosing a less adapted male than F_A did is approximately 0.244, the probability for her to choose an equally adapted male is ≈0.643 and the probability of her choosing a better adapted male is ≈ 0.112.

These probabilities become more 'egalitarian' with respect to the two females if there is more randomness in the outcome. Assuming $S_S = 25$, $Prob(F_A,M_A) = Prob(F_A,M_C) \approx 0.305$ and $Prob(F_A,M_B) \approx 0.391$. In this case the probability for female F_B to choose a less adapted male than F_A is still considerable, approximately 0.238, but the probability to choose an equally adapted male is clearly lower than before, 0.541, and the clear increase is in the probability of choosing a better adapted male, ≈0.221.

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Chapter 4

The role of mate-choice copying on species range expansion

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All figures, tables, and other sections denominated with the letter "S" can be found in Appendix III.

4.1 Abstract

Choosing individuals, mostly females, can change their preference after observing a mating event. This behaviour, called mate-choice copying (MCC), can target a single mate (individual MCC), or all similar mates (generalized MCC). By shaping mating preferences, MCC can cause selection, alter allelic frequencies, and potentially affect the ability of populations to adapt to new environments. We used individual-based models to analyse the effects of MCC on the speed of adaptation in populations expanding their range along an environmental gradient, simulating populations with no MCC, individual MCC, or generalized MCC. Additionally, we simulated conditions where preference can be based on a trait determined only by the male genotype (condition-independent information) or determined by genotype-by-environment interactions (condition-dependent information).

Results show that when preference is condition independent, populations with generalized MCC expanded faster than others, which was adaptive and potential copiers increased their frequency. This happens because the preference of non-copier females is not adaptive in the invasion, and generalization adds an intrinsic variance associated with the cognitive judgement of what constitutes a similar trait, allowing for copiers to make more adaptative choices.

When preference is condition dependent, populations with individual MCC expanded faster than other populations, but potential copiers lowered their frequency. The higher dispersal is explained by the fact that, when the same male is chosen multiple times in the same patch, kin competition is higher, encouraging dispersal. This effect disappears in simulations where dispersal was fixed.

Our study shows how MCC can have significant effects on population dynamics, especially how it can hamper or help population expansion and adaptation. It also highlights the importance of the type of information animals use for social learning. Knowing what information is relevant in different contexts is crucial to understanding the real effects of MCC for the adaptation of species in nature.

Keywords: Sexual selection, mate-choice copying, social information, population dynamics, individual-based simulations, local adaptation.

4.2 Impact Summary

Some animals copy the mate-choice decisions of others after observing them choosing. In theory, this behaviour, called mate-choice copying (MCC), can spread throughout the population, affecting how individuals choose their mates, and consequently affecting their evolution. Past theoretical studies have shown how MCC can be an adaptive strategy for animals when they disperse between patches because local individuals should be more informed about which individuals are the best to mate locally. But it is still unknown how this behaviour can affect adaptation when populations expand their distribution range. This benefit could disappear if a population expands to an empty habitat, because there are no longer local individuals from whom to copy. This study tackles this question by using computer simulations to understand how fast different populations, with and without MCC, can expand through an environmental gradient to a new empty habitat. We simulated different MCC modalities, such as copying types (allowing females to choose the same male or similar ones) and preference rules (allowing females to copy condition dependent or condition independent male traits) to evaluate whether their adaptive value differs during the process of range expansion. Results show that MCC can increase the speed of adaptation during range expansion but depends on the different copying modalities and preference rules. These results show another potential effect of MCC on populations evolutionary dynamics that have never been documented before, highlighting the importance of taking into account MCC modalities and preference rules when making predictions of the evolutionary effects of this behaviour.

4.3 Introduction

Choosing who to mate with is one of the most important decisions individuals make in their lifetime. If the choice falls on a maladapted mate, there is a risk of having maladapted offspring that might be eliminated from the population. Individuals can choose their mates based solely on their innate preferences, or by learning from experience or from the choices of others (Verzijden et al. 2012). The latter strategy, coined mate-choice copying (Pruett-Jones 1992), is a type of social learning found in numerous species across different taxa (DuVal et al. 2018; Davies et al. 2020).

Many theoretical studies tried to understand how mate-choice copying (hereafter MCC) can affect the evolution of secondary sexual traits in males (Agrawal 2001; Santos *et al.* 2014) and the evolution of copying behaviour in females (Servedio & Kirkpatrick 1996; Santos et al. 2017). Because MCC can lead females to make choices different from their innate preferences, it has the potential to change the course of sexual selection in a population, which has raised considerable interest among evolutionary biologists (Gibson & Höglund 1992; Kirkpatrick & Dugatkin 1994; Laland 1994; Brooks 1998; Danchin et al. 2004; Leadbeater 2009; Danchin & Wagner 2010; Witte et al. 2015). However, a detailed analysis of the role of this behaviour on wide-scale ecological and evolutionary processes is still in its infancy.

Varela et al. (2018) suggest that MCC should lead to convergence of mate preferences and reduced genetic differences between patches, since animals may share their preferences when traveling. This was confirmed by Sapage et al. (2021), who also found that MCC promote the evolution of dispersal because by copying local mating preferences individuals tend to produce offspring better adapted to the new patch, hence lowering dispersal costs. A side effect, however, is an overall reduction in local adaptation due to the increased rates of gene flow between patches. This effect raises an interesting question not tackled by Sapage et al. (2021), which is the role of MCC during range expansions. Because in expanding populations those individuals that arrive first to a new habitat would likely be the ancestors of future generations, the expectation is that by promoting dispersal MCC can quickly expand to new territories even if it is a neutral (or even slightly deleterious; e.g., Kirkpatrick & Dugatkin 1994) behaviour; i.e., a phenomenon akin to gene surfing (Klopfstein et al. 2006).

MCC can happen when individuals learn to prefer specific mates (individual MCC) or when they generalize the traits of model individuals to the entire population (generalized MCC or trait-copying) (Westneat et al. 2000). These types of MCC may interfere differently with the ability for populations to expand into new territories. Generalization is thought to have stronger consequences for evolution because copied preferences spread faster in the population, while individual MCC may affect only a few individuals (Danchin et al. 2020; Davies et al. 2020). This should be especially important during dispersal because it allows for individuals to assess mate quality in a new environment by learning from the choice of conspecifics, without focusing on a single mate that might be unavailable. Additionally, at least in theory, the effects of MCC on population expansion should also be affected by female preference. Among preference rules, individuals can prefer different types of information about sexual traits, namely information closely related to genotype, that is condition independent, or information based on genotype-by-environment interactions (e.g. performance), which is condition dependent (Wagner & Danchin 2010). Copying condition-dependent traits should have stronger consequences for evolution, because expectedly the offspring produced will be better adapted to the current local conditions, especially important during dispersal, as migrant individuals are not aware of the traits that have evolved locally (Holman & Kokko 2014; Sapage et al. 2021).

In this study, we use individual-based models to test the effects of different types of MCC and preference rules on the speed of population expansion.

4.4 Material and Methods

The model was adapted from Sapage et al. (2021), with some dispersal concepts taken from Phillips (2012). We considered a total of six polygynous population scenarios, crossing the type of strategy used in mate choice with the type of trait copied. For MCC types, females can either show (1) no MCC, (2) individual MCC, or (3) generalized MCC. For preference rules, females can either (1) choose males based on a trait directly related to the genotype (condition independent on the environment), or (2) a performance trait resulting from genotype-by-environment interactions (condition dependent).

The simulated world is represented by a matrix with $Y = 20$ rows and $X = 50$ columns, continuous in the *y* but not in the *x* axis (i.e., a pipe). Columns are subdivided into three groups: the 10 left-most columns (X_s) with the starting distribution of the population in the original habitat, the next 30 columns $\left(X_\mathrm{g}\right)$ define the environmental gradient, and the final 10 columns (X_f) where the endmost habitat is located. Each patch has an environmental value e_{ij} $(i = 1, \cdots, Y;\ j = 1, \cdots, X)$ sampled from a normal distribution with mean $\overline{e_j} = 0.9$ in X_s and $\overline{e_j} = 0.1$ in X_f and standard deviation 0.01. In the environmental gradient X_g, $\overline{e_j}$ decreases linearly from 0.9 to 0.1 (Figure S1 in Supporting Information).

We model an obligately sexual, haploid population with five independent loci, some with sex-limited expression. S (for sex) determines if individuals are females (0) or males (1). T (for trait) takes real values between 0 and 1 and defines the viability of the individual relative to the environmental value e_{ij} (see below). T has a pleiotropic effect in males, also coding for an observable phenotype that affects female choice. P (for preference), expressed only by females, takes real values between 0 and 1 and codes for the female preference relative to the male trait. C (for copy) is only expressed in females of populations with copying and has two alleles that code for the ability of females to mate-choice copy (C) or not (c). MCC did not involve direct costs in the models. Finally, the D locus codes for the probability of individuals to disperse to nearby patches and can take real values between 0 and 1.

Initially, all patches in $X_s(20 \times 10 = 200)$ are at carrying capacity $K = 64$ individuals, each with an equal probability of being female or male. Generations are discrete and nonoverlapping (this excludes the cultural evolution effect in generalized MCC). The order of events is mate choice, offspring production, viability selection, dispersal. This combination of events comprises one generation. All initial individuals carry allele *c* (i.e., females are non-copying), allelic D value set to 0.02, and are locally adapted, i.e., their allelic T values were sampled from a normal distribution centred on the environmental value of their patch $\overline{e_j} = 0.9$ with standard deviation 0.01. P allele values were sampled from the same distribution for condition-independent populations and remained equal to 0 for condition-dependent populations. Loci T, D and P have a mutation probability of 0.01 (for P only when preference is towards condition-independent traits). Once a mutation occurs, we add a normal random variable of mean zero and standard deviation 0.02, keeping the allelic value in the interval $[0,1]$. The C locus has a 0.005 probability of switching from c to C and vice versa.

The expansion starts after a warmup phase of 2,500 generations to reach a stable state. Provided that there is at least one female and one male in a patch, females can choose based on their own innate preference (non-copier) or perform MCC (copier). Females with the C allele can become non-copiers if there are no females with the c allele within the patch to copy from. Non-copier females assign a preference value towards a condition-independent or dependent trait. In the first case, they will score males as

$$\phi_{\mathrm{Pref}}(f,m) = e^{-S_{\mathrm{S}}\left(a_{\mathrm{P}f}-a_{\mathrm{T}m}\right)^2}, \tag{1}$$

where S_{S} is the strength of sexual selection (choosiness), $a_{\mathrm{P}f}$ is the allelic value from preference, and $a_{\mathrm{T}m}$ is male's trait value. In the second case, the score is

$$\phi_{\mathrm{Pref}}(f,m) = e^{-S_{\mathrm{S}}\left(a_{\mathrm{P}f}-\left|a_{\mathrm{T}m}-e_{ij}\right|\right)^2}. \tag{2}$$

Whenever the score is below 10^{-300} (a rare event), females ignore the male.

Copier females choose after non-copier ones. In the case of individual MCC, females count the number of times each male is chosen and mate with the most popular one (if there are tied values they choose randomly among the popular males). In generalized MCC, females give a social score to each male. Because allelic values $a_{\mathrm{T}m}$ are continuous in the interval $[0,1]$ the social score not only depends male's popularity but also on the popularity of similar males. The social score is

$$\phi_{\mathrm{Soc}}(m) = \sum_{m^*=1}^{M_{ij}} n_{m^*} e^{-S_{\mathrm{S}}\left(a_{\mathrm{T}m}-a_{\mathrm{T}m^*}\right)^2}, \tag{3}$$

where M_{ij} is the number of males in the patch and n_m is the number of times male $m^*$is chosen by non-copier females. Copier females replace their own $a_{\mathrm{P}f}$ value with the $a_{\mathrm{T}m}$ male's value if preference is for condition-independent traits, or with $\left|a_{\mathrm{T}m}-e_{ij}\right|$ for condition-dependent traits. Then copier females choose according to eqns. (1) or (2), respectively.

The expected number of offspring produced by each female is drawn from a Poisson distribution with mean $\lambda = 4$. Offspring inherits a random copy of the parental alleles. Survival probability depends on the survival score

$$\phi_{\mathrm{Surv}}(n) = e^{-S_{\mathrm{N}}\left(a_{\mathrm{T}m}-e_{ij}\right)^2}, \tag{4}$$

where $S_{\mathrm{N}} = 500$ is the strength of viability selection. Individuals with the highest survival score in each patch survive. The number of surviving individuals per patch is calculated as the sum of its $\phi_{\mathrm{Surv}}(n)$, with K as a hard upper bound. We used a relatively high strength of viability selection so that populations can only successfully expand if individuals in the invasion front can produce offspring with traits reasonably adapted to their patch. Under these conditions, the speed of expansion relates with the ability for populations to adapt to the new environment with their trait allele, although further adaptation to the patch can theoretically still be possible.

After passing the viability selection process, individuals can disperse to any of the neighbouring patches with the same probability, controlled by the allelic values at locus D. During dispersal, individuals have a 0.05 probability of dying, i.e., a risk of dispersal. Here we are implementing a hard selection model where the contribution of a patch to the migrant pool depends on its individuals' fitness (Christiansen 1975).

The simulation ends 1,000 generations after the endmost habitat is occupied at 80% carrying capacity, i.e., after the population is likely adapted to the new environment. In the rare event that the population did not adapt to the new habitat, we let the simulation run for another 9,000 generations. Here we only consider the time it takes for the population to breach the environmental gradient (i.e., to reach the 40th column of the simulated world) because in most cases populations adapted quickly to the endmost habitat after reaching that column. For each simulated run, we extracted the environmental matrix, the average allelic values at each column every generation, and the position of the invasion front.

We simulated different values of choosiness for the six population types by setting S_S to 100, 500, and 1000. Additionally, we made two simulations with $S_\mathrm{S} = 0$, where females choose randomly. With this parameter, populations with no MCC and with generalized MCC are conceptually identical, so we ran one set of simulations for both, allowing for preference to evolve neutrally. To study the effects of dispersal on the invasion process, we additionally ran the same simulations, but without allowing dispersal to evolve by setting D to 0.02 (close to the average value for most populations) and setting the mutation rate of D to 0. We ran each set of parameters 20 times.

The code is written in C with some functions from the GNU scientific library 2.3 (GSL) (Galassi et al. 2009), and can be found in the supplementary material. All data were analysed using the R software, version 4.1.1 (R Core Team 2021).

4.5 Results and Discussion

4.5.1 Case 1: When the preference is condition independent

We ran a set of simulations while considering preference to be condition independent and compared the performance of populations for MCC types: no MCC, individual MCC and generalized MCC.

4.5.1.1 Generalized MCC increases the speed of adaptation

We compared the behaviour of different populations considering that female preference is for a condition-independent trait. With this preference rule, populations with generalized MCC breached faster than individual MCC and no copying populations when $S_S > 0$ (Figure 1A and Table S1). This happens due to the intrinsic variation in generalized MCC. In each patch, copier females' choice is dependent on the average choice of non-copier females, plus on their own choosiness (i.e., the idea of what constitutes a 'similar enough' male). Since the innate preference of non-copier females in the invasion front is still maladapted, generalized copying can help to reframe female preference, and the margin created by choosiness helps some copier females to choose a slightly more adapted male than non-copiers, thus making the invasion faster. Studies of generalized MCC usually consider binary male traits, but generalization in the context of learning is a process that can introduce individual variability depending on individual experience and perception (Staddon 2016; Zaman et al. 2021). Therefore, with generalized copying, we show that range expansion occurs and can be accelerated even without the effect of cultural evolution – through oblique or vertical transmission of social information (Danchin et al. 2020; Davies et al. 2020) – which we did not include in our model.

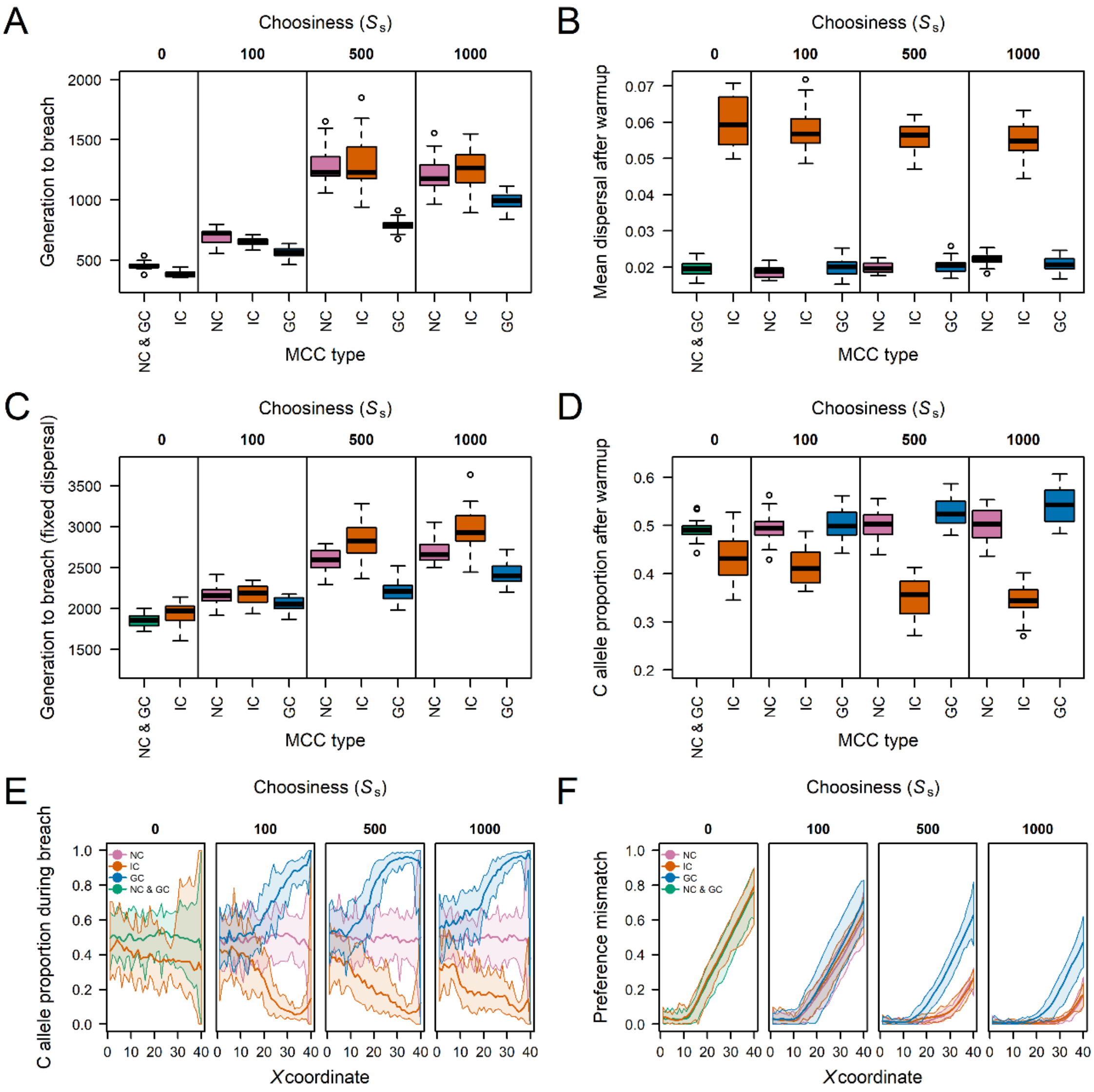

Figure 1. Results of simulations where preference is for condition-independent male traits. Except for panel C, all panels show results from simulations where dispersal is allowed to evolve. Panels A and C show the number of generations taken to breach the environmental gradient after warmup when dispersal is evolving or fixed, respectively. Panels B and D show, respectively, the mean dispersal allele value and the C allele proportion after warmup but before expansion. Panel E shows the C allele proportion per column during the generation where the population breaches the environmental gradient. Panel F shows the difference between the mean preference allele and the average environmental value within each column during the same generation as Panel E. In panels A–D, the thick line in each box plot represents the median value of 20 replicates, and the lower and upper margins of the box indicate the 25% and 75% interquartile range. Vertical dashed lines show extreme values within 1.5 times the interquartile range, while values outside this range are represented by open circles. NC = No MCC; IC = Individual MCC; GC = Generalized MCC.

4.5.1.2 Individual MCC promotes the evolution of dispersal

To understand if the speed of expansion was also related to differences in the tendency of dispersal, we compared simulations where dispersal can evolve (measured by changes in the average dispersal allele value in different populations after warmup but before expansion) with those where the dispersal allele is fixed. In the first scenario, simulations show that populations with individual MCC tend to disperse around three times more than in the other populations, even if non-copiers choose randomly (i.e., $S_S = 0$) (Figure 1B and Table S2). Faster dispersal in populations with individual MCC occurs because copier females from each patch tend to choose the exact same males, leading to a smaller variation not only in the target gene but in the entire genotype, including the dispersal allele. This effect leads to a higher variation in the dispersal allele between patches in the first generations, with selection subsequently favouring offspring from patches with high dispersal as they suffer less from kin competition. This result shows an important difference between individual MCC and generalized MCC, namely that individual MCC can reduce the effective size of a population, creating different ecological effects.

Another important aspect is the lack of differences in dispersal tendency between no MCC and generalized MCC, opposing to Sapage et al. (2021) where they found higher dispersal with generalization. However, Sapage et al. (2021) considered a positive spatial autocorrelation, so a higher dispersal means a higher probability to end up in a maladapted patch. In our case, the initial habitat grid has random noise which reduces the positive effects of dispersal. Additionally, we considered a maximum of 64 individuals per patch and hard selection, instead of an average 16 and soft selection considered by Sapage et al. (2021). This hinders the ability for migrants to compete with local ones because, although MCC can help migrant females to compete with local females, immigrant females are still, on average, due to their trait allele, less adapted than their local counterparts. Finally, although Sapage et al. (2021) considered generalized MCC in the sense that females can choose males with similar traits from the one they copied, they also considered that females copied the trait of the most popular male. This latter rule is more similar to individual MCC considered in this model. Although both models use different assumptions, they are complementary as they call attention to two different ecological problems: how social learning affects the evolution of populations within their home ranges (Sapage et al. 2021) and how it affects the evolution of populations during range expansion (our current work).

In the simulations where dispersal is fixed, all populations take more generations to breach the environmental gradient (cf. Figure 1A and C). However, individual MCC took more time to breach than generalized MCC, and more so (including no MCC) with $S_S \geq 500$ (Figure 1C and Table S3). This shows that the faster expansion of populations with generalized MCC was not related with the increase in dispersal through time. It also shows that individual MCC can hamper expansion if dispersal is fixed, especially when choosiness is high. The overall effect on expansion of individual MCC when preference is condition independent happens because the most popular males chosen by copier females in the invasion front are usually maladapted, so copying their choice exactly is also not a good strategy. In this case, it is better for individuals not to copy at all than to perform individual MCC, because there is intrinsic variation in female innate choice that would allow for some females to show more adaptive choices.

4.5.1.3 Generalized MCC favours the evolution of a copying allele

Furthermore, we analysed the evolution of copying. To control for mutation and genetic drift, we also introduced a “neutral” C allele in no MCC populations. In these populations, however, the C allele is not expressed, and all females are non-copiers. As expected, the proportion of individuals with the C allele after warmup but before expansion was always close to 0.5 (Figure 1D and Table S4). In populations with generalized MCC, the proportion of individuals with the C allele increased to a higher proportion during warmup than neutral expectation, particularly with higher choosiness (S_S), while this value decreased in populations with individual MCC (Figure 1D and Table S4). Additionally, the proportion of individuals with the C allele in individual MCC populations stayed below 0.5 even when non-copier females chose randomly. To characterize the variation in the distribution of copiers during expansion, we sampled the proportion of individuals with the C allele per column (X coordinate) at the generation when the population breached the gradient for the first time (Figure 1E and Table S5). The number of individuals with the C allele increased to around 0.95 close to the invasion front in populations with generalized MCC and decreased to around 0.05 in populations with individual MCC. These results show that, when preference is condition independent, it is not beneficial to show individual MCC in a patch, while it is beneficial for generalized MCC. Besides generalized MCC allowing for females to have more variation in mate choice within the same patch than individual MCC, females that copy using individual MCC cannot integrate information from multiple male targets, even from females that choose similar males. Given that copier females observe each target male independently, they might have a higher chance to choose maladaptively. In the invasion front, the proportion of individuals with individual MCC is even lower because non-copiers do not have adapted their preference allele yet, so copying the most popular male is also maladaptive. These results show the strong differences between the evolution of individual and generalized MCC, considering that in our model the only cost or benefit directly associated with MCC is related with the quality of the males being chosen. This contrasts with some other studies of evolution of MCC that consider additional costs or benefits, such as the time-saving aspect of copying (Stöhr 1998; Sirot 2001). Another important aspect to point out is that we considered females to have perfect information about all the non-copiers' matings in a patch. Eavesdropping is an important component of MCC (Danchin et al. 2004; Valone 2007), and the ability for females to observe other matings should depend on many different factors. Reducing the number of matings observed by females should increase the number of different males chosen by copiers inside each patch, thus making individual MCC more like generalized MCC. This, however, remains to be tested and is hard to implement given that individual subsampling would increase computational time to an unreasonable amount.

4.5.1.4 Generalized MCC weakens the adaptation of female preference to the environment

Finally, we checked if populations were adapting their innate preference during expansion by analysing the mismatch between the average preference allele and the expected environmental value ($\overline{e_J}$) for each column (X coordinate) during the generation where the population breached the gradient for the first time. Results show that populations with generalized MCC have the tendency to make the preference allele adapt much less to new environments (Figure 1E). This result can be due to the faster speed of expansion in generalized MCC populations, or due to the intrinsic properties of generalized MCC that can increase the mismatch between the preference and trait alleles (Sapage et al. 2021). Generalized copying can, therefore, serve as a shortcut for adapting to new environments, but individuals might need to ultimately align their innate preference towards the most adapted individuals in the long run. This, however, does not prevent generalized copying from increasing the speed of adaptation compared to the other populations.

4.5.2 Case 2: when preference is condition dependent

We ran the same set of simulations while considering preference to be condition dependent, excluding the scenario where non copier female choice is random ($S_S = 0$), given that the simulations would be identical with the ones in the first case. In this case we also did not analyse the adaptiveness of the preference allele, given that female innate preference is already towards the most adapted male trait in each patch.

4.5.2.1 Individual MCC increases the speed of adaptation

With this preference rule, all populations breach the environmental gradient faster than when preference is condition independent (Figure 2A and Table S1), and the effect is more evident with increasing choosiness. This is expected, because females are selected to prefer males with traits adapted to their local environment, so sexual selection opposes natural selection. In high contrast with what we saw in condition independent preference, we found that populations with individual MCC breached the environmental gradient much faster than the other populations (Figure 2A and Table S1). This happens again due to the intrinsic variation in generalized MCC, which becomes less adaptive when preference is condition dependent.

4.5.2.2 Individual MCC promotes the evolution of dispersal

Common to what was observed for condition independent preference, however, individual MCC populations showed a higher dispersal tendency than the other populations right before the population expands (Figure 2B and Table S2). Simulations with fixed dispersal show no difference in breaching time between all populations,

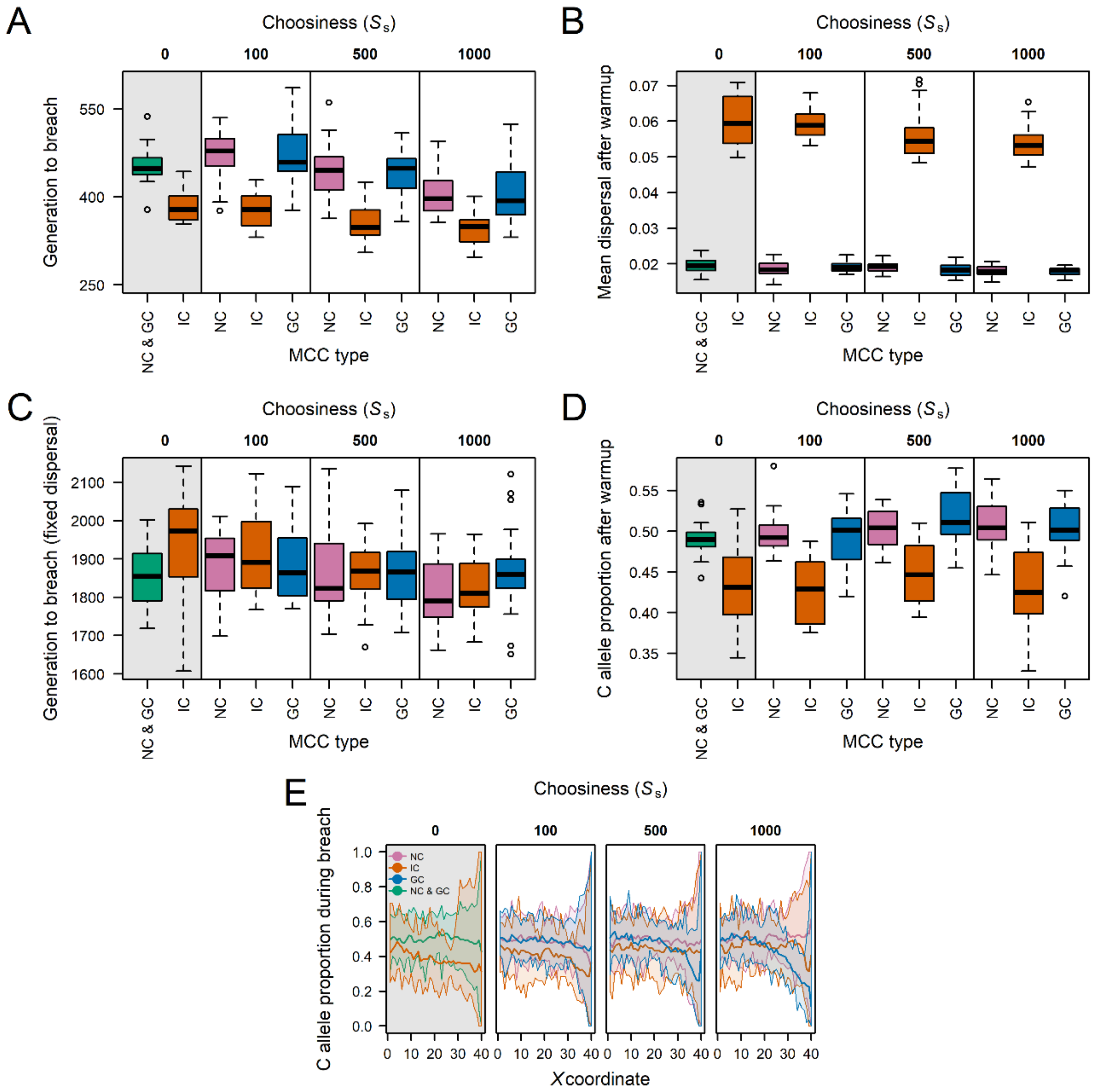

Figure 2. Results of simulations where preference is for condition-dependent male traits. Panels follow the same description as in Figure 1. Results with $S_S = 0$ (light grey background) are taken from the same simulations as in Figure 1 as they are equivalent for both simulations, and they are plotted comparison purposes.

confirming dispersal to be a determinant factor for the increase in expansion speed for individual MCC populations (Figure 2C and Table S3).

4.5.2.3 Individual MCC does not favour the evolution of a copying allele

Analysing the evolution of the copier allele, after warmup individual MCC is slightly lower than in the other populations, in common with the condition independent scenario (Figure 2D and Table S4). However, in this case the proportion of individuals with the C allele is not affected by choosiness. This may be because, since female preference is fixed and adapted to every patch, the proportion of individuals with the C allele does not change with choosiness.

There is a considerable difference in the fate of the copier allele after expansion comparing the two scenarios, condition independent preference mentioned above and this new scenario of condition dependence (cf. Figures 1E, 2E). In the latter case generalized copying decreases when choosiness is high ($S_S \geq 500$). This is because, since non-copiers always prefer the most adapted males, the strategy of generalization is worse than individual MCC. This is stronger in the invasion front where individuals are still in the process of fully adapting to the environment, and with higher choosiness where the stochastic effects are smaller (Figure 2E and Table S5).

Here, as when preference is condition independent, both types of copying errors also occur: generalized MCC allows for females to have variation in mate choice within the same patch, and individual MCC make females less able to integrate the information from multiple male targets. However, with condition dependent preference, these errors are no longer an advantage, particularly for generalized MCC, but a cost, making MCC poorly adaptive. This result shows, therefore, the importance of considering the interaction between female preference and the type of trait that a female is copying. In this case, because non-copier females are already choosing the most adapted males in each patch, copying can become trivial or even detrimental for females, especially if there are no additional benefits associated with this behaviour (e.g., reduced sampling costs).

4.5.3 Final considerations

Overall, our results show that generalized MCC increases the variability of female choice when compared to individual MCC, and it also allows for females to incorporate information from multiple matings more efficiently. While the effect of generalized MCC is adaptative when female preference is based on male traits that are condition independent, it can be maladaptive when female preference is based on male traits that are condition dependent. Additionally, we found an adaptative effect of individual MCC on dispersal, which happens because individual MCC can lead to stronger kin competition. These results further suggest that different mate-choice copying types, preference rules, and female choosiness can lead to different ecological and evolutionary effects, and they should be accounted for in future research. Many studies show that MCC has the potential to affect speciation (Gibson & Höglund 1992; Kirkpatrick & Dugatkin 1994; Danchin et al. 2004; Witte et al. 2015; Varela et al. 2018), hybridization (Varela et al. 2018), as well as dispersal and local adaptation (Sapage et al. 2021). While these studies suggest many possible ways MCC can affect ecology and evolution, our model shows that is imperative for researchers to understand the details surrounding this behaviour before making specific predictions on its effects.

There is still a lack of empirical studies exploring the effects of MCC in population dynamics, with only a few studies comparing the difference in copying behaviour between different populations (Heubel et al. 2008; Fowler-Finn et al. 2015). We acknowledge that it is difficult to empirically test some of the effects of MCC on population dynamics, but we urge empiricists to test which set of rules is prevalent in the species they study and why and how it may impact its ecology and evolution. Questions of who, what, and when to copy should all be considered for each population being studied. For example, related to the assumptions of the current model, empirical research has found that some species can, indeed, copy individuals or generalize what they have learned, or can copy condition dependent and condition independent traits. For example, female fruit flies *Drosophila melanogaster* are able to change their preference towards individual males with large or small size, a condition-dependent phenotype generated by subjecting young individuals to different growing conditions (Mery et al. 2009). Additionally, *D. melanogaster* is also able to generalize males powdered with different colours, one trait that is independent from the male’s condition (Mery et al. 2009). Generalized MCC of condition-independent traits has also been found in guppies (*Poecilia reticulata*), where females generalize the colour patterns of the males (Godin et al. 2005), a trait that is has high heritability in males (Houde 1992).

The current model also explores how MCC can impact how species can expand their distribution. Species distribution range has been one of the core questions in ecology and evolution, and extensive studies have been done to understand how populations disperse and adapt to new environments (Cox et al. 2016). On the other hand, only a few studies already show that social information might affect the decision for individuals to disperse (Cote et al. 2008), and MCC in particular, can be advantageous for dispersal, because it can help them adapt to a new environment by copying local individuals (Sapage *et al.* 2021). However, the effects of mate-choice copying in an expanding population had never been studied before. Here we show how it might impact a species range expansion in a scenario where the new habitat is empty. Scenarios that involve competition should enlighten us further. This question is important considering global environmental change for which the combined effects of social learning and sexual selection in shaping adaptation could be a promising new research avenue.

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Chapter 5

A comment and overview on recent mate-choice copying meta-analyses studies

This chapter contains a published commentary (Sapage and Varela 2020*) to a mate-choice copying meta-analysis study (Davies et al. 2020) that came out shortly after another meta-analysis study on the same topic (Jones and DuVal 2019). Given that Davies et al. (2020) heavily compare their study with Jones and DuVal (2019) and the studies complement each other, a summary of both studies is given in section 5.1, followed by the published commentary in section 5.2, and by an overview of other published commentaries on Davies et al. (2020) in section 5.3.

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SEE SECTION FOR DETAILS

5.1 Summary of two mate-choice copying meta-analyses

5.1.1 Summary of Jones and DuVal (2019)

In their meta-analysis, Jones and DuVal (2019) compared effect sizes of female mate-choice copying across 103 experiments from 40 non-human animal studies, covering 17 different species. The selected studies included both individual mate-choice copying and mate-choice copying generalization. All studies compared female copying behaviour with a control that could either be (1) the choice of females without social information, or (2) the assumption that if females do not copy, they have a 50% chance to pick either one of the males.

Jones and DuVal (2019) identified four key factors associated with the studies' experimental design that could affect the strength of mate-choice copying: (1) observer female mating status (virgin versus non-virgin); (2) model female age (older versus same age or younger); (3) model female choice (assigned to the less attractive male versus assigned randomly); and (4) experimental setting (conducted in captivity or in the wild). Additionally, the authors constructed a phylogenetic model with the 17 species, which are distributed into five different classes within Chordata and Arthropoda.

The meta-analysis found, as the mean effect across all studies, that social information increases the likelihood of female mate choice by an average of 2.71 times (odds ratio), with a 95% credible interval (a measure analogous to confidence interval for Bayesian statistics) of 1.6 to 4.8, and this effect seems to be independent of phylogenetic relationships. Although that is the case, the 95% prediction interval for any single effect size is from 0.31 to 22.75, meaning that mate-choice copying may not occur in some conditions or in some species. The authors found publication bias in these studies in favour of publishing non-null results ($p = 0.037$), but mate-choice copying remained statistically significant after adjustment (1.92 times more likely, 95% credible interval of 1.13 to 3.40).

The lack of a phylogenetic signal made the authors suggest that mate-choice copying is widespread in nature, although its occurrence may also differ between closely related species (e.g. *Drosophila melanogaster* and *D. serrata*, although the differences may also be methodological; see section 1.2). However, the authors point out that they only analysed a limited number of species due to their exclusion of studies reporting non-discrete choices (e.g. in mammals), and there are some other clades where many species show the ability to learn socially in other contexts (e.g., mammals as well as amphibians and cephalopods) that were never tested for mate-choice copying.

Because mate-choice copying is widespread and appears in species without complex sociality such as *D. melanogaster* and *Schizocosa* wolf spiders, Jones and DuVal (2019) suggest that mate-choice copying is not a discretely evolved trait, but part of a broader, conserved cognitive mechanism that gives the ability for animals in general to observe and copy others. The lack of a phylogenetic signal also lead the authors to suggest that this behaviour emerged in a common ancestor of all Nephrozoa (Jones and DuVal 2019).

Considering the factors that influence mate-choice copying, the authors found that virgin females are more likely to copy than their non-virgin counterparts ($p = 0.03$), as predicted by mate-choice copying theory that social information is more useful for unexperienced females (Nordell and Valone 1998). The authors did not find any statistical difference between the tendency for females to copy older females, versus the tendency to copy females younger or about the same age as themselves ($p = 0.88$), and they suggest further studies on the role of the demonstrator female quality, because they could not gather enough information to study other asymmetries. For this factor, is also important to point out that, in guppies, small females copy the mate choice of other small and large females, while large females only copy the choice of other large females (Vukomanovic and Rodd 2007). Given that age is associated with size in this species and females might still copy other individuals with the same age, I would argue that Jones and DuVal (2019) should have considered comparing younger demonstrator females with females that are of the same age or older.

Results also indicate that females are significantly more likely to copy when the model female's choice is assigned to the less attractive male (known as the "reversal of choice" protocol) then when it is assigned to a random male ($p = 0.004$). The authors justify this result due to the tendency of some species to switch their mate choice in second trials, with or without social information, and they recommend future studies to test the reversal of choice without social information (known as the "consistency of choice" control, see section 1.2). I agree with their assessment and discuss this point further in section 5.3, given that Davies et al. (2020) found similar results. Finally, mate-choice copying was found to be much stronger in natural conditions than in captivity ($p < 0.001$), where females are on average 14.4 times more likely to mate with males carrying positive social information in the wild, in contrast to the average of 2.31 times when tested in captivity. Two reasons are given for this effect. First, it is possible that the easiest populations and species to test mate-choice copying in the lab are also used in the wild, where the natural environmental setting improves their copying response. Alternatively, the authors suggest that animals in the wild are faced with more predation risk and competition, so they should rely more on mate-choice copying as a time-saving strategy. Additionally, mate-choice copying in lab tests are usually dichotomous, while females in the wild are typically faced with more mating options, thus increasing the importance of relying on social information. While studies of mate-choice copying in captivity have developed to a point where researchers are interested in understanding the conditions that favour or hamper copying behaviour, studies in the wild might be more focused on showing that a certain species can copy. If that is the case, the methodologies used might be quite different and the discrepancies in the results be, therefore, methodological. However, as the authors pointed out, an increase in mate-choice copying tendency can also be environmental or even genetic, as shown by studies from Trinidadian guppies that show mate-choice copying behaviour, while store-bought or feral guppies do not (see section 1.2). Hence, research is still needed to understand this discrepancies.

Based on their findings, Jones and DuVal (2019) make suggestions for future studies. First, they suggest more studies of mate-choice copying in the wild using species that have been demonstrated to copy in captivity, and for lab studies to test the effects of environmental factors on this behaviour. I agree that this is a good starting point for future research and the main argument of my published commentary (see below in section 5.2). Second, they suggest that future meta-analyses include other measures of mate choice, as they only considered discrete choice, while many studies rely on continuous variables (such as time spent near each mate). This was done by Davies et al. and the results are generally congruent (2020, see more details below in section 5.1.2). Third, they suggest contrasting individual mate-choice copying with mate-choice copying generalization, something that they could not do due to the lack of generalization studies with discrete choice measures, but that could be tested in Davies et al. (2020, see section 5.1.2). Fourth, they suggest testing the effects of mating systems on mate-choice copying behaviour, as most species tested for mate-choice copying are socially polygamous. This suggestion would also imply testing mate-choice copying in a wider range of species. Fifth, Jones and DuVal (2019) suggest to further explore how the amount and consistency of social information can influence the tendency of mate-choice copying. Although some studies suggest that mate-choice copying is stronger when multiple demonstrators reinforce the choices towards the non-preferred mate (Dugatkin 1998; Drullion and Dubois 2008), they were not enough to allow for Jones and DuVal (2019) to include it as a factor in their study. Unlike testing for mate-choice copying in species with different mating systems, this factor would better be tested in species where some of the effects of mate-choice copying are already known, such as guppies, mollies, or *Drosophila*, to reduce the effects of confounding factors. Finally, Jones and DuVal (2019) encourage other researchers to publish their studies independently of rejecting or supporting mate-choice copying. This suggestion is logical in theory, but it can be hard to publish negative results in mate-choice copying, especially because many factors can hamper this behaviour, as shown by the authors. I think that, for such studies to be true cases of no copying behaviour and, hence, be genuinely informative, researchers would need to develop more standardized methodologies, including for non-model species.

5.1.2 Summary of Davies et al. (2020)

Davies et al. (2020) used a phylogenetically controlled meta-analysis to understand what factors influence mate-choice copying, covering 158 effect sizes from 58 studies and 23 species. The authors highlight that although they used a similar dataset as Jones and DuVal (2019), they considered both males and females along with other factors not studied by the latter.

Davies et al. (2020) extracted effect size values from both discrete and continuous preferences, calculated from the difference between mating preference in the presence and absence of social information. Similar to Jones and DuVal (2019), the authors considered studies that assessed copying behaviour with a control test made without social information (the “before-and-after” experimental design) or simply through a statistical test with the assumption that if individuals do not copy, they have a random chance of choosing any one of the target mates (the “no pretest” experimental design), which, at the population level, generally corresponds to a 50% preference for either one of the males.

Davies et al. (2020) took into account eight key factors for their meta-analysis that could affect the strength of mate-choice copying, some not considered in Jones and DuVal (2019): (1) the taxonomic group (instead of only the phylogenetic relationships considered by Jones and DuVal 2019), for which the authors predict mate-choice copying to be strongest in mammals and birds followed by fish, then arthropods if cognitive capacity is important; (2) the sex of the copier (instead of only females considered by Jones and DuVal 2019), for which the authors predict females to have a stronger effect due to usually investing more in reproduction while males avoid sperm competition; (3) the rate of multiple mating (not considered in Jones and DuVal 2019), for which the authors suggest that a higher mating rate should result in weaker copying because individuals are less choosy; (4) the animal birth location (in the wild versus in captivity, instead of the location of the experiments used in Jones and DuVal 2019), for which the authors predict that individuals born in captivity would show stronger mate-choice copying, because many confounding variables that might weaken the effect of mate-choice copying in the wild (e.g., prior mating experience) are controlled in captivity; (5) the type of mate-choice copying (individual versus mate-choice copying generalization, discussed but not analysed in Jones and DuVal 2019), for which the authors give no prediction but highlight the importance of separating both types of copying, due to using different cognitive abilities (e.g., individual recognition versus the ability to generalize traits), and the potential for cultural evolution in generalization; (6) the type of experimental design (contrasting “before-and-after” and “no pretest” protocols, similar to Jones and DuVal 2019), for which the authors predict that the “no pretest” design (i.e. no initial choice treatment) will have a stronger copying effect because in these experiments random choice is often assumed as the control, and even a small variation in mate attractiveness might underestimate the preference for the most attractive mate and overestimate the strength of mate-choice copying; (7) the demonstrator choice (i.e. whether demonstrators were paired with the target individuals by choice or forcefully, not considered in Jones and DuVal 2019), for which the authors predict that mate-choice copying would be stronger when demonstrators were able to choose their target, because they might show subtle behavioural hints of such preference; and (8), the preference measure (contrasting discrete choice with continuous measures, in contrast to only discrete choices analysed by Jones and DuVal 2019), for which the authors predict a weaker discrete choice effect, because discrete choice might underestimate the degree of mate-choice copying due to being unable to capture subtle differences in preference. Although Davies et al. (2020) have more factors than Jones and DuVal (2019), they used separate statistic models for each different fixed factor instead of using a single model with all the factors.

Overall, Davies et al. (2020) found a positive effect of mate-choice coping (odds ratio 2.83, 95% CI: 1.85–4.35), similar to Jones and DuVal (2019). However, contrary to Jones & DuVal (2019), the authors also found little evidence for publication bias. Of all the tested factors, only the taxonomic group ($p = 0.04$) and the design type ($p = 0.01$) were statistically significant. Close to what was predicted, mammals seem to have stronger copying strength, followed by fish and birds, then arthropods. The authors urge to interpret these results with caution because of the small number of effect sizes for some groups, and the lack of studies for other taxonomic groups that might potentially show mate-choice copying, such as amphibians, reptiles, and nonhuman primates.

Contrary to the authors' prediction but consistent with Jones and DuVal (2019), the "before-and-after" design showed significantly stronger mate-choice copying effect than the "no pretest" design. The authors suggest that this effect could be due to the rapid succession of mating trials, and the experience gained by the observer in the first trial could affect the second one. The perception of a higher mate population density could make individuals choosier, for example.

Regarding the other factors, Davies et al. (2020) highlight the lack of difference in mate-choice copying behaviour between individuals born in captivity and in the wild. Based on the results of Jones and DuVal (2019), that individuals tested in the wild are more prone to copy, Davies et al. (2020) suggest that the environment during testing is an important factor for this behaviour. The authors also consider the small amount of data for some factor classes as the reason for some of the non-significant results, such as the rate of multiple matings and the male versus female studies. However, Davies et al. (2020) also consider alternative explanations for the lack of difference in mate-choice copying between sexes. One possibility is that the benefits of mate-choice copying are similar between males and females (e.g., to reduce sampling costs), and that males minimize the cost of sperm competition by strategically allocating sperm. Additionally, male mate-choice copying has often been tested in species with high reproductive investment, so males in these species should be as choosier as females and, therefore, equally prone to rely on mate-choice copying.

Davies *et al.* (2020) detected that many studies are focused on a small number of species. Out of 89 studies, 20 were on guppies, 9 on Japanese quails, and 9 on *Drosophila melanogaster*. However, the 16.7% of the heterogeneity was between-studies, 5.6% due to phylogenetic history and 0% to between-species differences, meaning that the overall effect of mate-choice copying was not due to a few well-studied species. The authors also note a high amount of heterogeneity due to observation-level differences (62.47%) that remained unexplained, meaning that there are still other unknown factors that might affect this behaviour. Davies et al. (2020) suggest that mate sampling costs might play an important role in mate-choice copying, but unfortunately there are not enough studies linking both variables, making broad-scale analysis difficult. However, the authors also point out that some empirical studies tried to study this cost indirectly by testing copying in high-cost environments (Briggs et al. 1996; Dugatkin and Godin 1998), and failed to find any significant effect. Another factor that the authors consider important for mate-choice copying is the ability to assess mate quality, something that is supported by some empirical studies that allowed females to choose between similar and non-similar males (Dugatkin 1996; Witte and Ryan 1998).

The aforementioned factors can be important topics for future studies, and in addition to that, Davies et al. (2020) suggest studying the role of memory in mate-choice copying, namely on how long the social information obtained during demonstration is remembered, and how easily it is forgotten or overwritten.

5.2 Two research avenues for future mate-choice copying studies: a comment on Davies et al.

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Since the early 1990s, when Pruett-Jones (1992) revised and formally defined the concept of mate-choice copying, this type of nonindependent mate choice has been consistently studied and a handful of experimental, theoretical, and conceptual works has been published every year. The accumulated amount of experimental studies is now allowing researchers to use meta-analytical methods to characterize mate-choice copying both in humans (Gouda-Vossos et al. 2018) and in nonhuman animals (Jones and DuVal 2019; Davies et al. 2020). The literature search of the two meta-analyses in nonhuman animals was carried out 1 month apart, showing that many researchers in the field today consider this analysis necessary. And, because the two studies show enough methodological differences, both are useful and complementary. Additionally, Davies et al. (2020) consistently discuss their results with those of Jones and Duval (2019), guiding the reader toward the nuances of both studies that, otherwise, could be confusing.

Davies et al. (2020) found two factors influencing significantly mate-choice copying across studies: the taxonomic group and the design type. For the taxonomic group, the effect of mate-choice copying is stronger in mammals and progressively less strong in birds, fish, and arthropods. Given that mate-choice copying is a form of social learning, this result may indicate general cognitive differences between taxonomic groups, but the authors caution against the overinterpretation of the data given the still small number of species that can be analyzed by group. Indeed, most studies on mate-choice copying have only been carried out on a small number of species, so it is still difficult to understand what factors—ecological, social, or cognitive—really affect the occurrence and strength of this behavior.

Regarding design type, Davies et al. (2020) show that mate-choice copying is stronger when focal individuals can make an initial choice before the demonstration (the “before-and-after” design) compared to when they can only choose after the demonstration (the “no pretest” design). This is important information to be considered by researchers in future experiments; however, it is also relevant to point out that most studies of mate-choice copying in arthropods use the “no pretest” design, and they are also found to be the less prone to copy by the authors. Given that the taxonomic group and the design type were analyzed in separate meta-analytic models, it is not possible to rule out the hypothesis that these two moderators are dependent on each other.

Meta-analyses are extremely important tools to point out where research is lacking and Davies et al. (2020) propose two research avenues for future studies: how mate-choice copying operates within a species and how widespread it is across taxonomic groups. We believe that these are indeed relevant recommendations and would like to expand on them. The first avenue leads to using model species, taking advantage of the tools available for them, to more deeply understand the mechanisms affecting the occurrence and strength of mate-choice copying. It implies using new designs adapted to the specific questions being asked. The second avenue leads to using nonmodel species with contrasting ecologies and life histories to investigate the factors that could predispose mate-choice copying evolution. It should imply using standard designs to make the results of different species more comparable. For example, the first study of mate-choice copying in the model species *Drosophila melanogaster* (Mery et al. 2009) uses, in one of its experiments, the standard before-and-after design only with the setup adaptations to a small animal as the fruit fly. Its second experiment and the studies that were published subsequently are about how mate-choice copying operates within the species and so use design adaptions to answer specific questions, such as mate-choice copying generalization (Mery et al. 2009), sperm depletion (Loyau et al. 2012), conformity (Danchin et al. 2018), costly variants (Nöbel et al. 2018), and neuronal mechanisms (Monier et al. 2018), among others.

More studies following these two research avenues would greatly help future meta-analyses to better characterize the occurrence, strength, and mechanisms of this fascinating behavior across species. Moreover, because mate-choice copying is likely to generate cultural evolution (Danchin et al., 2018) and affect the diversification processes of populations and species (Varela et al. 2018), studies are also needed to help characterize its evolutionary potential.

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5.3 Summary of other commentaries to Davies et al. (2020)

Besides my commentary to Davies et al. (2020) presented in section 5.2, there were three other Invited Commentaries from other authors to that study, along with a response commentary from the authors. In this section I briefly summarize all these contributions.

In their commentary, Danchin et al. (2020) focuses on three points. First, they highlight the use of the term “mate copying” instead of “mate-choice copying” used in Davies et al. (2020). According to these authors, the term “mate-choice copying” focuses too much on the information given by the demonstrator (that chooses their mate), instead of focusing on the information given by the target mate themselves (Wagner and Danchin 2010; Danchin et al. 2020). Both terms have been used interchangeably in recent literature, so there is still no consensus on the correct term. In this thesis, I choose to use the term ‘mate-choice copying’, because I consider that ‘mate copying’ can easily be mistaken for just individual mate-choice copying, excluding the process of mate-choice copying generalization. Second, they agree with the suggestion of Davies et al. (2020) that distinguishing between individual mate-choice copying and mate-choice copying generalization is important because of the ability for generalization to culturally evolve (see section 1.4). I agree that this distinction is important because, besides the argument presented by Danchin et al. (2020), as I demonstrate in chapter 4 (Sapage et al., in prep), individual mate-choice copying and generalization can have different ecological and evolutionary effects in populations. Third, they consider that the result of Davies et al. (2020) in finding stronger mate-choice copying in the “before-and-after” design versus the “no pretest” design to be a regression to the mean effect. According to the authors, there are two types of “before-and-after” designs, one where the experimenter chooses the less preferred target to receive positive social information using a demonstrator, and one where this information is assigned randomly to a target independently of the initial choice by the observer. In both designs, particularly the former, regression to the mean might happen if individuals, by chance, choose strongly in the initial choice and, by consequence, make a milder decision in the second, falsely suggesting a reduction in preference for the previously preferred male. Thereby, Danchin et al. (2020) recommend for “no pretest” designs. In my view, the suggestion to eliminate “before-and-after” designs is a double edge sword. On the one hand, it can eliminate the regression to the mean effect, as well as other confounding effects. One that I identify is the effect of gaining personal experience during the initial choice, which may create inertia in the subsequent acquisition of social information. On the other hand, “the before-and-after” design can identify which individuals are copiers and which are not, something that can only be inferred at the population level for the “no pretest design”. The discrimination between copiers and non-copiers can be important, for example, for the study of the genetics or neurobiology of this behaviour.

DuVal and Jones (2020), the authors of the first meta-analysis study summarized in section 5.1.1, consider that the stronger mate-choice copying of the “before-and-after” design might be caused by an increase in use of social information when target individuals are unattractive, or that females may change their choice in repeated testing. They suggest a broader use of the consistency of choice control described in section 1.2, which can also solve the problem of the regression to the mean raised by Danchin et al. (2020). DuVal and Jones (2020) find surprising that no difference was found between sexes and between individual mate-choice copying and mate-choice copying generalization, but caution that only a few studies were used for male mate-choice copying generalization. These authors also comment that Jones and DuVal (2019) found publication bias but Davies et al. (2020) did not. I agree that this is possibly due to the use of discrete instead of continuous variables by the former, along with a smaller number of studies, showing that discrete variables are less effective at capturing copying behaviour. In terms of statistical methods, DuVal and Jones (2020) criticize the use of separate models for each factor, because it can increase type 1 errors and assume no covariation of the factors. This is something that I also commented in section 5.2 specifically for the factors “taxonomic group” and “design type”. Finally, they recommend that future studies of sexual selection should more frequently consider the role of the social context.

Brooks (2020) takes a more personal approach and describes his difficulties in replicating mate-choice copying in his early studies with guppies (Brooks 1996, see section 1.2) and how there might be variations within the species. Then the author notes how meta-analysis methods have evolved to be able to filter all the noise from the signal in mate-choice copying studies ranging from mammals to fruit flies. Although these two studies are similar, Brooks (2020) is glad that they both got published and conclude by pointing out how far mate-choice copying studies have developed since he worked with it in the late-1990's.

The authors of Davies et al. (2020) meta-analysis replied to all the comments (Dougherty et al. 2020). They first thank all the authors for their comments and describe how hard it was to write their paper after Jones and DuVal (2019) was published, but they were able to do it with the support of the reviewers and editor. The authors address the issue of not considering correlations between factors as a possible reason for finding a significant effect in the "before-and-after" design versus the "no pretest" design by saying that there are many other explanations that were proposed by the other commentaries and in Jones and DuVal (2019). About the regression to the mean effect highlighted by Danchin et al. (2020), the authors suggest that future studies should account for it, or that they should preferably use the "no pretest" design, especially as a "standardized" procedure for non-model species, as suggested by Sapage and Varela (2020, section 5.2). Regarding the two research avenues proposed in Sapage and Varela (2020, section 5.2), Dougherty et al. (2020) suggest testing mate-choice copying in more non-model species to test for diversity, as 52% of effects sizes are from the family Poeciliidae, and researchers might be selective in the species they test for this behaviour. I agree that this should be one of the focuses in empirical research, as testing mate-choice copying in more diverse species would allow researchers to further understand the relationship between this behaviour and many environmental and life history factors.

As a general synthesis, it seems that researchers in the field are starting to look at the big picture, asking what the overall causes and effects of mate-choice copying are, not only in a few specific species, but in all animals capable of processing social information and subjected to mate choice decisions. These studies are focused on empirical research, but they can also help greatly to straighten the gap between empirical and theoretical studies of mate-choice copying, as they can help researchers to find general rules that might be applied to their theoretical models, such as the overall effects of mate-choice copying on ecology and evolution like the models presented in chapters 3 and 4.

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Chapter 6

General Discussion

Throughout the chapters of this thesis, I have introduced the concept of mate-choice copying (MCC) (chapter 1), showed, through individual-based models, various ways in which MCC can affect the evolutionary dynamics of populations (chapters 2 to 4), and developed ideas for two research avenues for future MCC studies (chapter 5). This thesis is innovative in the way it explores the role of MCC in population dynamics in a spatial setting, focusing on dispersal and local adaptation, and it suggests a framework for future empirical studies of MCC that also benefits the construction of future theoretical models.

Here I will present a synthesis of my work with a summary of the main results (section 6.1), an integrated discussion of how MCC can affect population dynamics (section 6.2), a discussion of the limitations of the models presented here (section 6.3), and perspectives for future research (section 6.4).

6.1 Results overview

Chapter 2 (Santos et al. 2017) explores the effects of MCC in a single habitat patch using individual-based models. Results show that if a more adaptive male trait is introduced into the population and female choosiness (i.e., “choice cost”) is not weak, MCC can evolve through indirect selection by hitchhiking on the new male trait. Unlike Servedio & Kirkpatrick (1996) who build a similar model to study the evolution of MCC, the model in chapter 2 uses non-overlapping generations. Despite this difference, both models show the evolution of the system in two timescales: the male trait evolves first, followed by MCC at a slower pace. Additionally, the presence of MCC in a population can increase its fitness by leading to a higher proportion of adapted males. As such, MCC, at a single habitat patch scale, has a positive effect on a population’s evolutionary dynamics. However, MCC only evolves when female preference does not coevolve with the male trait. The conditions in which this phenomenon can occur may be hard to imagine while considering a single patch, but it becomes more plausible if we consider a population distributed throughout multiple patches and connected through migration (Bakker & Pomiankowski 1995; Greenfield et al. 2014), where females develop a preference for the males of their own habitat patch, but where migrant females, by copying local mate choices, make better choices than if they followed their innate, no longer adapted mate preferences. This is what was simulated in chapter 3.

In chapter 3 (Sapage et al. 2021), the individual-based model was, therefore, built on a scale of many habitat patches, with a heterogeneous environment with spatial autocorrelation. This model shows that MCC is, as expected, advantageous to migrant females, and that it can even promote dispersal in both individuals with and without the copying allele. However, as expected under high migration rates, MCC reduces the degree of local adaptation of a population, promoting convergent mate preference between patches. The increase in dispersal tendency and the evolution of MCC is more evident when females copy only when they disperse. This model shows, for the first time, a link between the evolution of MCC, or social learning in general, and dispersal. The relevance of this finding is clear since dispersal is a trait with major implications to ecology and evolution. We then enlarged the study to a scenario of population range expansion and adaptation, which we simulated in chapter 4.

In chapter 4 (Sapage et al., in prep.), the individual-based model was, therefore, built on a scale of two habitats with an environmental gradient between them. Results show that MCC helps to increase expansion speed, but only under specific conditions: when generalized MCC is combined with female preference for condition-independent male traits, and when individual MCC is combined with female preference for condition-dependent ones. Both dispersal tendency and copying errors (the variation in copiers' mate-choice) help in affecting the speed of expansion. In this model generalized MCC did not affect dispersal, a result that can be explained by the assumptions of the model: to simulate a scenario of range expansion, I considered more demanding conditions, such as a higher carrying capacity, hard selection, and no spatial autocorrelation. On the other hand, individual MCC substantially increased dispersal, a result that can be explained by kin competition avoidance. These results show that MCC, on a multiple habitat scale, can still have a positive effect on a population's evolutionary dynamics, reinforcing and enlarging our previous finding of the importance of MCC, and social learning in general, to the evolutionary dynamics of populations. Additionally, the results highlight the importance of considering different copying types and preference rules while discussing the effects of mate-choice copying.

Chapter 5 (Sapage & Varela 2020) focuses on a published Invited Commentary to a meta-analysis where the authors show how most empirical studies of MCC are done in a few selected species, and how the results of MCC might depend on the methodology used (Davies et al. 2020). Given these findings, I suggest two different avenues for future research: firstly, the creation of a standardized experimental paradigm to help making the results from different species more comparable. Testing MCC on more species is necessary for a better understanding of the phylogenetic distribution of this behaviour and how it varies between taxa; and secondly, the creation of variations to the standardized paradigm, to test specific mechanisms of MCC in model species, for which there are more experimental tools available and knowledge of their behaviour and its mechanisms. An organization of work of this kind will be an important step to understand the effects of MCC on ecology and evolution because, as shown in the previous chapters, slight differences in MCC rules can have important implications on population dynamics.

6.2 General effects of MCC on population dynamics

6.2.1 Evolution of MCC

In this thesis, I have presented many models that simulate the evolution of MCC. The model in chapter 2 (Santos et al. 2017) focuses on genetic effects, while the models in chapters 3 (Sapage et al. 2021) and 4 (Sapage et al., in prep.), given the absence of genetic linkage between the copying gene and any other locus, focus on the costs and benefits of the copying behaviour itself (see sections 6.3.4 and 6.3.5). The two latter models show that generalized MCC can be a good strategy for individuals migrating to a new habitat patch, either because they are copying from local, more adapted, females; or because females adjust their preference towards an existing male in the patch, thus giving them a higher chance to choose more adapted males than non-copiers. This benefit, however, disappears if female preference is towards a male trait that is condition dependent, because in this situation non-copier females can choose the most adapted males in each patch not giving the copying females the opportunity to do better choices.

Although it is still not known how much MCC is genetic (see section 6.3.1), the models in this thesis show possible ways in which MCC might have evolved. Moreover, the costs and benefits of this behaviour in a spatially structured population are theoretically still valid even if the variation in MCC behaviour is not exclusively genetic.

6.2.2 MCC and dispersal

In this thesis, I have found two ways that MCC might affect dispersal. Chapter 3 shows that generalized MCC can make the choice of immigrants more adaptive, increasing the tendency for individuals to disperse; and chapter 4 shows that individual MCC can increase the degree of kin competition, such that individuals are selected to disperse to other patches, where competition is between non-related conspecifics. In both cases, the increase in dispersal not only affects copiers, but non-copiers as well. This effect appears mostly because there is no genetic linkage between the copying and dispersal, and both copier and non-copiers females tend to choose similar mates.

Many different factors have already been found that determine an individual's decision to disperse (Fowler 2005; Clobert et al. 2012; Matthysen 2012). A major finding in our models is that MCC can be intrinsically linked with dispersal in many ways, something never considered before

. According to these models, MCC can increase the average dispersal tendency of the entire population. This effect alone shows the importance of studying how MCC and social learning in general might affect ecology and evolution.

6.2.3 MCC, local adaptation, and expansion speed

Chapter 3 shows that MCC can decrease the degree of local adaptation in populations living in a heterogenous environment. This happens because MCC increases the competitiveness of migrant females – reducing the costs of dispersal – by allowing them to choose similar males as the local females. In chapter 4, because the model considers hard selection, expansion speed is directly related to the ability of individuals to adapt to an environmental gradient. In this case, because natural selection is strong, MCC can only affect the local adaptation of the preference allele, but not the trait. Many researchers consider MCC to be a shortcut in female choice, allowing females to quickly update their innate choice and make a more informed decision (Gibson & Höglund 1992; Vakirtzis 2011, section 1.3). Relying on the choice of others, however, lowers the selective pressure for female innate preference and/or assessment ability, so copier females can afford having their innate preference maladapted to the local conditions. During population expansion this effect might have some drawbacks: theoretically, if chooser females start rejecting males that are very different from their innate preference, expansion will halt in a certain threshold until the female innate preference becomes adapted enough to the new environment. A similar effect is found in Phillips (2012), which shows that the tendency of individuals to be maladapted at the invasion front, can help promote stable range edges. MCC can also affect local adaptation indirectly, through the increase in dispersal tendency (see section 6.2.2), since it promotes gene flow (Garant et al. 2007). In this case, even if the proportion of copiers in the population is small, if dispersal is increased, the population can still show the effects of MCC on local adaptation.

6.3 Models' assumptions and limitations

Box & Draper (1987) famously said that "essentially, all models are wrong, but some are useful". This is also true for MCC theoretical models. In this thesis, I have presented three different theoretical models, and I will discuss the reasons and the potential consequences for some of the assumptions I used. As a rule of thumb, the simplest possible assumptions were used in each model, while still trying to capture the essential dynamics of the biological processes.

6.3.1 Genetic background

An important assumption in all three models (chapters 2 to 4) is that MCC has a genetic basis. Many theoretical models use this assumption (Witte et al. 2015), but it is still not clear why some species, and even some specific individuals copy the mate choice of others while others do not (see section 1.4). An alternative assumption could be that all individuals are prone to copy if certain external conditions are met, such as those discussed in meta-analysis studies (Jones & DuVal 2019; Davies et al. 2020). However, this assumption is hard to model without knowing the precise conditions in which MCC occurs, which are not clear yet (Davies et al. 2020). Supporting the idea of MCC being non-genetic, Dugatkin & Druen (2007) did not find any heritability of MCC from mothers to offspring in fish. On the other hand, research with guppies (*Poecilia reticulata*) also show that females from wild Trinidadian populations and their descendants copy the mate choice of others, while feral or store-bought populations do not (see section 1.3). Overall, these results suggest that MCC should have at least some genetic basis, but can be influenced by external conditions, such as size and age of both the focal individual and the demonstrator (Amlacher & Dugatkin 2005), or the traits of the mates themselves (Dugatkin 1996). However, the introduction of these variables in a theoretical model would require many additional assumptions that would overcomplicate the model. Here, I decided on the simplest possible assumptions, namely that MCC is determined by a single locus in haploid populations. Despite the simplicity, I consider the models presented in my thesis to be illustrative of the possible effects of MCC to the evolutionary dynamics of populations. Still, further knowledge on what might affect MCC will certainly help in creating more accurate theoretical models in future.

6.3.2 Genetic linkage between alleles

Genetic linkage was used in the model from chapter 2 (Santos et al. 2017), where we showed that MCC can invade through indirect selection. Linkage was used here to account for Vakirtzis (2011) suggestion that innate preference and copying should have evolved together and been shaped by the same evolutionary forces, and to be comparable with Servedio & Kirkpatrick (1996).

On the other hand, genetic linkage was not considered in the models from chapters 3 and 4, where we studied the effect of MCC on migrant females dispersing to a new patch. Assuming genetic linkage within that framework would have added additional complications, given that these models also include the dispersal allele that, by the same logic, would also be linked to the remaining genes. Assuming that all genes are in the same chromosome and creating all the specific arrangements from which the loci are linked would make the model overly complex. For this reason, I modelled MCC without linkage, while still simulating a warmup period to allow for the population to reach a steady state. Nonetheless, it is possible that the models with linkage would lead to different results, such as promoting different dispersal strategies between copier and non-copier females: copiers might disperse to new locations while non-copiers might tend to stay in their natal patch. These dynamics are worth exploring in future studies.

6.3.3 Binary versus continuous traits

Another difference between the models is that chapter 2 considers a binary male trait (*x* and *y*) – like Servedio & Kirkpatrick (1996) – while the models from chapters 3 and 4 take a continuous trait into consideration. This change was needed because it would have been impossible to create a heterogeneous but autocorrelated environment (chapter 3), or an environmental gradient (chapter 4) using a single binary variable. The main problem with the continuous trait approach is that many aspects of MCC are studied in a binary way, usually reflected in a dichotomous choice (see section 1.2). This means that I had to create additional assumptions to cope with continuous traits, such as the functions related to individual survival, to female choice, and to the way copier females incorporate the information when they observe more than one mating. Again, these assumptions may not be correct, although I tried to use the most intuitive functions. On the other hand, defining the male trait as a continuous function is rather appealing, and this added complexity to the latter models has advantages of its own.

6.3.4 Copying criteria for multiple matings

How females assimilate information from multiple matings is also considered differently in the three models. In chapter 2, copier females would only consider the first mating they saw. This criterion was chosen for this model as it is the simplest, and given that the mating order is random (see section 6.3.5), we found that this assumption is adequate to reflect the evolution of MCC. In chapter 3, given that the model focuses on how migrant females acquire information when they arrive in a new patch, I decided that females should consider multiple matings. In chapter 3 I have considered that females copy the trait of the most popular male, using that trait as a criterion to choose similar males. This was a compromise for simplicity, given that, theoretically, there are many possible ways for individuals to compile that information. For example, females can prefer the average trait of all the males they observed mating, or they can have a higher preference towards the trait of the male they saw mating last.

The assumption was updated in chapter 4 by attributing a social score to each male considering not only the number of times they have been chosen by demonstrators, but also the similarity between them. This change was made to further contrast the differences between generalized and individual MCC, which was explored in this chapter. Migrant females from chapter 3 would possibly benefit even more from copying if that same criteria were used, given that they would be able to choose based on the average choice of demonstrator females.

6.3.5 Mating order and mate-choice of potential copiers that did not observe a mating

The mating order of the individuals is another assumption that might have affected the outcome of the models. In chapter 2, females (copiers and non-copiers) are chosen to mate in a random order, but copier females skip their turn if they have not witnessed a mating before being selected to mate. In chapters 3 and 4, copier females wait for all non-copiers to mate first and use their innate preference if they did not observe any mating. It is not known whether individuals that are prone to copy tend to wait longer to mate than non-copiers, but individuals that rely on social learning do actively prospect in other contexts (e.g., habitat selection, see section 1.8). Many other theoretical models of MCC are not individual-based, so the precise mating order is not clearly defined. However, some models assume that younger females copy older ones from different cohorts (Kirkpatrick 1982; Servedio & Kirkpatrick 1996; Stöhr 1998), allow for a few random females to choose first and the others to copy their choice (Agrawal 2001), or allow for copier females to copy both the choice of informed choosers and uninformed copiers (Pruett-Jones 1992).

In chapters 3 and 4, MCC would probably have a weaker effect in population dynamics if the mating order was random due to a smaller number of copiers, and it would be less adaptative if females with the tendency to copy decided to choose randomly when no social information is available. Random choice for this situation was used in past theoretical models (Losey et al. 1986), but I decided to avoid it because I wanted to contrast the effects of MCC versus innate mate choice, rather than the effects of random choice.

Chapter 2 also considers a threshold for mated females in each generation (85%), above which no more females are allowed to mate, making the mating order more important than in chapters 3 and 4. Because copier females only mate after observing another mating, this threshold creates a cost for copier females that is counteracted by the "choice cost". When "choice cost" is low, non-copier females will accept most males and copiers would tend to copy most males as well. However if "choice cost" is high, non-copier females will mostly accept their preferred male. In this situation, if non-copiers are surrounded by non-preferred males, they might miss their chance to mate. This threshold is important when studying the evolution of MCC itself, the goal of chapter 2. Since in chapters 3 and 4 I mainly wanted to test the population effects of MCC, these assumptions were removed. Copier females will necessarily breed last in these models, so not allowing for some of them to breed would create a strong selection against MCC.

6.3.6 Expression of the trait allele for viability

In chapter 2, male viability is determined by its genotype (x or y), while non-copier females may or may not pay a viability cost (s_c). This contrasts with the models from chapters 3 and 4, where both female and male viability are affected by their own *trait* allele. The different assumptions were created for several reasons. First, in chapter 2 the model was created to be comparable with Servedio & Kirkpatrick (1996), where similar assumptions about viability were used, while in the models of chapters 3 and 4 I wanted to make sure that the copying gene only affects viability through female choice. Furthermore, in chapters 3 and 4, I wanted to test the population effects of MCC in an environmental matrix, so both female and male offspring should be subjected to natural selection based on their trait. This is particularly relevant for chapter 4, where the model simulates a distribution expansion through an environmental gradient. In the model from chapter 2, if females were also to express the trait allele for viability, the selection for the most adapted allele y would probably have been stronger, along with the ability for the copy (social) allele to evolve by hitchhiking.

6.3.7 Natural selection

Natural selection (viability/survival) was also calculated using different methods in the different chapters. In chapter 2, only male offspring is subjected to viability (hard) selection, and it is dependent on their trait allele (*x* or *y*), as explained in section 6.2.6. In contrast, survival in chapter 3 is introduced as soft selection, meaning that offspring compete for a predetermined number of spots in a patch. This way of modelling selection may favour migrants because maladapted offspring may still survive in a patch if no better adapted individuals are present. The model was created this way mainly because we wanted to model localized phenomena, so even the maladapted individuals are considered adapted enough to survive in a patch when competition is low. In chapter 4, I added hard selection, because the objective of chapter 4 was to understand the speed of adaptation during population expansion. If maladapted individuals could also colonize a patch, the model would become trivial. To compensate for hard selection, I decided to increase substantially the population size for each patch (see section 6.3.9).

6.3.8 Non-overlapping generations

Models in chapters 2 to 4 consider non-overlapping generations, meaning that the social information created by mating events can only be transmitted horizontally, and they are created *de novo* at each generation. This assumption may be a simplification of the true effect of MCC, especially generalization, due to the potential for it to evolve culturally (Danchin et al. 2018) if social information can be also transmitted between generations (vertically and/or obliquely). The decision to use non-overlapping generations was mostly due to simplicity and technical limitations. However, in chapter 2, we found a similar effect in MCC evolution to Servedio & Kirkpatrick (1996), although they considered oblique transmission in their model (see section 6.1). Even with non-overlapping generations MCC still evolves and shows a significant effect in population dynamics, so if we were to consider overlapping generations in our models, we predict that the effects of MCC would remain the same or become more significant.

6.3.9 Technical limitations

Individual-based computer simulations are bound to be computationally intensive, given the computer requirements to explicitly simulate each interaction explicitly, making it susceptible to time and memory constraints. Although the assumptions of the model should always have a biological justification, technical limitations necessarily also play a role in creating these models.

All models considered an environment with a toroid (chapters 2 and 3) or cylindrical (chapter 4) shape to minimize the problem dealing with edges. In chapter 2, the model consists of a 900 grid squares with at most one individual per square, while in chapter 3 there are 625 grid squares with at most 16 individuals per patch, and in chapter 4 the model consists of 800 patches, with a carrying capacity of 64 offspring per patch. The increase in the number of individuals was needed because of the different scales considered by the different models, and it also means that the simplification of some of the algorithms was necessary. For example, in chapter 3 individuals were mapped using real coordinates in a matrix, and dispersal was calculated by choosing a random direction and a distance defined by the dispersal allele. In contrast, individuals from the model in chapter 4 were mapped using integers in a grid, and dispersal was calculated as the probability to move into a random adjacent patch.

In terms of mate sampling, females in chapter 2 could accept or reject a male during each turn (sequential sampling), while females from chapters 3 and 4 were only able to choose a mate from a set of possible candidates (single sampling). The latter assumption is computationally less intensive, but it also means that females tend to settle for males that are the closest to their preference, even when those males might be unattractive in absolute terms. In chapter 2, allowing for single sampling would have possibly given the same effect as increasing the “choice cost” because females would more likely choose males that they prefer the most. On the other hand, in chapters 3 and 4, given that generalized MCC creates a stronger mismatch between innate preference and trait, the effects of sequential sampling might depend on the threshold for rejection. A high threshold would lead non-copiers to reject males more often. Copier females, however, will match their preference with an existing male in the patch, so they might tend to choose earlier than many non-copiers (but not all, given that non-copiers still need to choose first). This effect could create some complex dynamics worth exploring in future.

6.4 Future perspectives

About 30 years after the first seminal papers about MCC, there is still much to be known about the subject. Witte et al. (2015) presents four main questions to be explored in the study of this behaviour: (1) the benefits of MCC; (2) the genetics of MCC; (3) the relevant information for MCC to occur; and (4) the role of the demonstrator (model) individual. More recently Jones & DuVal (2019) and Davies et al. (2020) also suggested additional topics for future MCC research, described in detail in sections 5.1.1 and 5.1.2. My thesis shows many other questions worth exploring and I will present them here. Some of these questions overlap with the ideas suggested by some of the aforementioned studies but reshaped within the framework of this thesis.

6.4.1 Distinction between different types of MCC

Future research should focus on the mechanisms behind individual and generalized MCC, an idea already discussed in Davies et al. (2020). Is generalization a by-product of individual MCC when individual recognition fails? Are they different mechanisms that evolved differently in different species? There has been an increasing interest in the study of MCC neurobiology (Kavaliers et al. 2017; Monier et al. 2019). Understanding the cognitive pathways behind MCC, along with its relation to other types of social learning, should indeed help answer these questions.

The distinction between individual and generalized MCC should also be clear while discussing its effects in ecology an evolution, as shown in chapter 4. Other distinct effects can also appear if cultural evolution is considered (Danchin et al. 2020; Davies et al. 2020, sections 1.2, 5.1.1, and 5.3), given that generalized copied preferences can carry over from generation to generation while individual MCC cannot. Cultural evolution might counteract the decrease in local adaptation caused by MCC if the population is initially well adapted to a patch, but it can also cause further delay when populations are trying to expand to a new environment. Another important aspect, although not considered in the models from chapters 3 and 4, is the cost of MCC, which may differ between the two types of copying, as the information transmitted during individual MCC is much more specific (unique to the individual) and depends on whether the copied mate is available for further mating. On the other hand, generalization might be neurologically and energetically more demanding, given that individuals would need to find and assess the similarity of potential mates.

6.4.2 Which traits to copy?

Given that individuals can generalize different kinds of traits, from artificial (e.g., colouring powders or artificial feathers) (White & Galef 2000; Mery et al. 2009; Kniel et al. 2015) to natural ones (e.g., body size: Mery et al. 2009; wing type: Nöbel et al. 2018), what are the traits most likely to be generalized? In chapter 4 the male traits that females innately preferred (and as such might also be chosen by copier females) were either condition dependent or condition independent. Both types of traits are documented in sexual selection research (Hamilton & Zuk 1982; Wagner & Danchin 2010; Roulin 2016) and include for example auricular patch colour chroma (condition independent) and auricular patch size (condition dependent) in the king penguin (*Aptenodytes patagonicus*) (Schull et al. 2018). However, empirical studies of MCC using one type or the other, have never been made. Because, in chapter 4, I found that generalization is more adaptive if females copy condition-independent traits, it would be enlightening to study this hypothesis empirically. In case of individual MCC, because copying happens at the individual level, this question does not occur. However, in both types of copying, it is still important to understand the preference of choosers and whether copying is conditional to any set of male traits.

Additionally, how do copier deal with multiple traits? Do they generalize one specific trait over another, or do they consider as many traits as possible while judging for similarities between mates? Are copiers more prone to generalize traits that are already part of their natural preference function, or traits that are rare and unusual? All the models in this thesis presented a single trait, so these questions remained to be explored.

6.4.3 Who, when, and what behaviours to copy?

Researchers have long been interested in finding the conditions that might affect the adaptive value of MCC (Jones & DuVal 2019; Scauzillo & Ferkin 2019; Davies et al. 2020). Chapters 3 and 4 show the importance of knowing the modalities of this behaviour (e.g., preference rules and copying types) before predicting its usefulness and evolutionary effects. These modalities resemble the concept of social learning strategies (or transmission biases) (Boyd & Richerson 1985; Laland 1994), recently reappraised for its importance in understanding the adaptive value of social learning (Kendal et al. 2018). The transmission biases are related to “who”, “when”, and “what behaviours” to copy, and they can be applied to MCC, although it has never been formally done.

There is some empirical evidence for “who to copy” strategies, linking the quality of model females to the likelihood of copying (Hill & Ryan 2006). Strategies concerning “what behaviour to copy” have been less studied, but, by the definition of MCC, individuals copy the mate choices of demonstrators. This can be the acceptance or the rejection of a mate. The copying of rejection has been shown in sailfin molly (*Poecilia latipinna*) (Witte & Ueding 2003) but failed to be demonstrated in *Drosophila melanogaster* (Nöbel et al. 2022).

Strategies concerning “when to copy” refer, in MCC theory, to situations when copiers lack information about mate quality, either due to inexperience or having outdated information (Nordell & Valone 1998). In fish, for example, females have a higher propensity to copy larger, supposedly older, and more experienced females (Dugatkin & Godin 1993; Amlacher & Dugatkin 2005). In chapter 3, I considered a hypothetical case where only immigrant females copy, because they have no information about local male quality. In that specific context, they might perceive other females to be more experienced than themselves or to have updated information. It would, therefore, be extremely interesting to empirically test MCC while simulating migration at the same time.

Conversely, individuals that have migrated together might try to copy each other instead, considering local females to be too different from themselves for their choice to matter. A study with sailfin mollies showed that only individuals in sympatry with Amazon mollies (*Poecilia formosa*) tend to copy Amazon’s mate choice (Heubel et al. 2008). On the other hand, one recent study in deer mice suggests that familiarity or kinship with demonstrator females does not affect olfactory MCC (Kavaliers et al. 2022). In the models from chapters 3 and 4, I assumed, for simplicity, that females were unable to distinguish between local and migrant demonstrators, so females copied indiscriminately. However, more studies, both empirical and theoretical, are needed to identify the specific criteria individuals use to decide whom to copy and what are the consequences of those choices.

6.4.4 How does multiple copying work?

Another important question to explore is related to how individuals combine the information of multiple matings. (Danchin et al. 2018) found that female fruit flies (*Drosophila melanogaster*) act in a conformist way, copying a trait that they saw most other females choosing. However, knowing that individuals might tend to copy some demonstrators more than others, as shown in the previous section, females can also be expected to give different weights to each mating event if they copied multiple demonstrators. Empirical studies are needed to specifically understand how individuals' weight and combine the choice of multiple matings. Both neurocognitive and empirical studies can be used to answer the question of mass copying. This question is related to the topic discussed in section 6.3.4, where I explore the differences in the assumptions I used for chapters 3 and 4.

6.4.5 Generalization of continuous traits

Many empirical studies of generalized MCC consider binary traits, such as males powdered with different food colouring (White & Galef 2000; Mery et al. 2009; Danchin et al. 2018). However, many traits involved in sexual choice are continuous in nature. For example, there are studies where females copy the choice of females for males of different sizes (Witte & Noltemeier 2002; Mery et al. 2009). In this situation, how do females generalize continuous traits? Do they generalize the absolute (e.g. a male of size *X*) or the relative value (the smaller the better) of the trait? What is the margin of error of such generalization? Is it related to individual memory, to the ability of females to discriminate different traits, or to the female preference function?

In chapter 4 I considered that the degree of what copiers consider similar is controlled by the sexual selection strength (or choosiness) and is identical with the criteria used by non-copiers. Continuous traits are important to be considered because the environment can also change in a continuous manner and understanding how MCC generalization operates in such scenario is important to determine its outcome.

6.4.6 Testing empirically the effects of MCC on population dynamics

Empirical tests of MCC can be hard, but the result of theoretical studies can help in finding specific hypotheses that are able to be empirically tested. This thesis showed various ways by which MCC might influence ecology and evolution, but it is important to empirically test these results.

Empirical tests for the effects in chapter 2 can include, for example, a comparative analysis to test whether populations with more variation in female preference are the ones that are more prone to copy. For chapter 3, it is interesting to test if populations with MCC are more prone to disperse and to show a lower degree of local adaptation than populations without MCC. Additionally, as suggested above (section 6.4.3), empirical tests could test if migrant females are those that are more prone to copy than resident ones. Researchers already found some behavioural differences between residents and dispersers in many species (Ronce & Clobert 2012). In some species, residents tend to explore less (Haughland & Larsen 2004) and take less risks than migrants (Cote & Clobert 2010). For chapter 4, empirical studies could try to assess how much females copy condition-independent versus condition-dependent traits and whether generalized MCC is more frequent when paired with condition-independent traits. Experimental evolution can also be used to study the correlation between dispersal syndromes and MCC. Torriani et al. (2010), for example, artificially selected moth populations based on their flight activity and compared their survival and reproductive output. In similar experiments, it would be interesting to compare flight/migration activity with MCC propensity.

These experiments will not be easy to implement, but they would be worth trying, given the importance that MCC appears to have for ecology and evolution, as revealed by my theoretical work.

6.4.7 Modelling specific examples of MCC

Chapters 2 to 4 are mostly proofs of concept to show various ways by which MCC might influence ecology and evolution, but further empirical and theoretical studies are needed to investigate the full magnitude of these effects. In chapter 5, based on the meta-analysis of empirical studies of MCC, I have suggested two new avenues of empirical research: one focused on model species to find specific mechanisms, and another focused on testing MCC in non-model species from different taxonomic groups to document how widespread this behaviour is. I suggest taking a similar approach for theoretical models. One avenue of theoretical research includes the approach that I followed in my thesis, where generic processes, with hypothetical species, are modelled to test and understand, in general terms, the potential effects of MCC in evolution. One example could be testing the effects of temporal variation on MCC. The second should be much more targeted, where specific examples of MCC are modelled, preferably recreating the life-history traits, mating systems and mating behaviours of the most studied species for this behaviour, such as the Amazon molly complex (sailfin molly, Amazon molly and Atlantic molly), the guppy, or the fruit fly. Even within the same species, there might be differences in MCC depending on the populations (Dugatkin 1998; Heubel et al. 2008), or the experimental setup (Belkina et al. 2021). Additionally, in some species, males can also copy the mate choice of other males (Schlupp & Ryan 1997; Widemo 2006; Bierbach *et al.* 2011). Understanding why male MCC occurs and how it can interact with female MCC can also lead to fruitful research.

There are already some theoretical models with targeted species or taxonomic groups (Stöhr 1998; Santos et al. 2014; Danchin et al. 2018), but none of them were used in an explicitly spatial context with a structured population living in an environmental matrix. While the first avenue of research is a good first step to create general hypotheses, the second avenue would allow for researchers to make specific predictions for each species that they could test empirically.

Theoretical and conceptual work on population ecology and evolution typically excludes learning processes (Ronce 2007; Lavergne et al. 2010; Hill et al. 2011), but this type of work has been considered essential to understand and predict evolutionary patterns, including species responses to environmental change (Hill et al. 2011). What I have shown with my thesis is that social learning in the sexual selection context, besides affecting the course of sexual selection, can also have significant effects outside the sexual selection domain, such as in dispersal, local adaptation, and expansion range. These are non-negligible effects that should raise interest among evolutionary ecologists, including to assess species adaptiveness and invasive potential (Whitney & Gabler 2008; Hoffmann & Sgrò 2011). Naturally, more studies, both theoretical and empirical are still needed. While I recognize that the role of MCC in ecology and evolution is a complex subject to tackle, this thesis has shown that the magnitude of the effects of this behaviour on the ecology and evolution of populations is worth exploring.

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Appendix I

Supporting material for Chapter 2: Mate-choice copying: A fitness-enhancing behavior that evolves by indirect selection

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Figure S1. Moore neighborhood applied in the simulations

Figure S1. Next page shows the Moore neighborhood applied in the simulations, defined on a two-dimensional lattice with periodic boundary conditions (column 1 and column *L* are neighbors, row 1 and row *L* are neighbors; indicated by the dotted arcs) that makes the space a torus. The model uses a haploid population of chromosomes but for illustrative purposes, we show fruit flies that also perform mate-choice copying (Mery *et al.* 2009). At each time step, we randomly choose a cell in the grid occupied by a virgin female (framed female) and the eight cells that surround it (thick grey square). The target female can accept or reject mating according to the phenotype of a neighbor male courting her, as well as to her innate/learned preference. If she accepts the male, the naïve neighbor females carrying the copying allele will set their (learned) preference towards the successful male trait. We therefore assume that social information acquired by copying female choices prevails over their fixed genetic preferences. Male and female *D. melanogaster* in the figure retrieved from

https://embryology.med.unsw.edu.au/embryology/index.php/File:Morgan_1925_fig06.jpg

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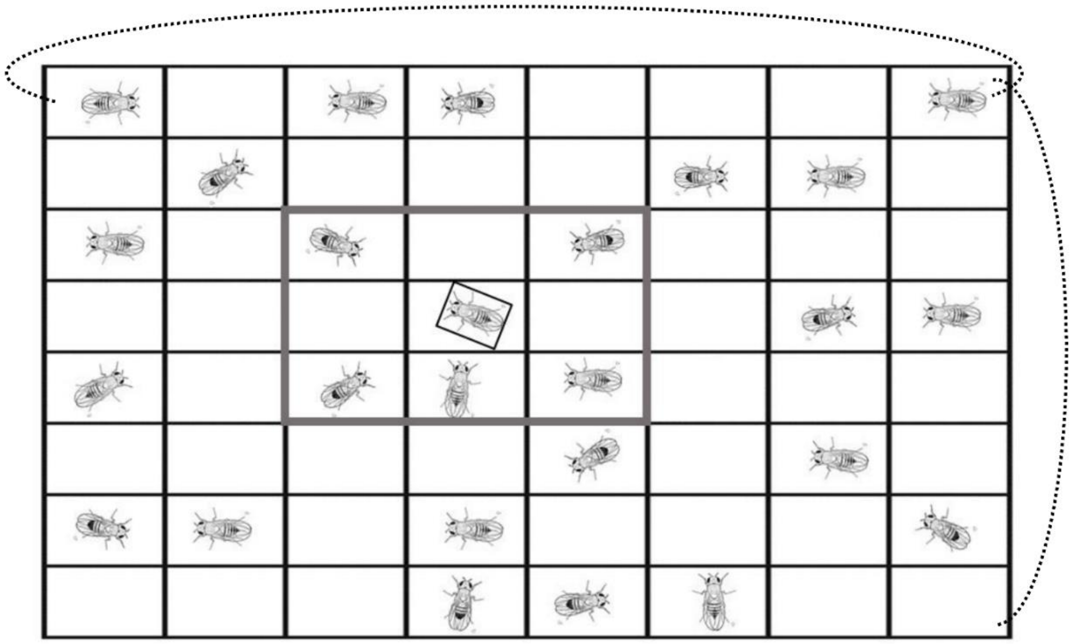

Figure S2. Schematic of female and male strings used in simulations

Figure S2. Next page shows a schematic of female and male strings used in simulations. Each chromosome is a string with three genes (bits):

Bit 1 – Innate preference gene ($pref$) expressed in females with two alleles: 0 → prefer male x; 1 → prefer male y

Bit 2 – 'Social' gene (soc) expressed in females with two alleles: 0 → no social influence; 1 → social influence

Bit 3 – Trait gene ($trait$) expressed in males (viability differences) with two alleles: 0 → phenotype x; 1 → phenotype y

Added to this, females have two extra bits to trace whether she will do copy or not, and whether she is virgin (unmated) or not:

Bit 4 – 'Public information'. If females are noncopiers ($\text{bit } 2 = 0$), this bit will always be NaN. If females are copiers ($\text{bit } 2 = 1$), this bit will be 0 if they have observed a demonstrator female mating with a x male, and will be 1 if they have observed the demonstrator female mating with a y male. Mating preferences of copier females will be based on this bit (i.e, socially acquired information will prevail over the fixed genetic preference defined by bit 1).

Bit 5 – Female status. NaN → unmated; 1 → mated

Once the female has mated a particular male, we append the male chromosome the female has mated with. This will be used for the recombination process.

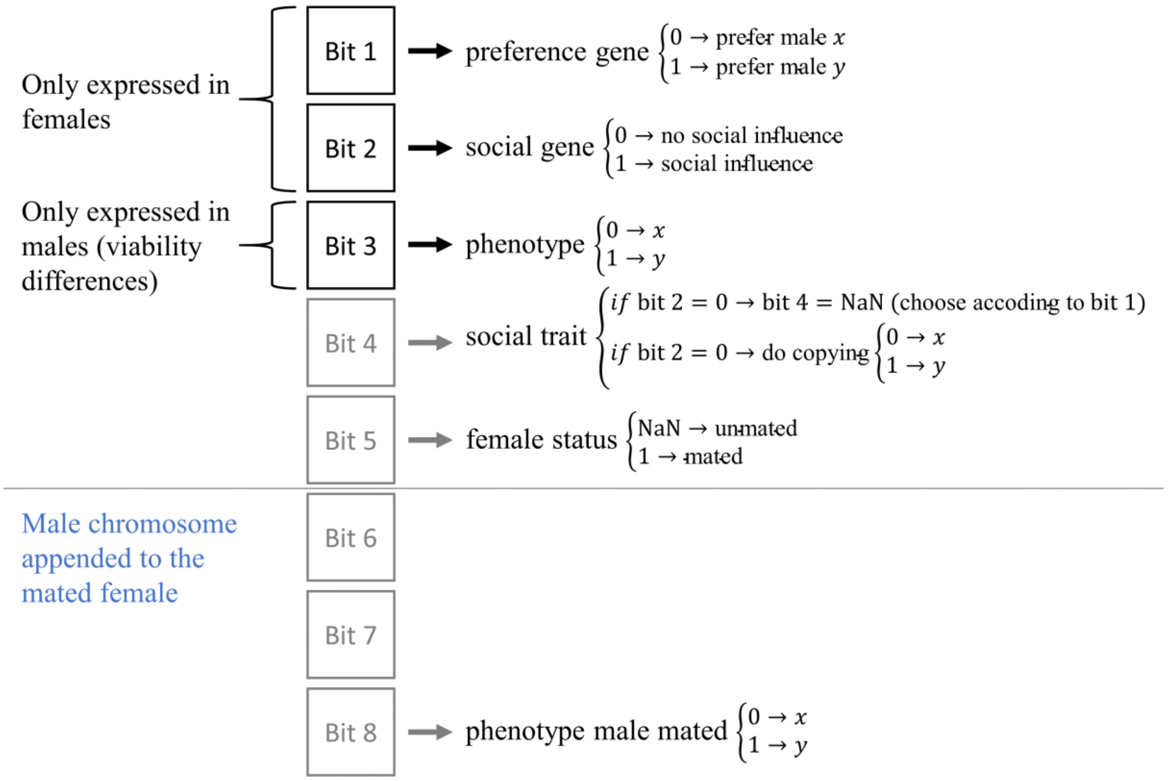
Only expressed in females
Only expressed in males (viability differences)
Bit 1
preference gene {0 → prefer male x, 1 → prefer male y}
Bit 2
social gene {0 → no social influence, 1 → social influence}
Bit 3
phenotype {0 → x, 1 → y}
Bit 4
social trait {if bit 2 = 0 → bit 4 = NaN (choose accoding to bit 1); if bit 2 = 0 → do copying {0 → x, 1 → y}}
Bit 5
female status {NaN → unmated, 1 → mated}
Male chromosome appended to the mated female
Bit 6
Bit 7
Bit 8
phenotype male mated {0 → x, 1 → y}

Table S1. Summary of simulation results for one-to-many horizontal cultural transmission and fixed innate preference

Conditions assayed to test if the trait and the copying allele can spread assuming a one-to-many horizontal cultural transmission and fixed innate preference (see text for details).

$p_{pref}^{t_0}$	s_x (a)	"choice cost"	Spread trait (b)	Spread copying
0.1	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.15$	No
0.2	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.15$	No
0.3	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.10$	No
0.4	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.10$	No
0.5	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.05$	No
0.6	(0 : 0.05 : 0.30)	0.3	Yes	No
0.7	(0 : 0.05 : 0.30)	0.3	Yes	No
0.8	(0 : 0.05 : 0.30)	0.3	Yes	No
0.9	(0 : 0.05 : 0.30)	0.3	Yes	No
0.1	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.25$	Yes if $s_x \geq 0.35$
0.2	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.25$	Yes if $s_x \geq 0.30$
0.3	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.20$	Yes if $s_x \geq 0.25$
0.4	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.15$	Yes if $s_x \geq 0.20$
0.5	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.05$	Yes if $s_x \geq 0.20$
0.6	(0 : 0.05 : 0.30)	0.5	Yes	Yes if $s_x \geq 0.25$
0.7	(0 : 0.05 : 0.30)	0.5	Yes	No
0.8	(0 : 0.05 : 0.30)	0.5	Yes	No
0.9	(0 : 0.05 : 0.30)	0.5	Yes	No
0.1	(0 : 0.05 : 0.35)	0.7	No	No
0.2	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.35$	No
0.3	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.30$	Yes if $s_x \geq 0.30$
0.4	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.20$	Yes if $s_x \geq 0.25$
0.5	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.10$	Yes if $s_x \geq 0.15$
0.6	(0 : 0.05 : 0.30)	0.7	Yes	Yes
0.7	(0 : 0.05 : 0.30)	0.7	Yes	Yes
0.8	(0 : 0.05 : 0.30)	0.7	Yes	Yes
0.9	(0 : 0.05 : 0.30)	0.7	Yes	No

The following parameters were held constant in the simulations: $L = 30$, $r = 0.05$, $p_{soc}^{t_0} = 0$, $p_{trait}^{t_0} = 0$, $\mu_{pref} = 0$, $\mu_{soc} = 0.001$, $\mu_{trait} = 0.01$, and $s_y = 0$. For each set of conditions, we performed three independent runs that behave qualitatively the same in all cases. (a) (0 : 0.05 ; 0.##) means that assayed conditions started with viability coefficient $s_x = 0$ and the strength of selection was increased at regular intervals until $s_x = 0.35$ ($p_{pref}^{t_0} \leq 0.5$) or $s_x = 0.30$ ($p_{pref}^{t_0} > 0.5$) by adding $\Delta s_x = 0.05$ to the previous value. (b) When $p_{pref}^{t_0} \leq 0.5$ we assumed that the trait spreads when its equilibrium frequency $\hat{p}_{trait} > p_{pref}^{t_0}$.

Table S2. Summary of simulation results for one-to-one horizontal cultural transmission and fixed innate preference

Conditions assayed to test if the trait and the copying allele can spread assuming a one-to-one horizontal cultural transmission and fixed innate preference (see text for details).

$p_{pref}^{t_0}$	s_x (a)	"choice cost"	Spread trait (b)	Spread copying
0.1	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.15$	No
0.2	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.15$	No
0.3	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.10$	No
0.4	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.10$	No
0.5	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.05$	No
0.6	(0 : 0.05 : 0.30)	0.3	Yes	No
0.7	(0 : 0.05 : 0.30)	0.3	Yes	No
0.8	(0 : 0.05 : 0.30)	0.3	Yes	No
0.9	(0 : 0.05 : 0.30)	0.3	Yes	No
0.1	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.25$	Yes if $s_x \geq 0.35$
0.2	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.25$	Yes if $s_x \geq 0.30$
0.3	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.20$	Yes if $s_x \geq 0.25$
0.4	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.15$	Yes if $s_x \geq 0.20$
0.5	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.05$	Yes if $s_x \geq 0.20$
0.6	(0 : 0.05 : 0.30)	0.5	Yes	Yes if $s_x \geq 0.25$
0.7	(0 : 0.05 : 0.30)	0.5	Yes	No
0.8	(0 : 0.05 : 0.30)	0.5	Yes	No
0.9	(0 : 0.05 : 0.30)	0.5	Yes	No
0.1	(0 : 0.05 : 0.35)	0.7	No	No
0.2	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.35$	No
0.3	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.30$	Yes if $s_x \geq 0.30$
0.4	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.20$	Yes if $s_x \geq 0.25$
0.5	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.10$	Yes if $s_x \geq 0.15$
0.6	(0 : 0.05 : 0.30)	0.7	Yes	Yes
0.7	(0 : 0.05 : 0.30)	0.7	Yes	Yes
0.8	(0 : 0.05 : 0.30)	0.7	Yes	Yes
0.9	(0 : 0.05 : 0.30)	0.7	Yes	No

The following parameters were held constant in the simulations: $L = 30$, $r = 0.05$, $p_{soc}^{t_0} = 0$, $p_{trait}^{t_0} = 0$, $\mu_{pref} = 0$, $\mu_{soc} = 0.001$, $\mu_{trait} = 0.01$, and $s_y = 0$. For each set of conditions, we performed three independent runs that behave qualitatively the same in all cases. (a) (0 : 0.05 ; 0.##) means that assayed conditions started with viability coefficient $s_x = 0$ and the strength of selection was increased at regular intervals until $s_x = 0.35$ ($p_{pref}^{t_0} \leq 0.5$) or $s_x = 0.30$ ($p_{pref}^{t_0} > 0.5$) by adding $\Delta s_x = 0.05$ to the previous value. (b) When $p_{pref}^{t_0} \leq 0.5$ we assumed that the trait spreads when its equilibrium frequency $\hat{p}_{trait} > p_{pref}^{t_0}$.

Figure S3. Sample simulations showing the dependence of the equilibrium frequency of the copying allele with the strength of innate preferences

Figure S3. Next page shows some sample simulations with the evolutionary fate of the fitter trait (male y) when the copying allele can coevolve but innate preference (pref. y) remains fixed throughout generations. For these plots, we have assumed a one-to-many horizontal cultural transmission. In all cases "choice cost" $= 0.7$ and viability selection coefficient against the resident males $s_x = 0.30$ (assuming no costs of copying; i.e., $s_c = 0$). These plots illustrate that in those situations where the copying allele spreads its equilibrium frequency is lower the higher is the frequency of the fixed innate preference towards the novel trait. A: $\hat{p}_{soc} \approx 0.79$ with $p_{pref}^{t_0} = 0.3$. B: $\hat{p}_{soc} \approx 0.75$ with $p_{pref}^{t_0} = 0.4$. C: $\hat{p}_{soc} \approx 0.70$ with $p_{pref}^{t_0} = 0.5$. D: $\hat{p}_{soc} \approx 0.63$ with $p_{pref}^{t_0} = 0.6$. E: $\hat{p}_{soc} \approx 0.50$ with $p_{pref}^{t_0} = 0.7$. F: $\hat{p}_{soc} \approx 0.12$ with $p_{pref}^{t_0} = 0.8$. G: $\hat{p}_{soc}$ usually drops below 0.05 with $p_{pref}^{t_0} = 0.9$ and the soc locus can be considered monomorphic in this case. These differences in the equilibrium frequency of the copying allele as a function of the strength of the fixed preference are expected from the analytical treatment in Servedio and Kirkpatrick (1996): copier females need to have a stronger preference towards the overall fitter males than the innate preference of noncopier females for the copying allele to spread (Appendix S1).

For comparative purposes, the equilibrium frequencies of the copying allele assuming the one-to-one horizontal cultural transmission rule are $\hat{p}_{soc} \approx 0.27$ with $p_{pref}^{t_0} = 0.3$; $\hat{p}_{soc} \approx 0.38$ with $p_{pref}^{t_0} = 0.4$; $\hat{p}_{soc} \approx 0.32$ with $p_{pref}^{t_0} = 0.5$; $\hat{p}_{soc} \approx 0.30$ with $p_{pref}^{t_0} = 0.6$; $\hat{p}_{soc} \approx 0.21$ with $p_{pref}^{t_0} = 0.7$; and $\hat{p}_{soc} \approx 0.08$ with $p_{pref}^{t_0} = 0.8$ ($\hat{p}_{soc}$ drops below 0.05 with $p_{pref}^{t_0} = 0.9$ and the soc locus can be considered monomorphic).

References

Servedio, M. R., and M. Kirkpatrick. 1996. The evolution of mate choice copying by indirect selection. *Am. Nat.* 148: 848-867.

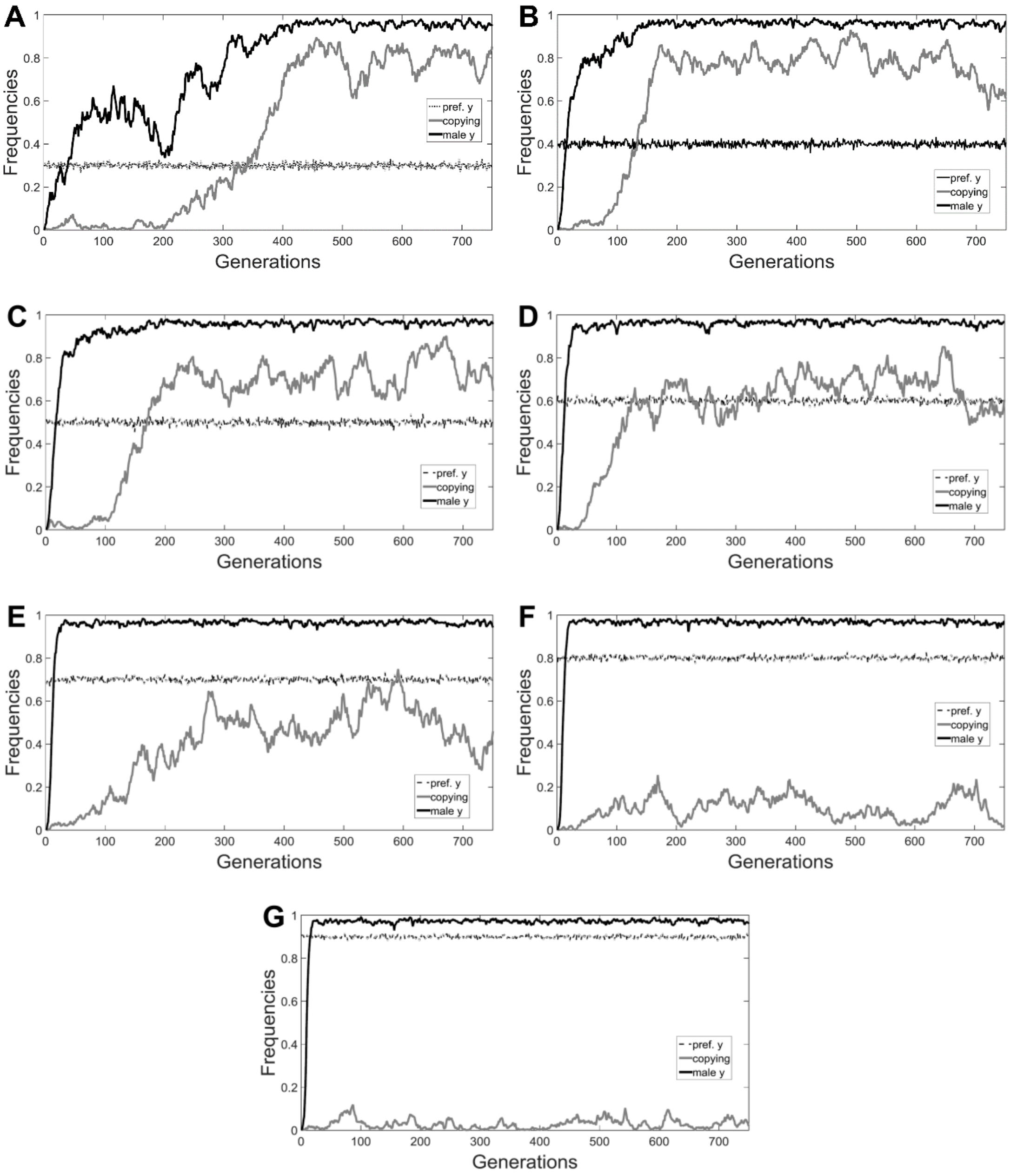
A
B
C
D
E
F
G
Frequencies
Generations
0
0.2
0.4
0.6
0.8
1
0
100
200
300
400
500
600
700
pref. y
copying
male y

Figure S4. Sample simulations when MCC is already established in the population and innate preference is kept fixed

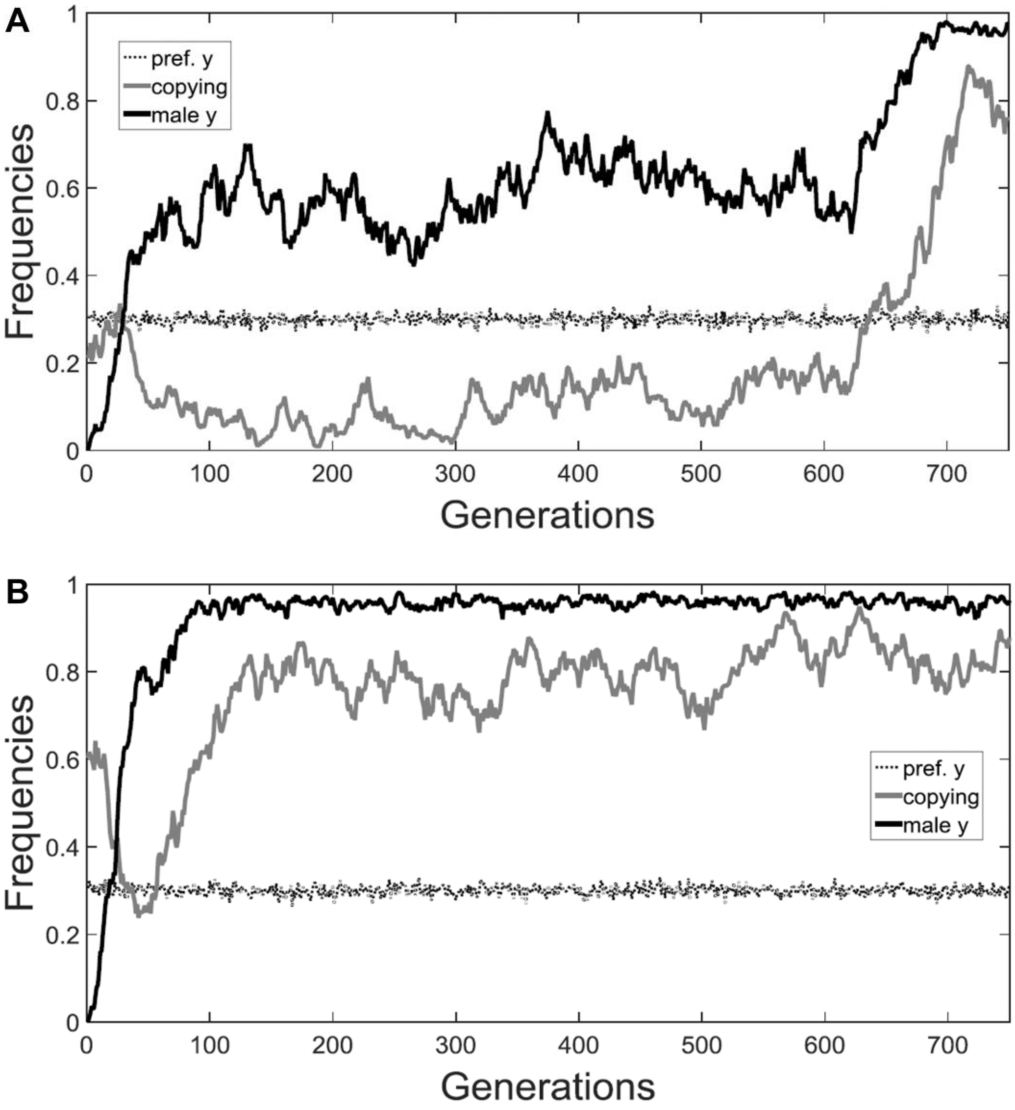

Figure S4. Evolutionary fate of the fitter trait (male y) when MCC is assumed to be initially established in the population and innate preference (pref. y) remains fixed throughout generations at the initial frequency $p_{pref}^{t_0} = 0.3$ (i.e., noncopier females tend to favor mating with resident males x). In all cases the initial frequencies and mutation rates for trait y were $p_{pref}^{t_0} = 0$ and $\mu_{trait} = 0.01$. In A the initial frequency of the copying allele was $p_{soc}^{t_0} = 0.20$ with $\mu_{soc} = 0.001$, whereas in B the values were $p_{soc}^{t_0} = 0.60$ with $\mu_{soc} = 0.001$. The frequency of the copying allele drops during the early generations and then rises in frequency following the spread of the trait. Other parameter values were $r = 0.05$, $\mu_{pref} = 0$, $s_x = 0.30$, $s_y = 0$ and 'choice cost' = 0.7.

Table S3. Summary of simulation results for one-to-many horizontal cultural transmission and coevolution of innate preference

Conditions assayed to test if the trait and the copying allele can spread assuming a one-to-many horizontal cultural transmission and coevolution of innate preference (see text for details).

$p_{pref}^{t_0}$	s_x [(a)]	"choice cost"	Spread trait [(b)]	Spread copying
0.1	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.20$	No
0.2	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.20$	No
0.3	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.15$	No
0.4	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.20$	No
0.5	(0 : 0.05 : 0.35)	0.3	Yes if $s_x \geq 0.15$	No
0.6	(0 : 0.05 : 0.30)	0.3	Yes if $s_x \geq 0.15$	No
0.7	(0 : 0.05 : 0.30)	0.3	Yes if $s_x \geq 0.05$	No
0.8	(0 : 0.05 : 0.30)	0.3	Yes if $s_x \geq 0.05$	No
0.9	(0 : 0.05 : 0.30)	0.3	Yes if $s_x \geq 0.05$	No
0.1	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.35$	No
0.2	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.35$	No
0.3	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.35$	No
0.4	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.35$	No
0.5	(0 : 0.05 : 0.35)	0.5	Yes if $s_x \geq 0.30$	No
0.6	(0 : 0.05 : 0.30)	0.5	Yes if $s_x \geq 0.30$	No
0.7	(0 : 0.05 : 0.30)	0.5	Yes if $s_x \geq 0.20$	No
0.8	(0 : 0.05 : 0.30)	0.5	Yes if $s_x \geq 0.10$	No
0.9	(0 : 0.05 : 0.30)	0.5	Yes	No
0.1	(0 : 0.05 : 0.35)	0.7	No	No
0.2	(0 : 0.05 : 0.35)	0.7	No	No
0.3	(0 : 0.05 : 0.35)	0.7	No	No
0.4	(0 : 0.05 : 0.35)	0.7	No	No
0.5	(0 : 0.05 : 0.35)	0.7	Yes if $s_x \geq 0.35$	No
0.6	(0 : 0.05 : 0.30)	0.7	Yes if $s_x \geq 0.30$	No
0.7	(0 : 0.05 : 0.30)	0.7	Yes if $s_x \geq 0.25$	No
0.8	(0 : 0.05 : 0.30)	0.7	Yes	No
0.9	(0 : 0.05 : 0.30)	0.7	Yes	No

The following parameters were held constant in the simulations: $L = 30$, $r = 0.05$, $p_{soc}^{t_0} = 0$, $p_{trait}^{t_0} = 0$, $\mu_{pref} = 0$, $\mu_{soc} = 0.001$, $\mu_{trait} = 0.01$, and $s_y = 0$. For each set of conditions, we performed three independent runs that behave qualitatively the same in all cases. Simulations where also running with $r = 0$ and $r = 0.25$ and qualitative results were basically the same. In no case the copying allele spread. [(a)] (0 : 0.05 ; 0.##) means that assayed conditions started with viability coefficient $s_x = 0$ and the strength of selection was increased at regular intervals until $s_x = 0.35$ $(p_{pref}^{t_0} \leq 0.5)$ or $s_x = 0.30$ $(p_{pref}^{t_0} > 0.5)$ by adding $\Delta s_x = 0.05$ to the previous value. [(b)] When $p_{pref}^{t_0} \leq 0.5$ we assumed that the trait spreads when its equilibrium frequency $\hat{p}_{trait} > p_{pref}^{t_0}$.

Figure S5. Sample simulations when innate preference is allowed to evolve

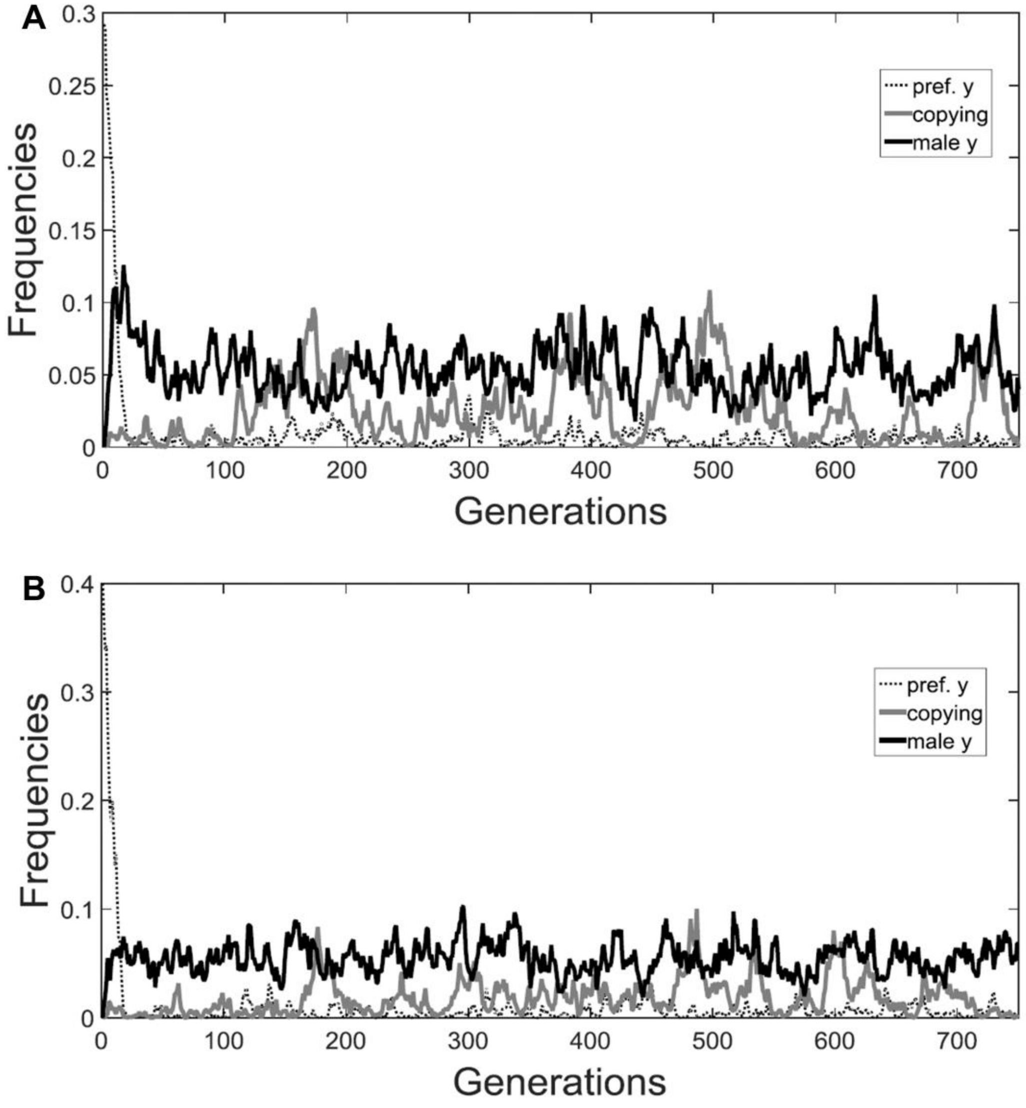

Figure S5. Evolutionary fate of the fitter trait (male y) when both innate preference (pref. y) and the copying allele can coevolve with the trait. In all cases the initial frequencies and mutation rates were $p_{trait}^{t_0} = 0$ and $\mu_{trait} = 0.01$ (trait y), $p_{soc}^{t_0} = 0$ and $\mu_{soc} = 0.001$ (copying allele), and recombination rate = $r = 0.05$. In A the initial frequency of allele 1 at the $pref$ locus was $p_{pref}^{t_0} = 0.30$ with $\mu_{pref} = 0.001$**,** whereas in B the values were $p_{pref}^{t_0} = 0.40$ and $\mu_{pref} = 0.001$**.** Innate preference quickly drops in frequency and strengthens the preference towards resident males x, which makes it more difficult for the new trait (and the copying allele) to spread. Other parameters values were $s_x = 0.35$, $s_y = 0$ and "choice cost" = 0.7.

Figure S6. Sample simulations with high mutation rate for innate preference

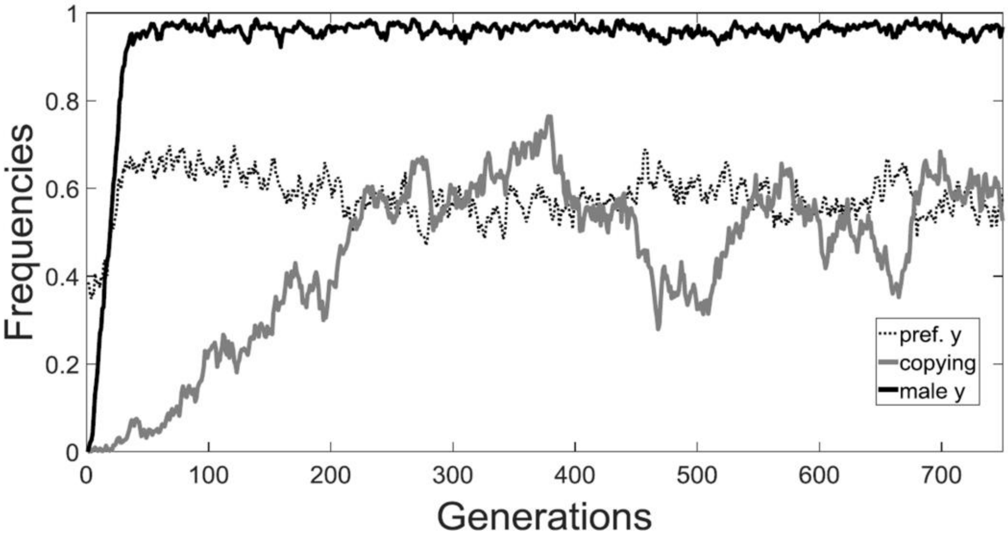

Figure S6. Evolutionary fate of the fitter trait (male y) when both innate preference (pref. y) and the copying allele can coevolve with the trait. The copying allele spreads because we have assumed a high mutation rate for the $pref$ locus ($\mu_{pref} = 0.1$) and, therefore, innate preference for the high-fitness trait remains segregating at approximately intermediate frequencies in the population. Other parameter values were $p_{pref}^{t_0} = 0.40$, $s_x = 0.30$, $r = 0.05$, $p_{soc}^{t_0} = 0$, $\mu_{soc} = 0.001$ and "choice cost" $= 0.7$.

Appendix S1. Mating pattern (with Figures S7 and S8)

Here we analyze the mating pattern – defined as the *a posteriori* deviation from random mating in mated individuals – between the copying and the trait alleles in some sampled simulations where the copying allele does or does not spread. To assess deviations from random mating, we will use the ‘pair sexual isolation index’ (*PSI*) because of some useful properties (Rolán-Alvarez and Caballero 2000; Pérez-Figueroa et al. 2005). The mating table is as follows:

Females

		Noncopier (A’)	**Copier (B’)**	
Males	**Trait x (A)**	aa	ab	$aa + ab$
	Trait y (B)	ba	bb	$ba + bb$
		$aa + ba$	$ab + bb$	t

(S1.1)

where aa, ab, ba, bb are the number of mating pairs and $t = aa + ab + ba + bb$. For every mating pair a PSI is defined as follows:

$$\begin{gathered} PSI_{aa} = \frac{(aa)t}{(aa+ab)(aa+ba)} \\ PSI_{ab} = \frac{(ab)t}{(aa+ab)(ab+bb)} \\ PSI_{ba} = \frac{(ba)t}{(aa+ba)(ba+bb)} \\ PSI_{bb} = \frac{(bb)t}{(ba+bb)(ab+bb)} \end{gathered} \tag{S1.2}$$

Values of PSI above/below one indicate excess/deficit of observed pairs relative to expected pairs under random mating using marginal frequencies. From these indexes, the following estimator for assortative mating is obtained:

$$I_{PSI} = \frac{(PSI_{aa} - PSI_{ab} - PSI_{ba} + PSI_{bb})}{(PSI_{aa} + PSI_{ab} + PSI_{ba} + PSI_{bb})} \qquad \textbf{(S1.3)}$$

This statistics ranges from -1 (complete disassortative or negative assortative mating; i.e. $aa = bb = 0$ S1.1) to $+1$ (complete assortative mating; $ab = ba = 0$).

Servedio and Kirkpatrick (1996) suggested that an allele for mate-choice copying will spread if it causes females to prefer the type of male that has the highest overall fitness. Therefore, assuming that the novel trait y has higher fitness than resident males x, the expectations are that $PSI_{aa} > PSI_{ab}$ and $PSI_{ba} < PSI_{bb}$, giving an $I_{PSI} > 0$ (i.e., an excess of matings involving noncopier females with the resident males x, and copier females with the novel males y). This assortative mating would establish and maintain a linkage disequilibrium between the copying allele and the trait. Conversely, when $I_{PSI} \leq 0$ the copying allele will not spread. For several sampled simulations, we have estimated these indexes at each generation. Some results are shown in Figures S7-S8.

References

Pérez-Figueroa, A., A. Caballero, and E. Rolán-Alvarez. 2005. Comparing the estimation properties of different statistics for measuring sexual isolation from mating frequencies. *Biol. J. Linn. Soc.* 85: 307-318.

Servedio, M. R., and M. Kirkpatrick. 1996. The evolution of mate choice copying by indirect selection. *Am. Nat.* 148: 848-867.

Rolán-Alvarez, E., and A. Caballero. 2000. Estimating sexual selection and sexual isolation effects from mating frequencies. *Evolution* 54: 30-36.

Figure S7. Evolution of sexual isolation index when the copying allele spreads

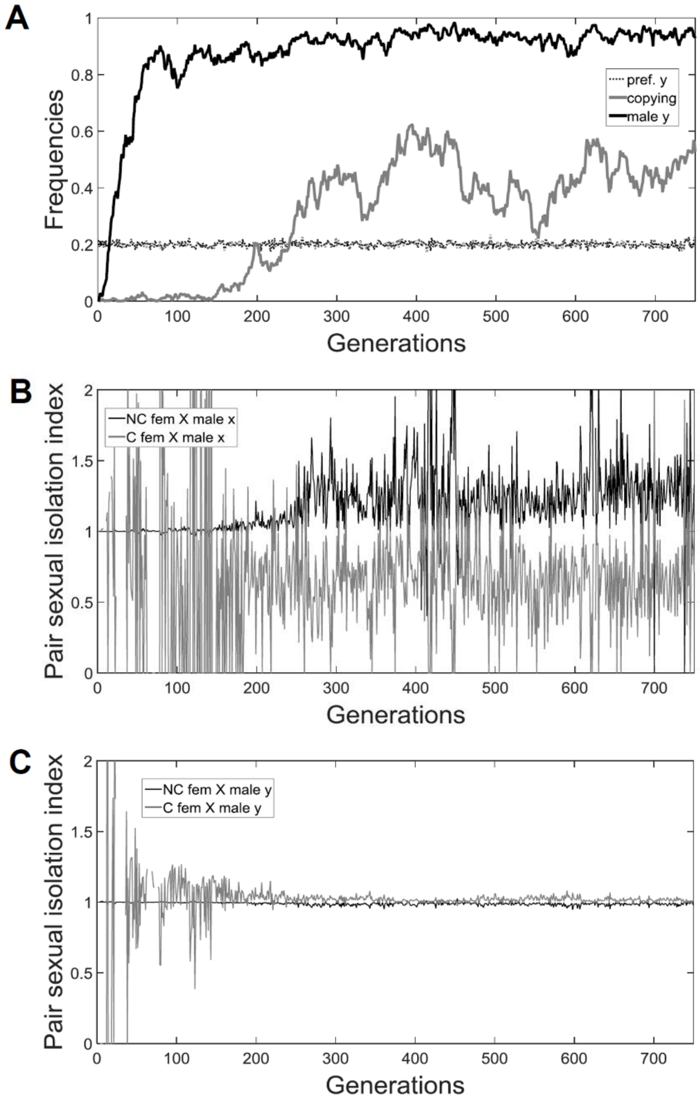

Figure S7. Sampled simulation assuming fixed innate preference (pref. y) where the copying allele spreads. A plots the allele frequencies of the invading trait (male y) and the copying allele. B plots the PSI for the mating pairs aa (i.e., Noncopier female × male x) and ab (Copier female × male x). C plots the PSI for the mating pairs ba (Noncopier female × male y) and bb (Copier female × male y). The copying allele coevolved with the trait from generation 150 on, and the average values of PSI were the following: $PSI_{aa} = 1.228$; $PSI_{ab} = 0.659$; $PSI_{ba} = 0.988$ and $PSI_{bb} = 1.022$. As expected, $PSI_{aa} > PSI_{ab}$ and $PSI_{ba} < PSI_{bb}$, which gives an average $I_{PSI} = 0.155$ (see text for details).

Figure S8. Evolution of sexual isolation index when the copying allele does not spread

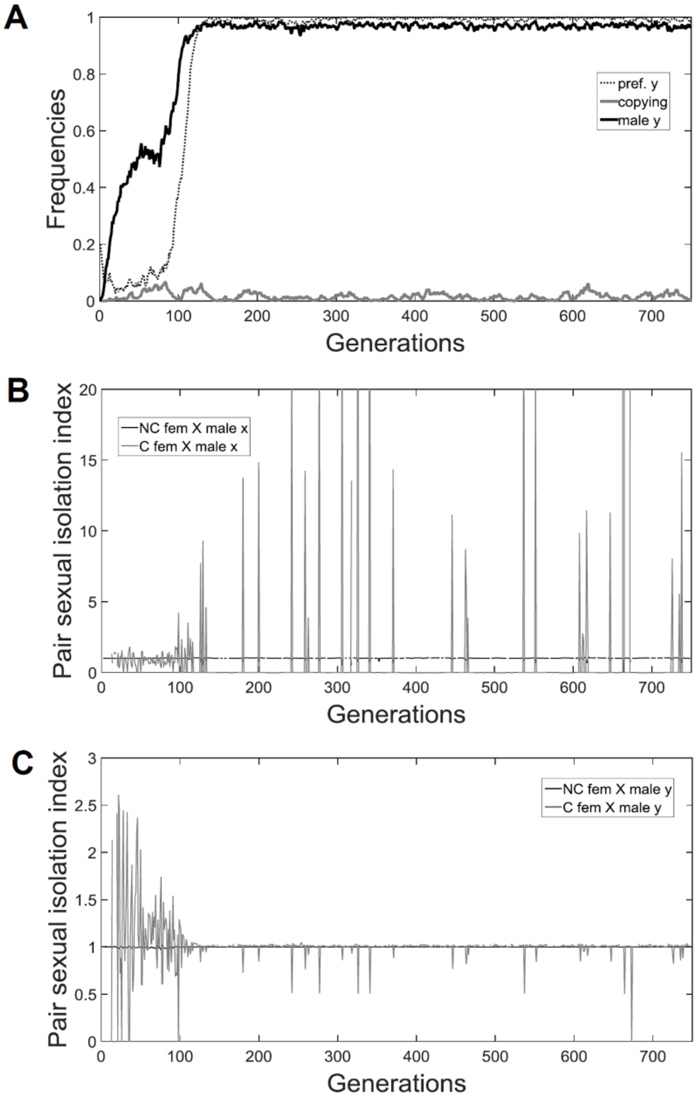

Figure S8. Sampled simulation assuming both innate preference (pref. y) and the copying allele can coevolve with the trait (the copying allele never spreads in these cases; Table S3). **A** plots the allele frequencies of the invading trait (male y), the innate preference allele, and the copying allele. **B** plots the PSI for the mating pairs aa (i.e., Noncopier female × male x) and ab (Copier female × male x). **C** plots the PSI for the mating pairs ba (Noncopier female × male y) and bb (Copier female × male y). The average values of PSI were the following: $PSI_{aa} = 1$; $PSI_{ab} = 1.266$; $PSI_{ba} = 1$ and $PSI_{bb} = 1.013$, which gives an average $I_{PSI} = -0.059$ (see text for details). Note the bursts with $PSI_{ab} \gg PSI_{aa}$, meaning that when copier females are at very low frequency they disproportionally mate with the low-fitness males x.

MATLAB Computer Code

The ‘INPUT PARAMETERS’ below are provided by an xls file as shown in Supplementary Table S4.

The Outputs are given in an xls file named 'My_Filename_', which has a number attached to it dependent on the number of conditions in the Input file. An example of the output file is shown in Supplementary Table S5.

Main file: Copying_batch.m

```
% Copying_batch.m
%
% We assume a two-dimensional regular lattice of linear length L with
% periodic boundary conditions, i.e., a torus.
%
% Written by Mauro Santos, June 2016 at Dept. Genètica i Microbiologia, Univ.
% Autònoma Barcelona, Spain.
%
% The program is written for Matlab R2015a
%-----------------------------------------------------------------------

clear
clc
  s = RandStream('mt19937ar','Seed',sum(100*clock));
  RandStream.setGlobalStream(s);

% INPUT PARAMETERS
[NUM,TXT] = xlsread('Input_Parameters.xls'); % See Table SI.3

for yy = 1:size(NUM,1)
    conditions = NUM(yy,:);
    L = conditions(1,1);
    f_pref = conditions(1,2);
    f_soc = conditions(1,3);
    f_male = conditions(1,4);
    rec_ = conditions(1,5);
    s_x = conditions(1,6);
    s_y = conditions(1,7);
    s_c = conditions(1,8);
    ch_cost = conditions(1,9);
    mut_pref = conditions(1,10);
    mut_soc = conditions(1,11);
    mut_phen = conditions(1,12);
    t_steps = conditions(1,13);
    runs = conditions(1,14);

    B = reshape(1:L^2,L,L); % matrix values to find Moore neighbors
    B1 = circshift(B, [1 1]);
    B2 = circshift(B1, [2 2]);

    for replicate = 1:runs % Number of runs
        fprintf('Run = %0.3d', replicate)
        gametes=[rand(L^2,1)<=f_pref,rand(L^2,1)<=f_soc,rand(L^2,1)<=f_male];
        Output_all = NaN*ones(t_steps,6);
        [~, Dprime] = ldiseq(gametes);
        Output_all(1,:) = [mean(gametes) Dprime];

        for xx = 2:t_steps
```

```
            fprintf('Generation = %0.3d', xx)
            oldpop = allocate(L,gametes,s_x,s_y,s_c);
            fem_mated = p_mated(oldpop); % calculates frequency mated females
            count=0;
            while (fem_mated<0.85 && count <10000)
                oldpop = mating_pooled(oldpop,B,B1,B2,L,ch_cost);
                fem_mated = p_mated(oldpop);
                count = count+1;
            end

            gametes = reproduction(oldpop,rec_,mut_pref,mut_soc,mut_phen);
            if mean(gametes(:,2)) >= 0.95 && mean(gametes(:,3)) >= 0.95
                break
            end

            % ##### TO KEEP f_pref fixed !
            aa = rand(size(gametes,1),1) <=f_pref;
            gametes(:,1) = aa;
            % REMEMBER TO REMOVE THIS IF f_pref IS ALLOWED TO EVOLVE

            [~, Dprime] = ldiseq(gametes);
            Output_all(xx,:) = [mean(gametes) Dprime];
        end

        Overall_output = Output_all;
        cell_output = {'f_pref' 'f_soc' 'f_male' 'Dprime 1-2' ...
            'Dprime 1-3' 'Dprime 2-3'};
        filename1 = ['My_Filename_' num2str(yy)];
        xlswrite(filename1,cell_output,replicate,'A1:F1');
        xlswrite(filename1,Overall_output,replicate,'A2:F751');
    end

    parameters = [L f_pref f_soc f_male rec_ s_x s_y s_c ch_cost ...
        mut_pref mut_soc mut_phen];
    cell_names = {TXT{1,1:12}};
    xlswrite(filename1,cell_names,runs+1,'A1:L1');
    xlswrite(filename1,parameters,runs+1,'A2:L2');
end
```

Function: allocate.m

```
function [out] = allocate(L,gametes,s_x,s_y,s_c)
% Allocate flies a random in the lattice L^2

f = size(gametes,1);

g = randperm(f);
gametes = gametes(g,:); % randomize gametes

grid = cell(L,L);
A = rand(L,L)<0.9; % average density is 0.9. With L=50 this results
                   % in a population size (fem + mal) higher than 2000
individuals.
for ii = 1:L
    for jj = 1:L
        if A(ii,jj) > 0
            sex = rand<0.5;
            if sex == 0 %female
                grid{ii,jj} = [gametes(1,:), NaN*ones(1,5)];
                if gametes(1,2) == 1 && rand < s_c
                    grid{ii,jj} = [];
                end
```

```
                gametes(1,:) = [];
            elseif sex ==1 %male
                grid{ii,jj} = gametes(1,:);
                if gametes(1,3) == 0 && rand < s_x
                    grid{ii,jj} = [];
                elseif gametes(1,3) == 1 && rand < s_y
                    grid{ii,jj} = [];
                end
                gametes(1,:) = [];
            end
        end
    end
end
out = grid;
end
```

Function: p_mated.m

```
function [out1,out2,out3] = p_mated(oldpop)
% Calculate proportion females mated

% bit 5. status: NaN -> naive (unmated); 1 -> mature (mated)

L = size(oldpop,1);

fem=[];
    for ii = 1:L
        for jj = 1:L
            if length(oldpop{ii,jj})>4
                fem = [fem; oldpop{ii,jj}];
            end
        end
    end

if (nargout == 1)
    out1 = nansum(fem(:,5))/(length(fem));
end

if (nargout > 1)
    out1 = nansum(fem(:,5))/(length(fem));
    copying = fem(:,2) == 1;
    out2 = nansum(fem(copying,5));
    noncopying = fem(:,2) == 0;
    out3 = nansum(fem(noncopying,5));
end
end
```

Function: mating_pooled.m

```
function [out] = mating_pooled(oldpop,B,B1,B2,L,ch_cost)
% Mating in the selected patches

[patches,target_female] = Moore(oldpop,B,B1,B2,L);
p_fem = [oldpop{target_female} target_female];

while ~isnan(p_fem(1,5)) % target female already mated
    [patches,target_female] = Moore(oldpop,B,B1,B2,L);
    p_fem = [oldpop{target_female} target_female];
end

l =length(patches);
females = []; males = [];
for ii=1:l
    if length(oldpop{patches(ii,1)}) > 5
        females = [females; [oldpop{patches(ii,1)}, patches(ii,1)]];
    elseif length(oldpop{patches(ii,1)}) == 3
        males = [males; [oldpop{patches(ii,1)}, patches(ii,1)]];
    end
end

if isempty(males) % mating is not possible
    out = oldpop;
    return
end

I = females(:,end)~=target_female; % to remove target female
females = females(I,:);

% Choose a male at random
rnd_m = ceil(size(males,1)*rand);
mal_c = males(rnd_m,1:3); % male phenotype is bit 3

% See if the male "suits" the female. We have to distinguish 2 posibilities:

if p_fem(1,2)==0 % Noncopier female
    if mal_c(1,3 )== p_fem(1,1) && p_fem(1,2) == 0
        p_fem(1,5) = 1; %bit 5. status: NaN (0) -> naive; 1 -> "mature"
        p_fem(1,6:8) = mal_c; % female mated with preferred male
    elseif mal_c(1,3)~=p_fem(1,1) && p_fem(1,2)==0
        if rand > ch_cost;
            p_fem(1,5) = 1;
            p_fem(1,6:8) = mal_c;
        else
            p_fem(1,5) = NaN;
            p_fem(1,6:8) = NaN;
        end
    end
end

if p_fem(1,2) == 1 && ~isnan(p_fem(1,4)) % Copier female with SI
    if mal_c(1,3)==p_fem(1,4) && p_fem(1,2)==1
        p_fem(1,5) = 1;
        p_fem(1,6:8) = mal_c;
    elseif mal_c(1,3)~=p_fem(1,4) && p_fem(1,2)==1
        if rand > ch_cost;
            p_fem(1,5) = 1;
            p_fem(1,6:8) = mal_c;
        else
            p_fem(1,5) = NaN;
            p_fem(1,6:8) = NaN;
        end
```

```
    end
end

% update oldpop
oldpop{p_fem(1,end)} = p_fem(1,1:8);

% Do copying.
K = females(:,2)==1 & isnan(females(:,4)) & isnan(females(:,5));
c_fem = females(K,:);

% One-to-many horizontal cultural transmision
if ~isempty(c_fem)
    c_fem(:,4) = p_fem(1,8); % Copy according to mated female
    for ii=1:size(c_fem,1)
        oldpop{c_fem(ii,end)} = c_fem(ii,1:8);
    end
end

% One-to-one horizontal cultural transmision
% ### Desactivate One-to-many and activate this ###

%if ~isempty(c_fem)
%    b = ceil(size(c_fem,1)*rand);
%    c_fem(b,4) = p_fem(1,8);
%    oldpop{c_fem(b,end)} = c_fem(b,1:8);
%end

out = oldpop;
end
```

Function: Moore.m

```
function [out1,out2] = Moore(oldpop,B,B1,B2,L)
% Obtain random patches from the L^2 lattice

mfem_target = randi(L,2,1)'; % pick a female at random
t_female = oldpop{mfem_target(1,1), mfem_target(1,2)};
while length(t_female)<5 % target is male or empty
    mfem_target = randi(L,2,1)';
    t_female = oldpop{mfem_target(1,1), mfem_target(1,2)};
end
% find the Moore neighborhood of the target
index_target = B(mfem_target(1,1), mfem_target(1,2));
t = B == index_target;
[~,ixn] = ixneighbors(B,t); % function by Wolfgang Schwanghart
neighbors1 = B(ixn);
if length(neighbors1) < 8
    t = B1 == index_target;
    [~,ixn] = ixneighbors(B1,t);
    neighbors2 = B1(ixn);
    t = B2 == index_target;
    [~,ixn] = ixneighbors(B2,t);
    neighbors3 = B2(ixn);
else
    neighbors2 = [];
    neighbors3 = [];
end
neighbors = sort(unique([neighbors1; neighbors2; neighbors3])); % Moore
neighborhs
out1 = sort([neighbors;index_target]); % patches to focus
out2 = index_target;
end
```

Function: ixneighbors.m (by Wolfgang Schwanghart)

```
function [ic,icd] = ixneighbors(varargin)
%
% [ic,icd] = ixneighbors(A);
% [ic,icd] = ixneighbors(A,ix);
% [ic,icd] = ixneighbors(A,I);
%
%
% ixneighbors returns the indices of neighbor cells in a n*m matrix A. ic
% and icd are column vectors of same length where ic are the indices of
% cells in A and icd are the indices of the neighbor cells.
%
% ixneighbors(A)       returns all neighbors of all cells in A
% ixneighbors(A,ix)    returns all neighbors of the cells in index
%                      vector ix
% ixneighbors(A,I)     returns all neighbors of the cells in the logical
%                      matrix I that are TRUE. I must be same size as A
%
% ixneighbors handles NaNs. Hence, it discards cells in A that are NaN both
% in ic and icd.
%
% ......................
% Example 1:
%
% A = magic(4);
% A(2,2) = NaN
%
% A =
%
%   16    2    3   13
%    5  NaN   10    8
%    9    7    6   12
%    4   14   15    1
%
% [ic,icd] = ixneighbors(A,3)
%
% ic =
%
%    3
%    3
%    3
%    3
%
%
% icd =
%
%    7
%    4
%    2
%    8
%
% .....................
% Example 2:
%
% Construct a sparse adjacency matrix S
%
% A = peaks(100);
% A(A<0) = NaN;
% nrc = numel(A);
% [ic,icd] = ixneighbors(A);
```

```
% S = sparse(ic,icd,ones(numel(icd),1),nrc,nrc);
% spy(S)
%
% Wolfgang Schwanghart
%


% handle input and error checking
if nargout~=2;
    error('wrong number of output arguments')
end

X = varargin{1};
siz = size(X);
nrc = siz(1)*siz(2);
In = isnan(X);

if nargin==1;
    method = 'getall';
elseif nargin==2;
    ix = varargin{2};
    if islogical(ix)
        if size(X) ~= size(ix);
            error('if I is logical I and X must have same size')
        end
    else
        ixvec = ix(:);
        ix = false(siz);
        ix(ixvec) = true;
    end
    ix = ~In & ix;
    method = 'getsome';
else
    error('wrong number of input arguments')
end

% replace values in X by index vector
X = reshape((1:nrc)',siz);
X(In) = NaN;

% Pad array
ic = nan(siz(1)+2,siz(2)+2);
ic(2:end-1,2:end-1) = X;

switch method
    case 'getall'
        I = ~isnan(ic);
    case 'getsome'
        % Pad logical array
        I = false(siz(1)+2,siz(2)+2);
        I(2:end-1,2:end-1) = ix;
end

icd = zeros(nnz(I),8);

% Shift logical matrix I across the neighbors
icd(:,1) = ic(I(:,[end 1:end-1]));                 % shift to the right
icd(:,2) = ic(I([end 1:end-1],:));                 % shift down
icd(:,3) = ic(I(:,[2:end 1]));                     % shift left
icd(:,4) = ic(I([2:end 1],:));                     % shift up
icd(:,5) = ic(I([2:end 1],[end 1:end-1]));         % shift up and right
icd(:,6) = ic(I([2:end 1],[2:end 1]));             % shift up and left
icd(:,7) = ic(I([end 1:end-1],[end 1:end-1]));     % shift down and right
icd(:,8) = ic(I([end 1:end-1],[2:end 1]));         % shift down and left

% Create output
ic = repmat(ic(I(:)),8,1);
```

```
icd = icd(:);
% Remove NaNs in neighbors
i = isnan(icd);
ic(i) = [];
icd(i) = [];
```

Function: ldiseq.m

```
function [D, Dprime] = ldiseq(gametes)
% in: matrix with gametes

if isempty(gametes)
    D = NaN*ones(1,3);
    Dprime = NaN*ones(1,3);
    return
end

f = size(gametes,1);

% LD 1 vs 2
I1=find(gametes(:,1)==0 & gametes(:,2)==0);
J1=find(gametes(:,1)==0 & gametes(:,2)==1);
K1=find(gametes(:,1)==1 & gametes(:,2)==0);
L1=find(gametes(:,1)==1 & gametes(:,2)==1);

D12 = (length(I1)/f)*(length(L1)/f)-(length(J1)/f)*(length(K1)/f);
p1 = 1-mean(gametes(:,1)); % freq 0 preference allele
q1 = mean(gametes(:,1)); % freq 1 preference allele

p2 = 1-mean(gametes(:,2)); % freq 0 social gene
q2 = mean(gametes(:,2)); % freq 1 social gene

if D12>=0
    Dmax = min(p1*q2, p2*q1);
elseif D12<0
    Dmax = min(p1*q1,p2*q2);
end
ld_12 = D12/Dmax;

% LD 1 vs 3
I1=find(gametes(:,1)==0 & gametes(:,3)==0);
J1=find(gametes(:,1)==0 & gametes(:,3)==1);
K1=find(gametes(:,1)==1 & gametes(:,3)==0);
L1=find(gametes(:,1)==1 & gametes(:,3)==1);

D13 = (length(I1)/f)*(length(L1)/f)-(length(J1)/f)*(length(K1)/f);
p1 = 1-mean(gametes(:,1)); % freq 0 preference allele
q1 = mean(gametes(:,1)); % freq 1 preference allele

p2 = 1-mean(gametes(:,3)); % freq 0 social gene
q2 = mean(gametes(:,3)); % freq 1 social gene

if D13>=0
    Dmax = min(p1*q2, p2*q1);
elseif D13<0
    Dmax = min(p1*q1,p2*q2);
end
ld_13 = D13/Dmax;

% LD 2 vs 3
I1=find(gametes(:,2)==0 & gametes(:,3)==0);
```

```
J1=find(gametes(:,2)==0 & gametes(:,3)==1);
K1=find(gametes(:,2)==1 & gametes(:,3)==0);
L1=find(gametes(:,2)==1 & gametes(:,3)==1);

D23 = (length(I1)/f)*(length(L1)/f)-(length(J1)/f)*(length(K1)/f);
p1 = 1-mean(gametes(:,2)); % freq 0 preference allele
q1 = mean(gametes(:,2)); % freq 1 preference allele

p2 = 1-mean(gametes(:,3)); % freq 0 social gene
q2 = mean(gametes(:,3)); % freq 1 social gene

if D23>=0
    Dmax = min(p1*q2, p2*q1);
elseif D23<0
    Dmax = min(p1*q1,p2*q2);
end
ld_23 = D23/Dmax;

D = [D12 D13 D23];
Dprime = [ld_12 ld_13 ld_23];

end
```

Function: reproduction.m

```
function [out] = reproduction(oldpop,rec_,mut_pref,mut_soc,mut_phen)
% Calculate gametes next generation

% A female is mated if bit 5 - > ~isnan

L = size(oldpop,1);
fem=[];
for ii = 1:L
    for jj = 1:L
        if length(oldpop{ii,jj})> 3
            fem = [fem; oldpop{ii,jj}];
        end
    end
end
M = fem(:,5) == 1;
fem_mated = fem(M,:);

% Now for each mated female we produce gametes
gametes = [];
for ii = 1:size(fem_mated,1)
    parent1 = fem_mated(ii,1:3); % female chromosome
    parent2 = fem_mated(ii,6:8); % male chromosome
    % produce gametes acording to fertility
    if parent2(end) == 0 % female mated with x male
        offsp = NaN*ones(5,3);
        for jj = 1:5
            if rand <= rec_ % produces 1 recombining offsprings
                rnd_ = ceil((3-1)*rand);
                offsp(jj,:) = [parent1(1:rnd_) parent2(rnd_+1:end)];
            else
                parents = [parent1; parent2];
                rnd_ = ceil(2*rand);
                offsp(jj,:) = parents(rnd_,:);
            end
        end
    elseif parent2(end) == 1 % female mated with y male
        offsp = NaN*ones(5,3);
```

```
        for jj = 1:5
            if rand <= rec_ % produces 1 recombining offsprings
                rnd_ = ceil((3-1)*rand);
                offsp(jj,:) = [parent1(1:rnd_) parent2(rnd_+1:end)];
            else
                parents = [parent1; parent2];
                rnd_ = ceil(2*rand);
                offsp(jj,:) = parents(rnd_,:);
            end
        end
    end
    gametes = [gametes;offsp];
end

% Now we introduce mutation
mm = size(gametes,1);
mutant_g = [rand(mm,1) < mut_pref, rand(mm,1) < mut_soc, rand(mm,1) <
mut_phen];
I = find(mutant_g == 1);
gametes(I) = ~gametes(I);
out = gametes;

if size(out,1) < L^2
    out = repmat(out,L^2,1); % to avoid an unlikely break in the program
end
end
```

Table S4. Input parameters (example of xls file for input data in MATLAB)

The first few lines of the xls file for the MATLAB input is represented below. The entire xls file can be downloaded from:

https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fevo.13235&file=evo13235-sup-0002-TableS4.xls

L	f_pref	f_soc	f_male	rec_	s_x	s_y	s_c	ch_cost	mut_pref	mut_soc	mut_phen	t_steps	runs
30	0.1	0	0	0	0.05	0	0	0.3	0	0.001	0.01	750	3
30	0.1	0	0	0	0.1	0	0	0.3	0	0.001	0.01	750	3
30	0.1	0	0	0	0.15	0	0	0.3	0	0.001	0.01	750	3
30	0.1	0	0	0	0.2	0	0	0.3	0	0.001	0.01	750	3
30	0.1	0	0	0	0.25	0	0	0.3	0	0.001	0.01	750	3
30	0.1	0	0	0	0.3	0	0	0.3	0	0.001	0.01	750	3
30	0.1	0	0	0	0.35	0	0	0.3	0	0.001	0.01	750	3
30	0.2	0	0	0	0.05	0	0	0.3	0	0.001	0.01	750	3
30	0.2	0	0	0	0.1	0	0	0.3	0	0.001	0.01	750	3
30	0.2	0	0	0	0.15	0	0	0.3	0	0.001	0.01	750	3
30	0.2	0	0	0	0.2	0	0	0.3	0	0.001	0.01	750	3
30	0.2	0	0	0	0.25	0	0	0.3	0	0.001	0.01	750	3
30	0.2	0	0	0	0.3	0	0	0.3	0	0.001	0.01	750	3
30	0.2	0	0	0	0.35	0	0	0.3	0	0.001	0.01	750	3
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮

Table S5. Output results (example of xls file output from MATLAB)

The first few lines one of the output results of the MATLAB output is represented below. The entire xls file can be downloaded from:

https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fevo.13235&file=evo13235-sup-0003-TableS5.xls

f_pref	f_soc	f_male	Dprime 1-2	Dprime 1-3	Dprime 2-3
0.10555556	0	0			
0.10182927	0.00304878	0.0097561	-0.10214067	-0.03971675	-0.00978593
0.10511364	0.00056818	0.0125	-0.10517339	-0.06041427	-0.01250711
0.09204545	0.00170455	0.02443182	-0.09220262	0.00107693	-0.02447353
0.08209366	0.00606061	0.02754821	0.00960384	-0.04328612	-0.02771619
0.10122699	0.00368098	0.04601227	-0.10160099	-0.0222508	-0.04618227
0.10112994	0.00225989	0.04915254	-0.101359	0.07930384	-0.04926387
0.11036415	0.00952381	0.05210084	-0.0520362	-0.05971174	-0.05260181
0.10697674	0.01104651	0.07325581	-0.00173273	-0.00410269	-0.07407407
0.10659026	0.00515759	0.07965616	0.00506022	0.0014813	-0.08006912
0.09740634	0.00461095	0.09567723	-0.09785756	0.03224007	-0.09612044
0.10457143	0.004	0.08914286	0.04275686	0.05502921	-0.08950086
0.10625	0.00170455	0.10681818	-0.10643142	-0.05370031	0.25360475
0.10445104	0.0041543	0.10979228	0.04288554	0.00431818	-0.1102503
0.1047619	0.00392157	0.12212885	-0.10517435	0.01926089	-0.12260967
0.1	0.00289017	0.14682081	-0.10028986	-0.01541426	-0.14724638
0.10393258	0.00280899	0.16235955	-0.10422535	0.01267062	-0.1628169
0.09529412	0.00235294	0.17705882	-0.09551887	-0.02513285	0.08863474
0.09833333	0.00444444	0.19166667	0.16820702	0.0005242	-0.06696429
0.1042735	0.0039886	0.19373219	-0.10469108	0.00370735	0.1140838
0.09575071	0.00623229	0.23342776	0.09518113	0.00425091	-0.23489168
0.09164087	0	0.2501548		-0.0671162	
0.09391304	0	0.30028986		-0.01122011	
0.10122699	0.00122699	0.3	-0.10135135	-0.0101148	0.28571429
0.1085044	0.00293255	0.26920821	-0.10882353	-0.02306188	0.17897271
0.10205279	0.0058651	0.28856305	-0.0020649	-0.02054476	0.57831822
0.09285714	0.00297619	0.31309524	-0.09313433	0.02946274	0.41767764
0.09317507	0.00593472	0.30148368	0.00752618	0.00608261	0.42735769
0.11702786	0.00619195	0.26315789	-0.01713396	-0.02838443	0.59285714
⋮	⋮	⋮	⋮	⋮	⋮

Appendix II

Supporting material for Chapter 3: Social learning by mate-choice copying increases dispersal and reduces local adaptation

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Figure S1. Examples of simulated environmental values landscapes

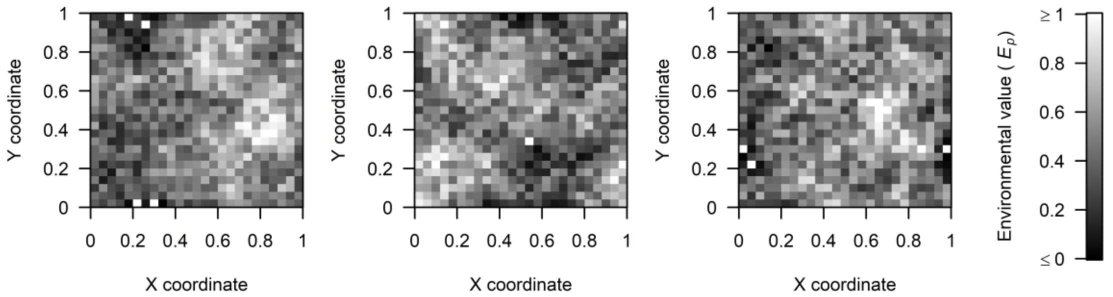

Figure S1. Examples of simulated environmental values landscapes for $\beta = 0.99$. Each small square in the landscape represents one of the 25^2 breeding patches, and its brightness represents its environmental value. The world is continuous, so the left border touches the right border, and the upper border touches the lower border.

Table S1. ANOVA comparison of the mean allelic value of D between control, unconditional, and conditional mate-choice copying scenarios at generations 7500 and 15000. Significant p-values are in bold.

Generation	S_S value	Degrees of freedom	F value	p-value	Bonferroni corrected p-value
7500	0	2 / 57	1.066	0.351	1.000
	25	2 / 57	0.045	0.956	1.000
	50	2 / 57	2.229	0.117	0.585
	75	2 / 57	1.011	0.370	1.000
	100	2 / 57	1.072	0.349	1.000
15000	0	2 / 57	0.747	0.479	1.000
	25	2 / 57	5.162	**0.009**	**0.044**
	50	2 / 57	36.368	**<0.001**	**<0.001**
	75	2 / 57	92.992	**<0.001**	**<0.001**
	100	2 / 57	54.646	**<0.001**	**<0.001**

Table S2. Pairwise t-tests comparing the mean allelic value of D of the control, unconditional, or conditional mate-choice copying scenarios between generations 7500 and 15000 (control scenario) or 12500 and 15000 (unconditional and conditional scenarios). Significant p-values are in bold.

Scenario	S_S	Generations compared	Mean difference* $(\times 10^{-4})$	95% Confidence Interval		Degrees of freedom	t-value	p-value	Bonferroni corrected p-value
				Lower* $(\times 10^{-4})$	Upper* $(\times 10^{-4})$				
Control	0	7500 / 15000	0.145	-2.801	2.512	19	-0.114	0.910	1.000
	25	7500 / 15000	-0.651	- 3.562	2.261	19	-0.467	0.645	1.000
	50	7500 / 15000	-0.520	- 4.041	3.002	19	-0.308	0.761	1.000
	75	7500 / 15000	- 0.693	-4.958	1.340	19	-0.713	0.485	1.000
	100	7500 / 15000	-2.460	- 2.725	0.039	19	-2.060	0.053	0.267
Unconditional	0	12500 / 15000	-0.041	-0.253	0.171	19	-0.404	0.691	1.000
	25	12500 / 15000	-0.158	-0.467	0.152	19	-1.067	0.300	1.000
	50	12500 / 15000	0.067	-0.360	0.493	19	0.328	0.747	1.000
	75	12500 / 15000	-0.232	-0.452	-0.012	19	-2.203	**0.040**	0.201
	100	12500 / 15000	0.308	-0.036	0.652	19	1.876	0.076	1.000
Conditional	0	12500 / 15000	-0.094	-0.273	0.086	19	-1.094	0.288	1.000
	25	12500 / 15000	-0.185	-0.409	0.040	19	-1.722	0.101	0.506
	50	12500 / 15000	0.326	0.011	0.642	19	2.168	**0.043**	0.215
	75	12500 / 15000	0.256	-0.189	0.701	19	1.203	0.244	1.000
	100	12500 / 15000	-0.141	-0.588	0.307	19	-0.658	0.518	1.000

*Value at generation 15000 minus the value at generation 7500 or 12500.

Table S3. Pairwise t-tests comparing the proportion of individuals with the C allele of the unconditional or conditional mate-choice copying scenarios between generations 12500 and 15000.

Scenario	S_S	Generations compared	Mean difference*	95% Confidence Interval		Degrees of freedom	t-value	p-value	Bonferroni corrected p-value
				Lower*	Upper*				
Unconditional	0	12500 / 15000	-0.023	-0.067	0.020	19	-1.123	0.276	1.000
	25	12500 / 15000	-0.041	-0.087	0.005	19	-1.858	0.079	0.394
	50	12500 / 15000	0.041	-0.034	0.115	19	1.132	0.272	1.000
	75	12500 / 15000	-0.003	-0.019	0.014	19	-0.329	0.746	1.000
	100	12500 / 15000	0.004	-0.006	0.014	19	0.823	0.421	1.000
Conditional	0	12500 / 15000	0.012	-0.048	0.071	19	0.409	0.687	1.000
	25	12500 / 15000	0.012	-0.051	0.076	19	0.409	0.687	1.000
	50	12500 / 15000	0.011	-0.040	0.063	19	0.460	0.651	1.000
	75	12500 / 15000	0.019	-0.034	0.071	19	0.751	0.462	1.000
	100	12500 / 15000	-0.004	-0.054	0.046	19	-0.163	0.872	1.000

*Value at generation 15000 minus the value at generation 12500.

Table S4. ANOVA comparisons of the local adaptation score (*L*) between control, unconditional, and conditional mate-choice copying scenarios at generations 7500 and 15000. Significant p-values are in bold.

Generation	S_S	Degrees of freedom	F value	p-value	Bonferroni corrected p-value
7500	0	2 / 57	0.679	0.511	1.000
	25	2 / 57	0.829	0.442	1.000
	50	2 / 57	0.645	0.528	1.000
	75	2 / 57	0.716	0.493	1.000
	100	2 / 57	1.294	0.282	1.000
15000	0	2 / 57	0.063	0.939	1.000
	25	2 / 57	4.562	**0.015**	0.073
	50	2 / 57	3.369	**0.041**	0.207
	75	2 / 57	7.362	**0.001**	**0.007**
	100	2 / 57	13.372	**<0.001**	**<0.001**

Table S5. Pairwise t-tests comparing the local adaptation score (L) of the control mate-choice copying scenario between generations 7500 and 15000.

Scenario	S_S	Generations compared	Mean difference* (10^{-3})	95% Confidence Interval Lower* ($\times 10^{-3}$)	95% Confidence Interval Upper* ($\times 10^{-3}$)	Degrees of freedom	t-value	p-value	Bonferroni corrected p-value
Control	0	7500 / 15000	0.0128	-0.2916	0.3173	19	0.088	0.931	1.000
	25	7500 / 15000	0.2080	-0.4677	0.8838	19	0.644	0.527	1.000
	50	7500 / 15000	0.1643	-1.1578	1.4864	19	0.260	0.798	1.000
	75	7500 / 15000	0.0237	-1.2952	1.3427	19	0.038	0.970	1.000
	100	7500 / 15000	-0.1407	-1.0326	0.7512	19	-0.330	0.745	1.000

*Value at generation 15000 minus the value at generation 7500.

Table S6. ANOVA comparisons of the Pearson correlation coefficient between the T and P alleles between control, unconditional, and conditional mate-choice copying scenarios at generations 7500 and 15000. Significant p-values are in bold.

Generation	S_S	Degrees of freedom	F value	p-value	Bonferroni corrected p-value
7500	0	2 / 57	0.250	0.780	1.000
	25	2 / 57	0.088	0.916	1.000
	50	2 / 57	1.801	0.174	0.872
	75	2 / 57	1.487	0.235	1.000
	100	2 / 57	1.353	0.267	1.000
15000	0	2 / 57	0.455	0.637	1.000
	25	2 / 57	39.867	**<0.001**	**<0.001**
	50	2 / 57	24.671	**<0.001**	**<0.001**
	75	2 / 57	61.226	**<0.001**	**<0.001**
	100	2 / 57	51.606	**<0.001**	**<0.001**

Table S7. Pairwise t-tests comparing the Pearson correlation coefficient between the T and P alleles of the control mate-choice copying scenario between generations 7500 and 15000.

Scenario	S_S	Generations compared	Mean difference*	95% Confidence Interval		Degrees of freedom	t-value	p-value	Bonferroni corrected p-value
				Lower*	Upper*				
Control	0	7500 / 15000	-0.005	-0.053	0.043	19	-0.219	0.829	1.000
	25	7500 / 15000	0.025	-0.038	0.087	19	0.825	0.420	1.000
	50	7500 / 15000	-0.002	-0.028	0.024	19	-0.143	0.888	1.000
	75	7500 / 15000	0.002	-0.015	0.018	19	0.219	0.829	1.000
	100	7500 / 15000	0.006	-0.020	0.032	19	0.474	0.641	1.000

*Value at generation 15000 minus the value at generation 7500.

C Computer Code

The computer code for this study has been published in the Dryad Digital Repository as:

Sapage, Manuel; Varela, Susana A. M.; Kokko, Hanna (2020), Social learning by mate-choice copying increases dispersal and reduces local adaptation, Dryad, Dataset, https://doi.org/10.5061/dryad.dncjsxkz1

The code has been published as a compressed folder with many files that are reproduced below. The published folder also includes an example of an output from the code that is not included here.

Instructions File: readme.txt

```
//Social learning by mate-choice copying increases dispersal and reduces local
adaptation
//Authors: Manuel Sapage; Susana A. M. Varela; Hanna Kokko
//Code created by Manuel Sapage (masapage@fc.ul.pt)


###
Instructions: to run the script in Cygwin using GCC, copy all the files to a
folder, open the '_input.h' as a text file to change the parameters before
compiling the executable.
Run the following three commands after setting Cygwin to the folder path where
the files are located:

gcc -c MCC_simulation.c -lm
gcc  MCC_simulation.c -lgsl -lgslcblas -lm -o MCC_simulation.exe
MCC_simulation.exe

The last line of the code can be ran multiple times for further replicates.

###
Output folder structure: The program will create a folder following the input
file name and number the simulations (starting from 0) accordingly.

/Local -> Folder for the variables by patch controlled by LSAMP. Each line
          is a sampled generation and values are sequential row-wise, i.e.,
          m[1,1],m[1,2],...,m[1,x],m[2,1],m[2,2],...,m[y,x]. First value for
          each line is the generation number. Values rounded to 3 decimal
          places
    ../Local_copy_sim_s****.txt -> Copy allele mean for each patch
    ../Local_disp_sim_s****.txt -> Disp allele mean for each patch
    ../Local_n_sim_s****.txt -> Number of adults in patch
    ../Local_pref_sim_s****.txt -> Pref allele mean for each patch
    ../Local_sex_sim_s****.txt -> Sex ratio for each patch
    ../Local_trait_sim_s****.txt -> Trait allele mean for each patch
/Main -> Main raw output controlled by GSAMP. Each line in the files is a
         sampled generation. First value for each line is the generation
         number. Values rounded to 3 decimal places
    ../Breed_coord_row_sim_s***.txt -> Individuals patch row position
    ../Breed_coord_col_sim_s***.txt -> Individuals patch col position
```

```
    ../Coord_row_sim_s***.txt -> Individuals row position
    ../Coord_col_sim_s***.txt -> Individuals col position
    ../Copy_sim_s****.txt -> Individuals copy allele
    ../Disp_sim_s****.txt -> Individuals disp allele
    ../Pref_sim_s****.txt -> Individuals pref allele
    ../Sex_sim_s****.txt -> Individuals sex: 0 = female; 1 = male)
    ../Trait_sim_s****.txt -> Individuals trait allele
/Log_name_s****.log -> Log file with all the variables. Is written so that it
                       can be run like an input file with the seed set to the
                       value of the run
/Extinction_sim.txt -> Common file for all simulations with the same name
                       Each line has the simulation name and the extinction
                       generation
                       No record if population do not extinguish
/Env_sim_s****.txt -> Environmental matrix
/Stats_sim_s****.txt -> Main stats for the generation with population number
                        after dispersal and mean, sd, or counts for the genes

###
```

Main File: MCC_simulation.c

```
//Social learning by mate-choice copying increases dispersal and reduces local
adaptation
//Authors: Manuel Sapage; Susana A. M. Varela; Hanna Kokko
//Code created by Manuel Sapage (masapage@fc.ul.pt)

// Importing some C libraries
#include <string.h>
#include <math.h>
#include <sys/stat.h>
#include <limits.h>
#include <stdarg.h>

// Importing some GNU scientific libraries (gsl)
#include<gsl/gsl_randist.h>
#include <gsl/gsl_sort.h>
#include <gsl/gsl_blas.h>

// Coded file
#include "_input.h" //parameters input file
#include "initialize.h" //population and environment initiation and management
#include "output.h" //creates and writes output files
#include "dynamics.h" //simulates population dynamics

void main(){
//main function for the simulation
    int g; //generation number
    initialize_objects();
    initialize_io();
    for(g=0;g<NG+1;g++){ //generation loop
        printf("\r\tGeneration %d out of %u",g,NG); fflush(stdout);
        survival_dispersal();
        if(adult.n_d==0) break;
        write_adult_status(g);
        breeding_reproduction(g);
    }
    free_objects();
    close_all_files();
    printf("\n\n### Simulation Complete ###\n");
}
```

Input File: _input.h

```
#ifndef PAR_CHOOSE_H_INCLUDED
#define PAR_CHOOSE_H_INCLUDED

// ### Parameters modified in the study ###
#define FN "Output_example" // Output Folder name
#define SSEX 100. // Scale of Sexual Selection Strength
#define LC 0 // Local Females Copy? (0 for conditional, 1 for unconditional,
not used in control)
#define MC 0.001 // Mutation Probability from c->C and C->c (0 in control)

// ### Other Modifiable Parameters ###
#define EB 0.99 // Patch Autocorrelation Beta (0<=EB<1)
#define K 16 // Patch Carrying Capacity, Produced Offspring is 2K
#define SENV 50. // Scale of Environmental Selection Strength
#define DMORT 0.05 // Dispersal Mortality
#define PSIZE 25 // The World has PSIZE^2 Patches

// # Mutation Probability
#define MT 0.01 // T
#define MP 0.01 // P
#define MD 0.01 // D

// # Mutation Amount in Standard Deviations
#define MTS 0.05 // T
#define MPS 0.05 // P
#define MDS 0.005 // D

// # Population Alleles Initialization
#define TPSD 0.05 // T and P Allele initial variation measured in sd in
relation the initial environment
#define DIN 0.005 // D initial distribution as an uniform distribution with
minimum of 0 and maximum of DIN

// # Simulation and Sample Options
#define NG 15000 // Number of Generations Simulated
#define MCA 7500 // Generation for the MC Mutation to Appear (irrelevant when
MC equals 0)
#define GW 2500 // Sample Interval
#define LSAMP 1 // Sample Local Patch Data (0 - No, 1 - Yes)
#define GSAMP 1 // Sample Individual Genetic Data (0 - No, 1 - Yes)

// # Randomness
#define RSEED 1 // Random Seed? (0 - No, 1 - Yes)
#define SEED 0 // Seed Value if RSEED 0

#endif
```

Supporting File: initialize.h

```
#ifndef INITIALIZE_H_INCLUDED
#define INITIALIZE_H_INCLUDED
//Functions to initiate the Simulation

//### GENERAL FUNCTIONS ###

//# objects
gsl_rng *r; //stores the instance of the random number generator
unsigned long seed; //stores seed value

//# functions
```

```
void rand_seed(const gsl_rng_type *R){
    //function to produce random of fixed seed
    if(RSEED){
        srand(time(NULL));
        seed=rand();
    }else seed=SEED;
    R=gsl_rng_default;
    r=gsl_rng_alloc(R);
    gsl_rng_set(r,seed);
}

void error_statement(const char* f, ...){
    //prints error and exits
    fflush(stdout);
    va_list arg;
    va_start(arg,f);
    vfprintf(stderr,f,arg);
    va_end(arg);
    exit(EXIT_FAILURE);
}

//### ENVIRONMENT CREATION FUNCTIONS ###

//# objects
gsl_matrix *env_grid; //environmental matrix

//# functions
double env_sample_neighbour(unsigned int row, unsigned int col){
    //returns the mean value of the neighboring patches
    unsigned int row_up, row_down, col_left, col_right;
    double v=0;
    row_up=(row==PSIZE-1)?0:row+1;
    row_down=(row==0)?PSIZE-1:row-1;
    col_right=(col==PSIZE-1)?0:col+1;
    col_left=(col==0)?PSIZE-1:col-1;
    v= gsl_matrix_get(env_grid,row_up,col_left)+
        gsl_matrix_get(env_grid,row_up,col)+
        gsl_matrix_get(env_grid,row_up,col_right)+
        gsl_matrix_get(env_grid,row_down,col_left)+
        gsl_matrix_get(env_grid,row_down,col)+
        gsl_matrix_get(env_grid,row_down,col_right)+
        gsl_matrix_get(env_grid,row,col_left)+
        gsl_matrix_get(env_grid,row,col_right);
    return(v/8);
}

void env_resample(){
    //selects and updates the patch value
    unsigned int row,col;
    if(EB<0 || EB>=1) error_statement("Wrong EB value");
    row=gsl_rng_uniform_int(r,PSIZE);
    col=gsl_rng_uniform_int(r,PSIZE);
    gsl_matrix_set(env_grid,row,col,gsl_rng_uniform_pos(r)*
        (1-EB)+env_sample_neighbour(row,col)*EB);
}

void env_rescale(){
    //rescales GEI for a mean of 0.5 and sd to 0.2
    unsigned int row,col;
    double sd=0, mean=0;
    for(row=0;row<PSIZE;row++) for(col=0;col<PSIZE;col++)
        mean+=gsl_matrix_get(env_grid,row,col);
    mean=(mean/(double)(PSIZE*PSIZE));
    for(row=0;row<PSIZE;row++) for(col=0;col<PSIZE;col++)
        sd+=pow(gsl_matrix_get(env_grid,row,col)-mean,2);
    sd=0.2/sqrt(sd/(double)(PSIZE*PSIZE));
    for(row=0;row<PSIZE;row++) for(col=0;col<PSIZE;col++)
```

```
        gsl_matrix_set(env_grid,row,col,
        (gsl_matrix_get(env_grid,row,col)-mean)*sd+0.5);
}

void main_env_construct_GEI(){
    //Constructs the environment matrix
    env_grid=gsl_matrix_alloc(PSIZE,PSIZE);
    unsigned int i,x,y;
    for(x=0;x<PSIZE;x++)for(y=0;y<PSIZE;y++)
        gsl_matrix_set(env_grid,y,x,gsl_rng_uniform_pos(r));
    for(i=0;i<100*PSIZE*PSIZE;i++) env_resample();
    env_rescale();
}

//### POPULATION INITIALIZATION FUNCTIONS ###

//# objects
struct population{ //population status
    gsl_vector *trait,*pref,*disp; //genotypes
    gsl_vector_char *sex,*copy; //sex: f=0,m=1; copy: no=0,yes=1;
    gsl_vector_char *survived; //marks if population survived during
        selection (no=0,yes=1)
    gsl_vector_char *changed; //marks if population changed their
        patch(no=0,yes=1)
    gsl_matrix *coord; //effective coordinates
    gsl_matrix_uint *breed_coord; //patch coordinates
    gsl_vector *value; //local adaptation value score (Offspring)
        //updated pref (Adult females) 0 to 1
    unsigned long n,n_d; //Population size before/after dispersal
} adult, offspring;

struct patch_selection{ //patch status
    gsl_vector_uint *select_id; //vector offspring id of the individuals in
        a patch
    gsl_vector_uint *male_id,*female_id; //vector of id of the (fe)males in
        the patch
    gsl_vector_uint *sampled_males; //number of times a male following
        male_id is chosen
    gsl_vector_uint *chosen_id; //id of the male of the chosen male by
        female_id
    unsigned int m,f; //number of males and females in the patch
} patch;

//# functions to initiate population struct data

void genotype_initiate_vector_char(gsl_vector_char *gen, double probability){
    //applies a vector with the value following the binomial distribution
         (for sex locus)
    unsigned int x;
    for(x=0;x<gen->size;x++)
        gsl_vector_char_set(gen,x,gsl_rng_uniform(r)<probability?1:0);
}

void genotype_initiate_vector_loc(gsl_vector *gen, double sigma){
    //places a value in a population genetic vector with a normal distribution
        centered on the local environmental value
    unsigned int x,patch_row,patch_col;
    double value;
    for(x=0;x<gen->size;x++){
        patch_row=(unsigned int) floor(gsl_matrix_get(offspring.coord,0,x)*
            PSIZE);
        patch_col=(unsigned int) floor(gsl_matrix_get(offspring.coord,1,x)*
            PSIZE);
        value=gsl_matrix_get(env_grid,patch_row,patch_col)+
            gsl_ran_gaussian_ziggurat(r,sigma);
        //standardizing to [0,1]
        if(value>1) value=1;
```

```
         if(value<0) value=0;
         gsl_vector_set(gen,x,value);
     }
}

void genotype_initiate_vector_unif(gsl_vector *gen, double n){
    //places random values in a population genetic vector
    unsigned int x;
    if(n>1) error_statement("Initiation error, value >1");
    if(n<0) error_statement("Initiation error, value <0");
    for(x=0;x<gen->size;x++) gsl_vector_set(gen,x,gsl_rng_uniform(r)*n);
}

void population_initiate(){
    //places the initial offspring data into random coordinates
    unsigned int n,coord;
    for(coord=0;coord<2;coord++) //coord = 0 for row; coord = 1 for col
        for(n=0;n<offspring.coord->size2;n++)
            gsl_matrix_set(offspring.coord,coord,n,gsl_rng_uniform_pos(r));
            genotype_initiate_vector_loc(offspring.trait,TPSD);
            genotype_initiate_vector_loc(offspring.pref,TPSD);
            genotype_initiate_vector_unif(offspring.disp,DIN);
            genotype_initiate_vector_char(offspring.copy,0);
            genotype_initiate_vector_char(offspring.sex,0.5);
}

//# functions to allocate and free memory for objects

void population_alloc(struct population *p, int n){
    //allocates memory for population struct
    p->trait=gsl_vector_alloc(n);
    p->pref=gsl_vector_alloc(n);
    p->disp=gsl_vector_alloc(n);
    p->copy=gsl_vector_char_alloc(n);
    p->sex=gsl_vector_char_alloc(n);
    p->coord=gsl_matrix_alloc(2,n);
    p->breed_coord=gsl_matrix_uint_alloc(2,n);
    p->value=gsl_vector_alloc(n);
    p->survived=gsl_vector_char_alloc(n);
    p->changed=gsl_vector_char_alloc(n);
}

void variables_alloc(){
    //allocates memory for population and patch_selection struct objects
    adult.n=K*PSIZE*PSIZE;
    offspring.n=2*K*PSIZE*PSIZE;
    population_alloc(&adult,adult.n);
    population_alloc(&offspring,offspring.n);
    patch.select_id=gsl_vector_uint_alloc(offspring.n);
    patch.male_id=gsl_vector_uint_alloc(adult.n);
    patch.sampled_males=gsl_vector_uint_alloc(adult.n);
    patch.female_id=gsl_vector_uint_alloc(adult.n);
    patch.chosen_id=gsl_vector_uint_alloc(adult.n);
}

void population_free(struct population *p){
    //frees memory for population struct
    gsl_vector_free(p->trait);
    gsl_vector_free(p->pref);
    gsl_vector_free(p->disp);
    gsl_vector_char_free(p->copy);
    gsl_vector_char_free(p->sex);
    gsl_matrix_free(p->coord);
    gsl_matrix_uint_free(p->breed_coord);
    gsl_vector_free(p->value);
    gsl_vector_char_free(p->survived);
    gsl_vector_char_free(p->changed);
```

```
}

void variables_free(){
    //frees memory for population and patch_selection struct objects
    population_free(&adult);
    population_free(&offspring);
    gsl_vector_uint_free(patch.select_id);
    gsl_vector_uint_free(patch.male_id);
    gsl_vector_uint_free(patch.sampled_males);
    gsl_vector_uint_free(patch.female_id);
    gsl_vector_uint_free(patch.chosen_id);
}

//# function to initiate and end simulation
void initialize_objects(){
    //initiates simulation
    const gsl_rng_type *R; //object to store randomizer
    variables_alloc();
    rand_seed(R);
    main_env_construct_GEI();
    population_initiate();
}

void free_objects(){
    //frees memory for all objects
    variables_free();
    gsl_matrix_free(env_grid);
}

#endif
```

Supporting File: output.h

```
#ifndef OUTPUT_H_INCLUDED
#define OUTPUT_H_INCLUDED
// Funtions to record output

//### CREATING FILES AND FOLDERS ###

// Objects
mode_t oldumask;

struct input_output{
    //creates files for output
    char dir[100],str[10];
    FILE *log,*stats,*env_variable;
    //Main folder
    FILE *trait,*copy,*pref,*sex,*disp;
    FILE *coord_row,*coord_col,*breed_coord_row,*breed_coord_col;
    //Local folder
    FILE *local_trait,*local_copy,*local_pref;
    FILE *local_sex,*local_disp,*local_n;
}io;

// functions
FILE* create_file(FILE *file, char name[]){
    //creates a generic output file
    char dir[120];
    snprintf(dir,sizeof(dir),"%s%s%s%s%s",io.dir,name,"_sim",io.str,".txt");
    file=fopen(dir,"w");
}

void create_extra_folder(char name[]){
    //creates extra folder if it doesn't exist
```

```
    char dir[120];
    snprintf(dir,sizeof(dir),"%s%s%s",io.dir,"/",name);
    oldumask=umask((mode_t)0);
    mkdir(dir,0777);
    umask(oldumask);
}

void create_all_files(){
    //create sampling files
    io.stats=create_file(io.stats,"/Stats");
    if(GSAMP){
        create_extra_folder("Main");
        io.trait=create_file(io.trait,"/Main/Trait");
        io.copy=create_file(io.copy,"/Main/Copy");
        io.pref=create_file(io.pref,"/Main/Pref");
        io.sex=create_file(io.sex,"/Main/Sex");
        io.disp=create_file(io.disp,"/Main/Disp");
        io.coord_row=create_file(io.coord_row,"/Main/Coord_row");
        io.coord_col=create_file(io.coord_col,"/Main/Coord_col");
        io.breed_coord_row=create_file(io.breed_coord_row,
            "/Main/Breed_coord_col");
        io.breed_coord_col=create_file(io.breed_coord_col,
            "/Main/Breed_coord_row");
    }
    if(LSAMP){
        create_extra_folder("Local");
        io.local_trait=create_file(io.local_trait,"/Local/Local_trait");
        io.local_copy=create_file(io.local_copy,"/Local/Local_copy");
        io.local_pref=create_file(io.local_pref,"/Local/Local_pref");
        io.local_sex=create_file(io.local_sex,"/Local/Local_sex");
        io.local_disp=create_file(io.local_disp,"/Local/Local_disp");
        io.local_n=create_file(io.local_n,"/Local/Local_n");
    }
}

int c_file_exists(const char* filename){
    //checks if file exists, returns 1 if it doesn't
    struct stat buffer;
    int exist=stat(filename,&buffer);
    return(exist==0?1:0);
}

void create_folder(){
    //creates new folder if it doesn't exist or adds new number based on log
        number
    int n=0;
    char dir[100], str[10];
    strcpy(io.dir,FN);
    oldumask=umask((mode_t)0);
    mkdir(io.dir,0777);
    umask(oldumask);
    while(n!=-1){
        sprintf(str,"_s%04d",n); n++;
        snprintf(dir,sizeof(dir),"%s%s%s%s%s",FN,"/Log_",FN,str,".h");
        if(!c_file_exists(dir))n=-1;
    }
    strcpy(io.str,str);
}

void close_all_files(){
    //close sampling files
    fclose(io.stats);
    if(GSAMP){
        fclose(io.trait); fclose(io.copy); fclose(io.pref);
        fclose(io.sex); fclose(io.disp); fclose(io.coord_row);
        fclose(io.coord_col); fclose(io.breed_coord_row);
        fclose(io.breed_coord_col);
```

```
    }
    if(LSAMP){
        fclose(io.local_trait); fclose(io.local_copy);
        fclose(io.local_pref); fclose(io.local_sex);
        fclose(io.local_disp); fclose(io.local_n);
    }
}

//### PRINTS STATUS AND SIMULATION LOG ###

//# objects
struct tm* t; //stores time

struct tm* present_time(){
    //records time
    time_t rawtime;
    struct tm* timeinfo;
    time(&rawtime);
    timeinfo=localtime(&rawtime);
    return timeinfo;
};

//# functions
void print_input(FILE *out){ //check new input
    //display in log and console output
    char buffer[80];
    fprintf(out,"//Log data for simulation: %s%s%s","Log_",io.dir,io.str);
    fprintf(out,"\r\n//Simulation code written by Manuel Sapage");
    fprintf(out,"\r\n//Can be used as input code");
    fprintf(out,"\r\n\r\n#ifndef VAR_CHOOSE_H_INCLUDED");
    fprintf(out,"\r\n#define VAR_CHOOSE_H_INCLUDED");
    fprintf(out,"\r\n\r\n//#Simulation started on ");
    strftime(buffer,80,"%d %b %Y, %H:%M:%S",t);
    fprintf(out,"%s",buffer);
    fprintf(out,"\r\n\r\n\t//Generator type = %s",gsl_rng_name(r));
    fprintf(out,"\r\n\t//Maximum int = %d",INT_MAX);
    fprintf(out,"\r\n\r\n// ### Parameters modified in the study ###");
    fprintf(out,"\r\n#define FN \"%s\" // Folder name",io.dir);
    fprintf(out,"\r\n#define SSEX %f // Scale Sexual Selection
        Strength",SSEX);
    fprintf(out,"\r\n#define LC %d // Do Local Females Copy? ",LC);
    fprintf(out,"(0 for conditional, 1 for unconditional, not used in
        control)");
    fprintf(out,"\r\n#define MC %f //  Mutation Probability from c->C and
        C->c (0 in control)",MC);
    fprintf(out,"\r\n\r\n// ### Other Modifiable Parameters ###");
    fprintf(out,"\r\n#define EB %f // Patch Autocorrelation Beta
        (0<=EB<1)",EB);
    fprintf(out,"\r\n#define K %u // Patch Carrying Capacity, Produced
        Offspring is 2K",K);
    fprintf(out,"\r\n#define SENV %f // Scale of Environmental Selection
        Strength",SENV);
    fprintf(out,"\r\n#define DMORT %f // Dispersal Mortality",DMORT);
    fprintf(out,"\r\n#define PSIZE %u // The World has PSIZE^2
        Patches",PSIZE);
    fprintf(out,"\r\n\r\n// # Mutation Probability");
    fprintf(out,"\r\n#define MT %f // T",MT);
    fprintf(out,"\r\n#define MP %f // P",MP);
    fprintf(out,"\r\n#define MD %f // D",MD);
    fprintf(out,"\r\n\r\n// # Mutation Amount in Standard Deviations");
    fprintf(out,"\r\n#define MTS %f // T",MTS);
    fprintf(out,"\r\n#define MPS %f // P",MPS);
    fprintf(out,"\r\n#define MDS %f // D",MDS);
    fprintf(out,"\r\n\r\n// #  Population Alleles Initialization");
    fprintf(out,"\r\n#define TPSD %f // T and P Allele initial variation
        measured in sd in relation the initial environment",TPSD);
    fprintf(out,"\r\n#define DIN %f // D initial distribution as an uniform
```

```
        distribution with minimum of 0 and maximum of DIN",DIN);
    fprintf(out,"\r\n\r\n// # Simulation and Sample Options");
    fprintf(out,"\r\n#define NG %u // Number of Generations Simulated",NG);
    fprintf(out,"\r\n#define MCA %d // Generation for the MC Mutation to
        Appear (irrelevant when MC equals 0)",MCA);
    fprintf(out,"\r\n#define GW %u // Sample Interval",GW);
    fprintf(out,"\r\n#define LSAMP %d // Sample Local Patch Data (0 - No, 1
        - Yes)",LSAMP);
    fprintf(out,"\r\n#define GSAMP %d // Sample Individual Genetic Data (0
        - No, 1 - Yes)",GSAMP);
    fprintf(out,"\r\n\r\n// # Randomness");
    fprintf(out,"\r\n//#define RSEED %d // Random Seed? (0 - No, 1 -
        Yes)",RSEED);
    fprintf(out,"\r\n#define RSEED 0 // Redefine as 0 for SEED to repeat");
    fprintf(out,"\r\n#define SEED %u // Seed Value",seed);
    fprintf(out,"\r\n\r\n#endif");
    fprintf(out,"\r\n\r\n");
}

void create_log(){
    //create log file
    char dir[120];
    snprintf(dir,sizeof(dir),"%s%s%s%s%s",io.dir,"/Log_",io.dir,io.str,
        ".h");
    vio.log=fopen(dir,"w");
}

//### WRITES INTO OUTPUT FILES ###

//# functions
void write_genotype_vector(FILE *file, gsl_vector *gen, gsl_vector_char *surv,
    unsigned int n, int g){
    //writes a one line genetic matrix
    unsigned int j;
    fprintf(file,"%d\t",g);
    for(j=0;j<n;j++){
        if(gsl_vector_char_get(surv,j)==1)
            fprintf(file,"%.3f\t", gsl_vector_get(gen,j));
        if(j%500==0) fflush(file);
    }
    fprintf(file,"\r\n");
}

void write_genotype_vector_char(FILE *file, gsl_vector_char *gen,
    gsl_vector_char *surv, unsigned int n, int g){
    //writes a genetic char vector (ex. sex)
    unsigned int j;
    fprintf(file,"%d\t",g);
    for(j=0;j<n;j++){
        if(gsl_vector_char_get(surv,j)==1)
            fprintf(file,"%c\t",gsl_vector_char_get(gen,j)+48); //ascii48 = 0
        if(j%500==0) fflush(file);
    }
    fprintf(file,"\r\n");
}

void write_coord_matrix(FILE *file_row, FILE *file_col, gsl_matrix *coord,
    gsl_vector_char *surv, unsigned int n, int g){
    //writes a double vector for 2 files with row and col coord
    unsigned int j;
    fprintf(file_row,"%d\t",g); fprintf(file_col,"%d\t",g);
    for(j=0;j<n;j++){
        if(gsl_vector_char_get(surv,j)==1){
            fprintf(file_row,"%f\t",gsl_matrix_get(coord,0,j));
            fprintf(file_col,"%f\t",gsl_matrix_get(coord,1,j));
        }
    }
```

```
    fprintf(file_row,"\r\n");
    fprintf(file_col,"\r\n");
}

void write_coord_uint_matrix(FILE *file_row, FILE *file_col, gsl_matrix_uint
    *coord, gsl_vector_char *surv, unsigned int n, int g){
    //writes a uint vector for 2 files with row and col coord
    unsigned int j;
    fprintf(file_row,"%d\t", g); fprintf(file_col,"%d\t", g);
    for(j=0;j<n;j++){
        if(gsl_vector_char_get(surv,j)==1){
            fprintf(file_row,"%u\t",gsl_matrix_uint_get(coord,0,j));
            fprintf(file_col,"%u\t",gsl_matrix_uint_get(coord,1,j));
        }
    }
    fprintf(file_row,"\r\n");
    fprintf(file_col,"\r\n");
}

void write_genotype_vector_local_mean(FILE *file, gsl_vector *gen){
    //writes the mean genotype value per patch
    unsigned int i;
    double sum=0;
    if(patch.m+patch.f>0){
        for(i=0;i<patch.m;i++)sum+=gsl_vector_get(gen,gsl_vector_uint_get
            (patch.male_id,i));
        for(i=0;i<patch.f;i++)sum+=gsl_vector_get(gen,gsl_vector_uint_get
             (patch.female_id,i));
        sum=sum/(double)(patch.m+patch.f);
        fprintf(file,"%.3f\t",sum);
    }else fprintf(file,"NA\t");
}

void write_genotype_vector_local_mean_char(FILE *file, gsl_vector_char *gen){
    //writes the mean genotype value per patch
    unsigned int i;
    double sum=0;
    if(patch.m+patch.f>0){
        for(i=0;i<patch.m;i++)sum+=gsl_vector_char_get(gen,gsl_vector_uint_get
            (patch.male_id,i));
        for(i=0;i<patch.f;i++)sum+=gsl_vector_char_get(gen,gsl_vector_uint_get
            (patch.female_id,i));
        sum=sum/(double)(patch.m+patch.f);
        fprintf(file,"%.3f\t",sum);
    }else fprintf(file,"NA\t");
}

void write_environment_status(){
    //writes the environment status
    io.env_variable=create_file(io.env_variable,"/Env");
    unsigned int col,row;
    for(row=0;row<PSIZE;row++){
        for(col=0;col<PSIZE;col++)fprintf(io.env_variable,"%f\t",
            gsl_matrix_get(env_grid,row,col));
        fprintf(io.env_variable,"\r\n");
    }
    fclose(io.env_variable);
}

void write_main_stats_initiate(){
    //writes header for stats file
    fprintf(io.stats,"%s\t%s\t%s\t%s\t%s\t%s\t%s\t%s\t%s\t%s\r\n",
        "Generation","N","C","c","Trait_mean","Trait_sd","Pref_mean",
        "Pref_sd","Disp_mean","Disp_sd");
}

void write_main_stats(int g){
```

```
    //writes stats file
    unsigned int i, copy=0, no_copy=0;
    double t_mean=0, t_sd=0, p_mean=0, p_sd=0, d_mean=0, d_sd=0;
    for(i=0;i<adult.n;i++) if(gsl_vector_char_get(adult.survived,i)==1){
        if(gsl_vector_char_get(adult.copy,i)==1) copy++; else no_copy++;
        t_mean+=gsl_vector_get(adult.trait,i);
        p_mean+=gsl_vector_get(adult.pref,i);
        d_mean+=gsl_vector_get(adult.disp,i);
    }
    t_mean=t_mean/adult.n_d;
    p_mean=p_mean/adult.n_d;
    d_mean=d_mean/adult.n_d;
    for(i=0;i<adult.n;i++) if(gsl_vector_char_get(adult.survived,i)==1){
        t_sd+=pow(gsl_vector_get(adult.trait,i)-t_mean,2);
        p_sd+=pow(gsl_vector_get(adult.pref,i)-p_mean,2);
        d_sd+=pow(gsl_vector_get(adult.disp,i)-d_mean,2);
    }
    t_sd=sqrt(t_sd/(adult.n_d-1));
    p_sd=sqrt(p_sd/(adult.n_d-1));
    d_sd=sqrt(d_sd/(adult.n_d-1));
    fprintf(io.stats,"%d\t%u\t%u\t%u\t%f\t%f\t%f\t%f\t%f\t%f\r\n",
        g,adult.n_d,copy,no_copy,t_mean,t_sd,p_mean,p_sd,d_mean,d_sd);
}

void write_adult_status(int g){
    //recorded after dispersal in adults
    if(g%GW==0 && GSAMP){
        write_genotype_vector(io.trait,adult.trait,adult.survived,adult.n,g);
        write_genotype_vector(io.pref,adult.pref,adult.survived,adult.n,g);
        write_genotype_vector(io.disp,adult.disp,adult.survived,adult.n,g);
        write_genotype_vector_char(io.copy,adult.copy,adult.survived,
            adult.n,g);
        write_genotype_vector_char(io.sex,adult.sex,adult.survived,adult.n,g);
        write_coord_matrix(io.coord_row,io.coord_col,adult.coord,
            adult.survived,adult.n,g);
        write_coord_uint_matrix(io.breed_coord_row,io.breed_coord_col,
            adult.breed_coord,adult.survived,adult.n,g);
    }
    write_main_stats(g);
}

void write_local_adult_status(){
    //recorded after individual placement in patches before selection
    fprintf(io.local_n,"%u\t",patch.m+patch.f);
    write_genotype_vector_local_mean(io.local_trait,adult.trait);
    write_genotype_vector_local_mean(io.local_pref,adult.pref);
    write_genotype_vector_local_mean(io.local_disp,adult.disp);
    write_genotype_vector_local_mean_char(io.local_copy,adult.copy);
    if(patch.m+patch.f>0)fprintf(io.local_sex,"%.3f\t",
        ((double)patch.m)/(double)(patch.m+patch.f));
    else fprintf(io.local_sex,"NA\t");
}

void write_local_adult(char *s){
    //recorded after selection in all patches to get new line
    fprintf(io.local_n,s);
    fprintf(io.local_trait,s);
    fprintf(io.local_pref,s);
    fprintf(io.local_copy,s);
    fprintf(io.local_disp,s);
    fprintf(io.local_sex,s);
}

void initialize_io(){
    //initiates sampling folders and files and writes initial information
    create_folder();
    printf("\r\nMCC simulation");
```

```
    t=present_time();
    create_log();
    print_input(stdout);
    print_input(io.log);
    fclose(io.log);
    create_all_files();
    write_environment_status();
    write_main_stats_initiate();
}

#endif
```

Supporting File: dynamics.h

```
#ifndef DYNAMICS_H_INCLUDED
#define DYNAMICS_DISPERSAL_H_INCLUDED
// Funtions for population dynamics

//### OFFSPRING SURVIVAL AND DISPERSAL ###

void set_patch(struct population *pop, char after){
    //Identify individuals patch and checks if adults changed patch
    //Also kills some dispersed individuals if mortality is set
    unsigned int i,row,row_new,col,col_new;
    char ch;
    for(i=0;i< pop->n;i++){
        row_new=(unsigned int)floor(gsl_matrix_get(pop->coord,0,i)*PSIZE);
        col_new=(unsigned int)floor(gsl_matrix_get(pop->coord,1,i)*PSIZE);
        ch=after;
        if(ch==1){
            row=gsl_matrix_uint_get(pop->breed_coord,0,i);
            col=gsl_matrix_uint_get(pop->breed_coord,1,i);
            if(row!=row_new||col!=col_new){ //changed patch
                gsl_vector_char_set(pop->changed,i,1);
                if(gsl_rng_uniform(r)<DMORT){
                    gsl_vector_char_set(pop->survived,i,0);
                    pop->n_d--;
                }
                ch=0;
            }
        }
        if(ch==0){
            gsl_matrix_uint_set(pop->breed_coord,0,i,row_new);
            gsl_matrix_uint_set(pop->breed_coord,1,i,col_new);
        }
    }
}

//# offspring survival

void survival_select(unsigned int size, unsigned int add){
    //adds 1 to offspring that survives
    //"size" = number of individuals, "add" = number to be selected
    unsigned int i,id;
    if(size<=add)for(i=0;i<size;i++) //Less offspring than carrying capacity
        gsl_vector_char_set(offspring.survived,
            gsl_vector_uint_get(patch.select_id,i),1);
    else{
        size_t index[add];
        double value[size];
        for(i=0;i<size;i++){
            id=gsl_vector_uint_get(patch.select_id,i);
```

```
value[i]=gsl_ran_exponential(r,gsl_vector_get(offspring.value,id));
        }
        const double *c_value = (const double*)value;
        gsl_sort_largest_index(index,add,c_value,1,size);
        for(i=0;i<add;i++){
            id=gsl_vector_uint_get(patch.select_id,index[i]);
            gsl_vector_char_set(offspring.survived,id,1);
        }
    }
}

unsigned int survival_transfer(){
    //transfers the offspring to the adult population struct
    unsigned int i,j=0;
    for(i=0;i<offspring.n;i++)
        if(gsl_vector_char_get(offspring.survived,i)==1){
            gsl_vector_set(adult.trait,j,gsl_vector_get(offspring.trait,i));
            gsl_vector_set(adult.pref,j,gsl_vector_get(offspring.pref,i));
            gsl_vector_set(adult.disp,j,gsl_vector_get(offspring.disp,i));

gsl_vector_char_set(adult.copy,j,gsl_vector_char_get(offspring.copy,i));

gsl_vector_char_set(adult.sex,j,gsl_vector_char_get(offspring.sex,i));
            gsl_vector_char_set(adult.changed,j,0);
            gsl_vector_char_set(adult.survived,j,1);

gsl_matrix_set(adult.coord,0,j,gsl_matrix_get(offspring.coord,0,i));

gsl_matrix_set(adult.coord,1,j,gsl_matrix_get(offspring.coord,1,i));
            gsl_matrix_uint_set(adult.breed_coord,0,j,
            gsl_matrix_uint_get(offspring.breed_coord,0,i));
            gsl_matrix_uint_set(adult.breed_coord,1,j,
            gsl_matrix_uint_get(offspring.breed_coord,1,i));
            j++;
        }
    if(j>K*PSIZE*PSIZE)error_statement("More viable than adults");
    return(j);
}

void survival_calculate(){
    //calculates survival values for each offspring related to the patch value
    unsigned int i;
    double difference;
    for(i=0;i<offspring.n;i++){
        difference=gsl_vector_get(offspring.trait,i)-gsl_matrix_get(env_grid,
            gsl_matrix_uint_get(offspring.breed_coord,0,i),
        gsl_matrix_uint_get(offspring.breed_coord,1,i));
        gsl_vector_set(offspring.value,i,exp(-SENV*pow(difference,2)));
       }
}

unsigned int survival(){
    //processes the entire survival step returning the total value of adults
    unsigned int row,col,k,n;
    set_patch(&offspring,0);
    survival_calculate();
    gsl_vector_char_set_zero(offspring.survived);
    for(row=0;row<PSIZE;row++)for(col=0;col<PSIZE;col++){
        n=0;
        for(k=0;k<offspring.n;k++){
            if(gsl_matrix_uint_get(offspring.breed_coord,0,k)==row &&
                gsl_matrix_uint_get(offspring.breed_coord,1,k)==col){
                gsl_vector_uint_set(patch.select_id,n,k);
                n++;
            }
        }
```

```
        survival_select(n,K);
    }
    return(survival_transfer());
}

//# dispersal
void dispersal(struct population pop){
    unsigned int i;
    double theta, dist;
    for(i=0;i<pop.n;i++){
        theta=gsl_rng_uniform(r)*M_PI*2; //dispersal angle
        dist=gsl_ran_exponential(r,gsl_vector_get(pop.disp,i));
        //dispersal in vertical (row)

gsl_matrix_set(pop.coord,0,i,gsl_matrix_get(pop.coord,0,i)+(sin(theta)*dist));
        gsl_matrix_set(pop.coord,0,i,gsl_matrix_get(pop.coord,0,i)-
            floor(gsl_matrix_get(pop.coord,0,i))); //readjust to [0,1]
        //dispersal in horizontal (col)

gsl_matrix_set(pop.coord,1,i,gsl_matrix_get(pop.coord,1,i)+(cos(theta)*dist));
        gsl_matrix_set(pop.coord,1,i,gsl_matrix_get(pop.coord,1,i)-
            floor(gsl_matrix_get(pop.coord,1,i))); //readjust to [0,1]
    }
}

void survival_dispersal(){
    adult.n=survival();
    adult.n_d=adult.n;
    dispersal(adult);
    set_patch(&adult,1);
}

//### MATING AND REPRODUCTION ###

void adult_value(){
    //transfers female preference from integer to [0,1]
    unsigned int i;
    for(i=0;i<adult.n;i++)if(gsl_vector_char_get(adult.sex,i)==0)
        gsl_vector_set(adult.value,i,gsl_vector_get(adult.pref,i));
}

void place_individuals_patch(unsigned int row, unsigned int col){
    //places individuals that survived dispersal into the patch struct for
mate choice
    patch.m=0; patch.f=0;
    unsigned int k;
    for(k=0;k<adult.n;k++)
        if(gsl_vector_char_get(adult.survived,k)==1 &&
            gsl_matrix_uint_get(adult.breed_coord,0,k)==row &&
            gsl_matrix_uint_get(adult.breed_coord,1,k)==col){
            if(gsl_vector_char_get(adult.sex,k)==0){
                gsl_vector_uint_set(patch.female_id,patch.f,k);
                patch.f++;
            }else{
                gsl_vector_uint_set(patch.male_id,patch.m,k);
                patch.m++;
            }
        }
}

unsigned int female_choice(unsigned int f, char set){
    // female choice, set=1 mate-choice is used as demonstration for copiers
    unsigned int i;
    double difference, exp_values[patch.m], chosen, total;
    total=0;
    for(i=0;i<patch.m;i++){
```

```
difference=gsl_vector_get(adult.trait,gsl_vector_uint_get(patch.male_id,i))-

gsl_vector_get(adult.value,gsl_vector_uint_get(patch.female_id,f));
        exp_values[i]=exp(-SSEX*pow(difference,2));
        total+=exp_values[i];
    }
    chosen=gsl_rng_uniform(r)*total;
    for(i=0;i<patch.m;){
        chosen-=exp_values[i];
        if(chosen<0) break;
        i++;
    }
    if(set)gsl_vector_uint_set(patch.sampled_males,i,
        gsl_vector_uint_get(patch.sampled_males,i)+1);
    return(gsl_vector_uint_get(patch.male_id,i));
}

void local_female_selection_single(){
    //female choice within each patch
    unsigned int i,j=0,max,copied,copy[patch.m];
    double x;
    for(i=0;i<patch.m;i++) gsl_vector_uint_set(patch.sampled_males,i,0);
    for(i=0;i<patch.f;i++){ // Non-copiers

if(gsl_vector_char_get(adult.copy,gsl_vector_uint_get(patch.female_id,i))==0
||
            (LC==0?(gsl_vector_char_get(adult.copy,gsl_vector_uint_get
            (patch.female_id,i))==1 &&
            gsl_vector_char_get(adult.changed,gsl_vector_uint_get
            (patch.female_id,i))==0):0)){
            gsl_vector_uint_set(patch.chosen_id,i,female_choice(i,1));
        }
    }
    //find the most chosen males by non-copiers
    max=gsl_vector_uint_get(patch.sampled_males,0);
    for(i=1;i<patch.m;i++) if(max<gsl_vector_uint_get(patch.sampled_males,i))
        max=gsl_vector_uint_get(patch.sampled_males,i);
    //to account for multiple males to be the most chosen ones
    for(i=0;i<patch.m;i++)
if(gsl_vector_uint_get(patch.sampled_males,i)==max){
        copy[j]=gsl_vector_uint_get(patch.male_id,i);
        j++;
    }
    for(i=0;i<patch.f;i++){ // Copiers

if(gsl_vector_char_get(adult.copy,gsl_vector_uint_get(patch.female_id,i))==1
&&
           (LC==0?gsl_vector_char_get(adult.changed,gsl_vector_uint_get
            (patch.female_id,i))==1:1)){
           if(max!=0){ //if there are no demonstrators
               copied=gsl_rng_uniform_int(r,j);

gsl_vector_set(adult.value,gsl_vector_uint_get(patch.female_id,i),
                   gsl_vector_get(adult.trait,copy[copied]));
           }
           gsl_vector_uint_set(patch.chosen_id,i,female_choice(i,0));
        }
    }
}

void genotype_mutation_char(gsl_vector_char *dest, unsigned int o, double
mut){
    //binary mutation
    if(gsl_rng_uniform(r)<mut){
        if(gsl_vector_char_get(dest,o)==0) gsl_vector_char_set(dest,o,1);
        else if(gsl_vector_char_get(dest,o)==1) gsl_vector_char_set(dest,o,0);
```

```
        else error_statement("Mutation value error");
    }
}

void genotype_mutation(gsl_vector *dest, unsigned int o, double mut, double
sigma){
    //continuous mutation
    if(gsl_rng_uniform(r)<mut){
        gsl_vector_set(dest,o,gsl_vector_get(dest,o)+
            gsl_ran_gaussian_ziggurat(r,sigma));
        if(gsl_vector_get(dest,o)<0) gsl_vector_set(dest,o,0);
        else if(gsl_vector_get(dest,o)>1) gsl_vector_set(dest,o,1);
    }
}

void inheritance(unsigned int g, unsigned int j, unsigned int i){
    //construction of each offspring genotype
    char parent=gsl_rng_uniform(r)<0.5?0:1; //0 for mother, 1 for father
    gsl_vector_set(offspring.trait,offspring.n+i,parent==0?
        gsl_vector_get(adult.trait,gsl_vector_uint_get(patch.female_id,j)):
        gsl_vector_get(adult.trait,gsl_vector_uint_get(patch.chosen_id,j)));
    genotype_mutation(offspring.trait,offspring.n+i,MT,MTS);
    parent=gsl_rng_uniform(r)<0.5?0:1;
    gsl_vector_set(offspring.pref,offspring.n+i,parent==0?
        gsl_vector_get(adult.pref,gsl_vector_uint_get(patch.female_id,j)):
        gsl_vector_get(adult.pref,gsl_vector_uint_get(patch.chosen_id,j)));
    genotype_mutation(offspring.pref,offspring.n+i,MP,MPS);
    parent=gsl_rng_uniform(r)<0.5?0:1;
    gsl_vector_char_set(offspring.copy,offspring.n+i,parent==0?

gsl_vector_char_get(adult.copy,gsl_vector_uint_get(patch.female_id,j)):

gsl_vector_char_get(adult.copy,gsl_vector_uint_get(patch.chosen_id,j)));
    if(g>MCA) genotype_mutation_char(offspring.copy,offspring.n+i,MC);
    parent=gsl_rng_uniform(r)<0.5?0:1;
    gsl_vector_set(offspring.disp,offspring.n+i,parent==0?
        gsl_vector_get(adult.disp,gsl_vector_uint_get(patch.female_id,j)):
        gsl_vector_get(adult.disp,gsl_vector_uint_get(patch.chosen_id,j)));
    genotype_mutation(offspring.disp,offspring.n+i,MD,MDS);
}

unsigned int local_breeding_determined(unsigned int g){
    //construction of all offspring genotype in a patch
    unsigned int i,j,local_n;
    local_n=2*K;
    for(i=0;i<local_n;i++){
        j=(unsigned int)gsl_rng_uniform_int(r,patch.f);
        inheritance(g,j,i);
        gsl_vector_char_set(offspring.sex,offspring.n+i,
            (gsl_rng_uniform(r)<0.5)?1:0);
        gsl_matrix_set(offspring.coord,0,offspring.n+i,gsl_matrix_get
            (adult.coord,0,gsl_vector_uint_get(patch.female_id,j)));
        gsl_matrix_set(offspring.coord,1,offspring.n+i,
        gsl_matrix_get(adult.coord,1,gsl_vector_uint_get(patch.female_id,j)));
    }
    return(i);
}

void select_individuals_patch(int g){
    //breeding and selection per breeding patch
    if(patch.m>0 && patch.f>0){
        local_female_selection_single();
        offspring.n+=local_breeding_determined(g);
    }
}

void breeding_reproduction(int g){
```

```
    //breeding for all patches each generation
    unsigned int row,col;
    offspring.n=0;
    adult_value();
    if(g%GW==0 && LSAMP){
        char s[10];
        snprintf(s,sizeof(s),"%d\t", g);
        write_local_adult(s);
    }
    for(row=0;row<PSIZE;row++){
        for(col=0;col<PSIZE;col++){
            place_individuals_patch(row,col);
            if(g%GW==0 && LSAMP) write_local_adult_status();
                select_individuals_patch(g);
        }
    }
    if(g%GW==0 && LSAMP) write_local_adult("\r\n");
}

#endif
```

Appendix III

Supporting material for chapter 4: The Role of mate-choice copying on species range expansion

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Figure S1. Representation of the simulated world, segmented into 20 × 50 patches

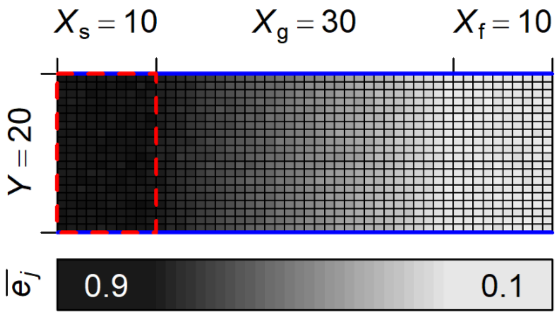

Figure S1. The environmental value e_{ij} of each patch is represented by a colour that might go from black (high values) or white (low values). The bar on the bottom represents the mean $\overline{e}_j$ value sampled for each column X. There are slight random variations of e_{ij} within each column (amplified here for representation purposes). The world wraps around itself in the y axis (the two blue lines are adjacent to each other) while the population is trying to expand from left to right in the X axis. At the beginning of each simulation the population is restricted in the X_S columns (dashed red rectangle). After a warmup phase the population expands its distribution to a new habitat through X_g until it reaches X_f, where it adapts to the new habitat.

Table S1. Number of generations taken by each type of population after warmup to breach the environmental gradient with evolving dispersal.

Preference rule*	S_S value	MCC type†	Min	Quantile 25%	Median	Quantile 75%	Max
CI	0	NC & GC	378	438.5	448	464.75	537
		IC	354	360.75	378.5	401	443
	100	NC	556	648.5	723.5	735.5	797
		IC	583	635.5	657	673.5	712
		GC	464	538.5	562	592	638
	500	NC	1055	1206.25	1230.5	1356.5	1651
		IC	940	1176.75	1229	1422.5	1849
		GC	676	770.5	786	809.75	912
	1000	NC	962	1124.5	1175.5	1285.75	1554
		IC	892	1148.25	1264.5	1370.75	1549
		GC	841	951.75	995	1034.75	1114
CD	100	NC	376	454.75	478	498.25	535
		IC	331	353.75	378	400.5	429
		GC	377	444.75	459	506.25	586
	500	NC	363	411.75	445.5	465.25	561
		IC	305	336	348	372.75	425
		GC	358	415.75	449	465	509
	1000	NC	356	379	396.5	426	495
		IC	297	325.25	349	360.25	401
		GC	331	369	393.5	439.25	524

* CI = Condition-independent; CD = Condition-dependent

* NC = No MCC; IC = Individual MCC; GC = Generalized MCC.

Table S2. Mean dispersal allele D value for each type of population at the end of the warmup phase.

Preference rule*	S_S value	MCC type†	Min	Quantile 25%	Median	Quantile 75%	Max
CI	0	NC & GC	0.0155	0.0183	0.0195	0.0208	0.0238
		IC	0.0499	0.0538	0.0594	0.0668	0.0709
	100	NC	0.0163	0.0172	0.0188	0.0197	0.0218
		IC	0.0486	0.0543	0.0568	0.0609	0.0718
		GC	0.0153	0.0182	0.0201	0.0214	0.0253
	500	NC	0.0177	0.0187	0.0196	0.0209	0.0226
		IC	0.0471	0.0532	0.0564	0.0588	0.0621
		GC	0.0168	0.0189	0.0204	0.0212	0.0258
	1000	NC	0.0182	0.0215	0.0223	0.0229	0.0254
		IC	0.0444	0.0522	0.0548	0.0585	0.0633
		GC	0.0168	0.0195	0.0206	0.0221	0.0246
CD	100	NC	0.0141	0.0173	0.0183	0.0200	0.0226
		IC	0.0532	0.0562	0.0588	0.0619	0.0679
		GC	0.0171	0.0181	0.0190	0.0200	0.0224
	500	NC	0.0164	0.0180	0.0193	0.0199	0.0223
		IC	0.0483	0.0512	0.0543	0.0581	0.0717
		GC	0.0153	0.0167	0.0182	0.0195	0.0219
	1000	NC	0.0149	0.0171	0.0179	0.0191	0.0206
		IC	0.0472	0.0506	0.0532	0.0558	0.0654
		GC	0.0154	0.0170	0.0181	0.0186	0.0196

* CI = Condition-independent; CD = Condition-dependent

* NC = No MCC; IC = Individual MCC; GC = Generalized MCC.

Table S3. Number of generations taken by each type of population after warmup to breach the environmental gradient in the simulations with fixed dispersal.

Preference rule*	S_S value	MCC type†	Min	Quantile 25%	Median	Quantile 75%	Max
CI	0	NC & GC	1719	1800.25	1854	1913.25	2002
		IC	1607	1856.75	1973	2026.75	2142
	100	NC	1915	2095.25	2159	2229.5	2415
		IC	1936	2096.5	2192	2268.25	2348
		GC	1870	2001.75	2055	2129.25	2174
	500	NC	2294	2508.75	2595.5	2706	2789
		IC	2364	2690.75	2826	2974.5	3281
		GC	1982	2131.5	2210.5	2279	2521
	1000	NC	2502	2591.75	2661.5	2779	3055
		IC	2445	2828.5	2927.5	3133.25	3634
		GC	2200	2341.5	2400.5	2514.5	2722
CD	100	NC	1699	1825	1908	1951.75	2011
		IC	1767	1823.75	1891	1997	2122
		GC	1770	1808.75	1864	1948.5	2089
	500	NC	1704	1791.5	1822.5	1931	2135
		IC	1670	1834.75	1868.5	1914.75	1992
		GC	1708	1798.5	1865	1903.5	2079
	1000	NC	1662	1748.25	1790.5	1886	1965
		IC	1683	1780.25	1810	1887.75	1964
		GC	1651	1833.25	1860	1894.25	2121

* NCD = Condition-independent; CD = Condition-dependent

* NC = No MCC; IC = Individual MCC; GC = Generalized MCC.

Table S4. Proportion of individuals with the C allele after warmup.

Preference rule*	S_S value	MCC type†	Min	Quantile 25%	Median	Quantile 75%	Max
CI	0	NC & GC	0.4423	0.4823	0.4900	0.4980	0.5355
		IC	0.3445	0.4006	0.4315	0.4673	0.5271
	100	NC	0.4292	0.4806	0.4945	0.5063	0.5628
		IC	0.3636	0.3818	0.4102	0.4435	0.4878
		GC	0.4420	0.4843	0.4987	0.5269	0.5615
	500	NC	0.4398	0.4864	0.5024	0.5202	0.5558
		IC	0.2720	0.3214	0.3569	0.3808	0.4131
		GC	0.4792	0.5060	0.5233	0.5502	0.5866
	1000	NC	0.4363	0.4754	0.5026	0.5311	0.5535
		IC	0.2702	0.3309	0.3436	0.3662	0.4013
		GC	0.4824	0.5112	0.5425	0.5702	0.6071
CD	100	NC	0.4634	0.4821	0.4922	0.5068	0.5801
		IC	0.3753	0.3868	0.4288	0.4620	0.4875
		GC	0.4199	0.4651	0.5009	0.5141	0.5460
	500	NC	0.4613	0.4871	0.5040	0.5245	0.5387
		IC	0.3946	0.4143	0.4465	0.4785	0.5100
		GC	0.4548	0.4967	0.5109	0.5473	0.5774
	1000	NC	0.4464	0.4904	0.5040	0.5301	0.5645
		IC	0.3280	0.3990	0.4251	0.4719	0.5106
		GC	0.4204	0.4903	0.5014	0.5248	0.5500

* CI = Condition-independent; CD = Condition-dependent

* NC = No MCC; IC = Individual MCC; GC = Generalized MCC.

C Computer Code

Instructions File: readme.txt

```
###
Instructions: to run the script in Cygwin using GCC, copy all the files to a
folder, open the 'input.h' as a text file to change the parameters before
compiling the executable.
Run the following three commands after setting Cygwin to the folder path where
the files are located:

gcc -c main.c -lm
gcc  main_test.c -lgsl -lgslcblas -lm -o main.exe
main.exe

The last line of the code can be ran multiple times for further replicates.

###
Output folder structure: The program will create a folder following the input
file name and number the simulations (starting from 0) accordingly.

/Local -> Folder for the variables by patch controlled by WRITELOCAL. Each
          line is a sampled generation and values are sequential row-wise,
          i.e.,m[1,1],m[1,2],...,m[1,x],m[2,1],m[2,2],...,m[y,x]. First value
          for each line is the generation.
    ../Copy_sim_s****.txt -> Copy allele mean for each patch
    ../Disp_sim_s****.txt -> Dispersal allele mean for each patch
    ../Population_n_sim_s****.txt -> Number of adults for each patch
    ../Pref_sim_s****.txt -> Pref allele mean for each patch
    ../Sex_sim_s****.txt -> Sex ratio for each patch
    ../Trait_sim_s****.txt -> Trait allele mean for each patch
/Main -> Main raw output controlled by WRITEMAIN. Each line in the files is a
         sampled generation. First value for each line is the generation
         number except for Coord_sim_s****.txt that has one line for the
         generation number (preceded by #), one line for the X coordinate, and
         one line for the Y coordinate.
    ../Copy_sim_s****.txt -> Copy allele for each individual
    ../Disp_sim_s****.txt -> Dispersal allele for each individual
    ../Coord_sim_s****.txt -> Coordinates for each individual
    ../Pref_sim_s****.txt -> Pref allele for each individual
    ../Sex_sim_s****.txt -> Sex for each individual
    ../Trait_sim_s****.txt -> Trait allele for each individual
/Column -> Column raw output controlled by WRITECOLUMN. Each line in the files
           is a sampled generation. First value for each line is the
           generation number. Files have the same name as in the Local folder
           but each value corresponds to the average value or the number of
           adults in each column.
/Log_name_s****.log -> Log file with all the variables.
/Environment_sim_s****.txt -> Environmental matrix.
/Summary_sim_s****.txt -> Summary statistics for each generation.

###
```

Main File: main.c

```
//Mate-Choice Copying Generalization invasion fronts
//Written by Manuel Sapage,
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// Headers
#include <string.h>
#include <math.h>
#include <sys/stat.h>
#include <stdarg.h>
#include <unistd.h>

//GNU scientific library (gsl)
#include <gsl/gsl_randist.h>
#include <gsl/gsl_sort.h>
#include <gsl/gsl_blas.h>

//Fixed Parameters
#define XA 10 //Width of original area
#define XG 30 //Gradient width
#define XF 10 //Final columns
#define YSIZE 20 //Height of the world
#define NOISE 0.01 // SD of the noise for the environmental matrix
#define K 64 // Patch carrying capacity
#define ROFF 4 //Mean number of offspring
#define GENOCUP 0.8 //Percentage occupied new environment to be considered
                    //adapted
#define GENMAX 10000 //Maximum number of generations for adaptation to new
                     //habitat
#define GENWARM 2500 //Generations before barrier removal
#define GENEND 1000 //Generations after population is adapted to new habitat
                    //before ending
#define CSUR 500 //Natural Selection Strength SN
#define CDISP 0.05 //Dispersal cost

//Coded file
#include "input.h" //input file name
#include "initialize.h" //create environment & population
#include "output.h" //creates and writes output
#include "dynamics.h" //simulates population dynamics

// Main //
void ending(int g){
       write_end_invasion(g);
       //ends the simulation
       if(adult.n==0)printf("\n### Extinction at generation %d ###\n",g);
       else if(other.end==-1){
              write_population(g,2);
              printf("\rGeneration %d, x = %d",g,other.xpos);
              printf("\n### Generation limit of %d achieved ###\n",g);
       }else{
              write_population(g,2);
```

```
			printf("\n### End at generation %d ###\n",g);
		}
		variables_free();
		close_all_files();
		sleep(1);
		exit(0);
}

int generation_loop(){
		//runs each generation loop
		int g,xpos=XA-1;
		printf("\r\n");
		for(g=0;g<GENMAX+GENEND;g++){
			printf("\rGeneration %d, x = %d",g,other.xpos); fflush(stdout);
			if(adult.n==0) break;
			place_individual(g);
			if(other.end==g) break;
			if(g>=GENMAX && other.end==-1) break;
			if(xpos!=other.xpos){
				write_population(g,1);
				xpos=other.xpos;
			}else if(g==0 || g==GENWARM || g==other.end-GENEND){
				write_population(g,2);
			}else{
				write_population(g,0);
			}
			world_dynamics(g);
		}
		return(g);
}

void main(){
		//main function
		int g;
		const gsl_rng_type *R;
		rand_seed(R);
		initialize();
		main_info_all();
		g=generation_loop();
		ending(g);
}
```

Input File: input.h

```
#ifndef VAR_CHOOSE_H_INCLUDED
#define VAR_CHOOSE_H_INCLUDED


//Population Type
#define COPYTYPE 2 //0=Individual based-copying, 1=Copying Generalization,
		//2=No Copying
#define PREFTYPE 0 //0=Conditional independent, 1=Conditional dependent
#define CHOOSY 0 //Lambda for choosiness and score effect
#define DINIT 0.02 //Initial dispersal value
#define ADAPT 0.01 //Initial population Trait (and Preference if TB) standard
		//deviation
```

```
//Mutation
#define MU_TRAIT 0.01
#define SD_TRAIT 0.02
#define MU_PREF 0.01
#define SD_PREF 0.02
#define MU_DISP 0.01
#define SD_DISP 0.02
#define MU_COPY 0.005

// Sampling
// When generations are sampled: Positive number constant sample,
// -1 for generation with breaches, other negative numbers for both, 0 for
// none
#define WRITEMAIN 0 //Samples data for all individuals
#define WRITELOCAL 0 //Samples mean data for each patch
#define WRITECOLUMN -1 //Samples mean data for each column
#define FN "test" //Output file name

// Randomness
#define RSEED 1 //1 for random seed 0 for fixed seed 'SEED'
#define SEED 0 //seed value

#endif
```

Supporting File: initialize.h

```
#ifndef INITIATION_H_INCLUDED
#define INITIATION_CREATE_H_INCLUDED

//### GENERAL FUNCTIONS ###

//# objects
gsl_rng *r; //stores the instance of the random number generator
unsigned long seed; //stores seed value

//# functions
void rand_seed(const gsl_rng_type *R){
       //function to set random or fixed seed
       if(RSEED){
              srand(time(NULL));
              seed=rand();
       }else seed=SEED;
       R=gsl_rng_default;
       r=gsl_rng_alloc(R);
       gsl_rng_set(r,seed);
}

void error_statement(const char* f, ...){
       //prints error and exits
       fflush(stdout);
       va_list arg;
       va_start(arg,f);
       vfprintf(stderr,f,arg);
       va_end(arg);
```

```
        exit(EXIT_FAILURE);
}

//### ENVIRONMENT & POPULATION CREATION FUNCTIONS ###

//# objects
struct population_data{
        gsl_vector *disp,*trait,*pref; //dispersal, trait and innate preference
                                        //values
        gsl_vector_char *copy; //copy gene value (0=never copies)
        gsl_vector_char *sex; //0=female, 1=male
        gsl_matrix_ushort *coord; //patch (X,Y)
        unsigned long n; //population size
}adult, offspring;

struct patch_data{
        //all patches data
        gsl_vector_ushort *f,*m;  //number of (fe)males in each patch
        gsl_matrix_uint *f_id,*m_id; //id of individuals in each patch
        gsl_vector *pref_v; //effective female preference value (after copying)
        gsl_vector *social_trt_v; //social score - tracks witch males females
copy
        gsl_vector_ushort *m_select; //track the number of times a male is
chosen
        gsl_vector_ushort *m_popular; //track the most popular males in a patch
}patch;

struct patch_offspring{
        //temporary offspring values for each patch (before survival)
        gsl_vector_uint *f_id,*m_id; //parents id
        gsl_vector *trait; //offspring trait value
        unsigned int n; //number of offspring in the patch
}patch_off;

struct other_obj{
        gsl_matrix *env_mat; //environment matrix
        int limit; //limit individuals in new habitat to trigger ending
        int end; //checks ending condition before maximum
        int xpos; //position of the invasion front
}other;

// Functions //
void env_construct(){
        //Constructs the environment vector     with gradient from 0.9 to 0.1
        int i,j;
        //Original habitat
        for(i=0;i<XA;i++) for(j=0;j<YSIZE;j++)
                gsl_matrix_set(other.env_mat,i,j,0.9+gsl_ran_gaussian(r,NOISE));
        //Gradient
        for(;i<XA+XG;i++) for(j=0;j<YSIZE;j++)
                gsl_matrix_set(other.env_mat,i,j,0.9+
                        gsl_ran_gaussian(r,NOISE)-(((double)(i-XA+1)*0.8)/(XG)));
        //New habitat
        for(;i<XA+XG+XF;i++) for(j=0;j<YSIZE;j++)
                gsl_matrix_set(other.env_mat,i,j,0.1+gsl_ran_gaussian(r,NOISE));
}

void genotype_initiate(struct population_data *p){
```

```
	//initializes genotype
	unsigned int x,y,i,k,n=0;
	double env_val,trait,pref;
	for(x=0;x<XA;x++)for(y=0;y<YSIZE;y++){
		env_val=gsl_matrix_get(other.env_mat,x,y);
		for(k=0;k<K;k++){
			gsl_matrix_ushort_set(p->coord,0,n,x);
			gsl_matrix_ushort_set(p->coord,1,n,y);
			gsl_vector_set(p->disp,n,DINIT);
			trait=env_val+gsl_ran_gaussian(r,ADAPT);
			if(trait>1) trait=1; else if (trait<0) trait=0;
			gsl_vector_set(p->trait,n,trait);
			if(PREFTYPE==1) pref=0;
			else if(PREFTYPE==0){
				pref=env_val+gsl_ran_gaussian(r,ADAPT);
				if(pref>1) pref=1; else if (pref<0) pref=0;
			}
			else error_statement("PREFTYPE value error");
			gsl_vector_set(p->pref,n,pref);
			gsl_vector_char_set(p->copy,n,0);
			gsl_vector_char_set(p->sex,n,gsl_rng_uniform(r)<0.5?1:0);
			n++;
		}
	}
}

void population_alloc(struct population_data *n, int inds){
	//allocates memory for population struct
	n->disp=gsl_vector_alloc(inds);
	n->trait=gsl_vector_alloc(inds);
	n->pref=gsl_vector_alloc(inds);
	n->copy=gsl_vector_char_alloc(inds);
	n->sex=gsl_vector_char_alloc(inds);
	n->coord=gsl_matrix_ushort_alloc(2,inds);
}

void variables_alloc(){
	//allocates memory for all objects
	adult.n=K*XA*YSIZE;
	population_alloc(&adult,(XA+XG+XF)*YSIZE*K*ROFF);
	population_alloc(&offspring,(XA+XG+XF)*YSIZE*K*ROFF);
	patch.m=gsl_vector_ushort_alloc((XA+XG+XF)*YSIZE);
	patch.f=gsl_vector_ushort_alloc((XA+XG+XF)*YSIZE);
	patch.m_select=gsl_vector_ushort_alloc((XA+XG+XF)*YSIZE);
	if(COPYTYPE==0)patch.m_popular=gsl_vector_ushort_alloc((XA+XG+XF)*YSIZE
);
	else if(COPYTYPE==1)patch.social_trt_v=gsl_vector_alloc(K*9);
	else if (COPYTYPE!=2)error_statement("COPYTYPE value error");
	patch.m_id=gsl_matrix_uint_alloc((XA+XG+XF)*YSIZE,K*9);
	patch.f_id=gsl_matrix_uint_alloc((XA+XG+XF)*YSIZE,K*9);
	patch.pref_v=gsl_vector_alloc(K*9);
	patch_off.f_id=gsl_vector_uint_alloc(ROFF*K*9);
	patch_off.m_id=gsl_vector_uint_alloc(ROFF*K*9);
	patch_off.trait=gsl_vector_alloc(ROFF*K*9);
	other.env_mat=gsl_matrix_alloc(XA+XG+XF,YSIZE);
	other.end=-1;
	other.limit=(int)(GENOCUP*XF*YSIZE*K);
	other.xpos=XA-1;
```

```
}

void initialize(){
        //initiates adult data
        variables_alloc();
        env_construct();
        genotype_initiate(&adult);
}

void population_free(struct population_data *n){
        //frees population struct
        gsl_vector_free(n->disp);
        gsl_vector_free(n->trait);
        gsl_vector_free(n->pref);
        gsl_vector_char_free(n->copy);
        gsl_vector_char_free(n->sex);
        gsl_matrix_ushort_free(n->coord);
}

void variables_free(){
        //frees all struct
        population_free(&adult);
        population_free(&offspring);
        gsl_vector_ushort_free(patch.m);
        gsl_vector_ushort_free(patch.f);
        gsl_vector_ushort_free(patch.m_select);
        if(COPYTYPE==0)gsl_vector_ushort_free(patch.m_popular);
        else if(COPYTYPE==1)gsl_vector_free(patch.social_trt_v);
        gsl_matrix_uint_free(patch.m_id);
        gsl_matrix_uint_free(patch.f_id);
        gsl_vector_free(patch.pref_v);
        gsl_vector_uint_free(patch_off.f_id);
        gsl_vector_uint_free(patch_off.m_id);
        gsl_vector_free(patch_off.trait);
        gsl_matrix_free (other.env_mat);
}

#endif
```

Supporting File: output.h

```
#ifndef OUTPUT_H_INCLUDED
#define OUTPUT_H_INCLUDED

//### CREATING FILES AND FOLDERS ###

// objects
mode_t oldumask;

struct input_output{
        //creates files for output
        char dir[200], str[10];
        FILE *sim_log,*sim_env,*sim_end,*sim_sum;
        //Main folder
        FILE *sim_disp,*sim_trait,*sim_pref,*sim_copy,*sim_sex,*sim_coord;
        //Local folder
```

```
       FILE *sim_local_disp,*sim_local_trait,*sim_local_pref,*sim_local_copy,
              *sim_local_sex,*sim_local_n;
       //Column folder
       FILE
*sim_col_disp,*sim_col_trait,*sim_col_pref,*sim_col_copy,*sim_col_sex,
              *sim_col_n;
}io;

//functions
FILE* create_file(FILE *file, char name[]){
       //creates a generic output file
       char dir[220];
       snprintf(dir,sizeof(dir),"%s%s%s%s%s",io.dir,name,"_sim",io.str,
              ".txt");
       file=fopen(dir,"w");
}

void create_extra_folder(char name[]){
       //creates extra folder if it doesn't exist
       char dir[220];
       snprintf(dir,sizeof(dir),"%s%s%s",io.dir,"/",name);
       oldumask=umask((mode_t)0);
       mkdir(dir,0777);
       umask(oldumask);
}

int c_file_exists(const char* filename){
       //checks if file exists, returns 1 if it doesn't
       struct stat buffer;
       int exist = stat(filename,&buffer);
       if(exist==0)return 1; else return 0;
}

void get_columns_header(FILE* file, int start, char summary){
       //appends the breaching columns header in the End_Generation and column
       files
       int i;
       for(i=start;i<XA+XG+XF;i++)
              fprintf(file,"%d\t",i);
       if(summary==1) fprintf(file,"adapt\tend");
       fprintf(file,"\r\n");
}

void append_file_expansion(char name[]){
       //creates file to track expansion
       char dir[220];
       snprintf(dir,sizeof(dir),"%s%s%s%s",io.dir,name,"_sim",".txt");
       if(c_file_exists(dir)){
              io.sim_end=fopen(dir,"a");
       }else{
              io.sim_end=fopen(dir,"w");
              fprintf(io.sim_end,"name\t");
              get_columns_header(io.sim_end,XA,1);
       }
       fprintf(io.sim_end,"%s_sim%s",io.dir,io.str);
}

void write_columns_header(FILE* file){
```

```
        fprintf(file,"gen\t");
        get_columns_header(file,0,0);
}

void create_all_files(){
        //creates output files
        io.sim_env=create_file(io.sim_env,"/Environment");
        io.sim_sum=create_file(io.sim_sum,"/Summary");
        fprintf(io.sim_sum,"gen\tN\tDisp\tTrait\tPref\tCopy\tSex");
        fprintf(io.sim_sum,"\tXPOS");
        fprintf(io.sim_sum,"\r\n");
        append_file_expansion("/End_Generation");
        if(WRITEMAIN!=0){
                create_extra_folder("Main");
                io.sim_disp=create_file(io.sim_disp,"/Main/Disp");
                io.sim_trait=create_file(io.sim_trait,"/Main/Trait");
                io.sim_pref=create_file(io.sim_pref,"/Main/Pref");
                io.sim_copy=create_file(io.sim_copy,"/Main/Copy");
                io.sim_sex=create_file(io.sim_sex,"/Main/Sex");
                io.sim_coord=create_file(io.sim_coord,"/Main/Coord");
        }
        if(WRITELOCAL!=0){
                create_extra_folder("Local");
                io.sim_local_disp=create_file(io.sim_local_disp,"/Local/Disp");

        io.sim_local_trait=create_file(io.sim_local_trait,"/Local/Trait");
                io.sim_local_pref=create_file(io.sim_local_pref,"/Local/Pref");
                io.sim_local_copy=create_file(io.sim_local_copy,"/Local/Copy");
                io.sim_local_sex=create_file(io.sim_local_sex,"/Local/Sex");

        io.sim_local_n=create_file(io.sim_local_n,"/Local/Population_n");
        }
        if(WRITECOLUMN!=0){
                create_extra_folder("Column");
                io.sim_col_disp=create_file(io.sim_col_disp,"/Column/Disp");
                io.sim_col_trait=create_file(io.sim_col_trait,"/Column/Trait");
                io.sim_col_pref=create_file(io.sim_col_pref,"/Column/Pref");
                io.sim_col_copy=create_file(io.sim_col_copy,"/Column/Copy");
                io.sim_col_sex=create_file(io.sim_col_sex,"/Column/Sex");
                io.sim_col_n=create_file(io.sim_col_n,"/Column/Population_n");
                write_columns_header(io.sim_col_disp);
                write_columns_header(io.sim_col_trait);
                write_columns_header(io.sim_col_pref);
                write_columns_header(io.sim_col_copy);
                write_columns_header(io.sim_col_sex);
                write_columns_header(io.sim_col_n);
        }
}

void create_folder(){
        //creates new folder if it doesn't exist or adds new number based on
        //log number
        int n=1;
        char dir[200],str[10];
        strcpy(io.dir,FN);
        oldumask=umask((mode_t)0);
        mkdir(io.dir,0777);
        umask(oldumask);
```

```
        while(n!=0){
                sprintf(str,"_s%04d",n); n++;
                snprintf(dir,sizeof(dir),"%s%s%s%s%s",FN,"/Log_",FN,str,".log");
                if(!c_file_exists(dir))n=0;
        }
        strcpy(io.str, str);
}

void create_log(){
        //creates log file
        char dir[220];
        snprintf(dir,sizeof(dir),"%s%s%s%s%s",io.dir,"/Log_",io.dir,io.str,".lo
                g");
        io.sim_log = fopen(dir, "w");
        fprintf(io.sim_log,"//Log data for simulation: %s%s",io.dir,io.str);
        fprintf(io.sim_log,"\r\n//Simulation written by Manuel Sapage");
}

//### PRINTS STATUS AND SIMULATION LOG ###

//# objects
struct tm* sim_t; //stores time

struct tm* present_time(){
        //records time
        time_t rawtime;
        struct tm* timeinfo;
        time(&rawtime);
        timeinfo=localtime(&rawtime);
        return timeinfo;
};

void print_input(FILE *out){
        //display in log and console output
        char buffer[80];
        fprintf(out,"\r\n\r\n//Fixed Parameters");
        fprintf(out,"\r\nWorld Size: XA = %d; XG = %d; XF = %d; Y = %d; Noise =
                %f",
                XA,XG,XF,YSIZE,NOISE);
        fprintf(out,"\r\nPatch K = %d\r\nMean Offspring Number =
                %f",K,(double)ROFF);
        fprintf(out,"\r\nPercentage in new habitat to be adapted =
                %f",GENOCUP);
        fprintf(out,"\r\nWarmup Generations = %d\r\nMaximum Simulated
                Generations = %d",GENWARM,GENMAX);
        fprintf(out,"\r\nGenerations after adaptation to end simulation =
                %d",GENEND);
        fprintf(out,"\r\nNatural Selection Strength SN = %f",(double)CSUR);
        fprintf(out,"\r\nDispersal cost = %f",(double)CDISP);
        fprintf(out,"\r\n\r\n//Input Parameters");
        if(COPYTYPE==0) fprintf(out,"\r\nIndividual copying ");

        else if(COPYTYPE==1) fprintf(out,"\r\nGeneralization copying ");
        else if(COPYTYPE==2) fprintf(out,"\r\nNo copying ");
        if(PREFTYPE==0) fprintf(out,"with conditional independent trait
                preference");
        else if(PREFTYPE==1) fprintf(out,"with conditional dependent trait
                preference");
```

```
        fprintf(out,"\r\nFemale Choosiness SS = %f",(double)CHOOSY);

        fprintf(out,"\r\nInitial Dispersal Value = %f",DINIT);
        if(PREFTYPE==0) fprintf(out,"\r\nInitial Trait and Preference SD =
               %f",ADAPT);
        if(PREFTYPE==1) fprintf(out,"\r\nInitial Trait SD = %f; Pref Fixed to
               0",ADAPT);
        fprintf(out,"\r\nTrait Mutation Probability = %f and amount in SD =
               %f",
               MU_TRAIT,SD_TRAIT);
        fprintf(out,"\r\nPreference Mutation Probability = %f and amount in SD
               = %f",
               MU_PREF,SD_PREF);
        fprintf(out,"\r\nDispersal Mutation Probability = %f and amount in SD =
               %f",
               MU_DISP,SD_DISP);
        fprintf(out,"\r\nCopy Mutation Probability = %f",MU_COPY);
        fprintf(out,"\r\n\r\n//Technical Parameters");
        fprintf(out,"\r\nData for all individuals ");
        if(WRITEMAIN==0) fprintf(out,"not sampled");
        else if(WRITEMAIN>0) fprintf(out,"sampled every %d generation(s)",
               WRITEMAIN);
        else if(WRITEMAIN==-1) fprintf(out,
               "sampled when population breaches to a new column", WRITEMAIN);
        else fprintf(out,
               "sampled every %d generations and when population breaches to a
               new column",
               -WRITEMAIN);
        fprintf(out,"\r\nData for all patches ");
        if(WRITELOCAL==0) fprintf(out,"not sampled");
        else if(WRITELOCAL>0) fprintf(out,"sampled every %d generation(s)",
               WRITELOCAL);
        else if(WRITELOCAL==-1) fprintf(out,"sampled when population breaches
               to a new column",
               WRITELOCAL);
        else fprintf(out,
               "sampled every %d generations and when population breaches to a
               new column",
               -WRITELOCAL);
        fprintf(out,"\r\nData for all columns ");
        if(WRITECOLUMN==0) fprintf(out,"not sampled");
        else if(WRITECOLUMN>0) fprintf(out,"sampled every %d generation(s)",
               WRITECOLUMN);
        else if(WRITECOLUMN==-1) fprintf(out,
               "sampled when population breaches to a new column",
               WRITECOLUMN);
        else fprintf(out,
               "sampled every %d generations and when population breaches to a
               new column",WRITECOLUMN);
        fprintf(out,"\r\nSimulation Name = %s",FN);
        fprintf(out,"\r\n%s seed = %u",RSEED==0?"Fixed":"Random",seed);
        fprintf(out,"\r\n\r\n//Simulation %s%s started on ",FN,io.str);
        strftime(buffer,80,"%d %b %Y, %H:%M:%S",sim_t);
        fprintf(out,"%s",buffer);
        fprintf(out,"\r\n//Ending condition: %d individuals in the end
               environment"
               ,other.limit);
        fprintf(out,"\r\n//Random generator type = %s",gsl_rng_name(r));
```

```
        fprintf(out,"\r\n");
}

//### WRITING OUTPUTS ###

//# functions
void write_vector(FILE *file, gsl_vector *gen, unsigned int n, int g){
        //writes disp, trait, and pref matrices
        unsigned int i;
        double val;
        if(g>=0)fprintf(file,"#\t%d\r\n",g);
        for(i=0;i<n;i++){
                val=gsl_vector_get(gen,i);
                if(fabs(round(val)-val)<0.0001) fprintf(file,"%0.1f\t",val);
                else fprintf(file,"%0.4f\t",val);
                if(i%500==0) fflush(file);
        }
        fprintf(file,"\r\n");
}

void write_vector_char(FILE *file, gsl_vector_char *gen, unsigned int n, int
        g){
        //writes sex and copy vectors
        unsigned int i;
        fprintf(file,"#\t%d\r\n",g);
        for(i=0;i<n;i++){
                fprintf(file,"%c\t",gsl_vector_char_get(gen,i)+48); //ascii48 =
                        0; ascii49=1
                if(i%500==0) fflush(file);
        }
        fprintf(file,"\r\n");
}

void write_matrix(FILE *file, gsl_matrix *gen, unsigned int x, unsigned int
y,      int g){
        //writes env matrix
        unsigned int i,j;
        double val;
        if(g>=0)fprintf(file,"#\t%d\r\n",g);
        for(j=0;j<y;j++){
                for(i=0;i<x;i++){
                        val=gsl_matrix_get(gen,i,j);
                        if(fabs(round(val)-val)<0.0001)
        fprintf(file,"%0.1f\t",val);
                        else fprintf(file,"%0.4f\t",val);
                        if(j%500==0) fflush(file);
                }
                fprintf(file,"\r\n");
        }
}

void write_matrix_ushort(FILE *file, gsl_matrix_ushort *coord, unsigned int
n, int g){
        //writes a uint matrix with X and Y coord
        unsigned int i,j;
        fprintf(file,"#\t%d\r\n",g);
        for(i=0;i<2;i++){
                for(j=0;j<n;j++){
```

```
                        fprintf(file,"%hu\t",gsl_matrix_ushort_get(coord,i,j));
                        if(j%500==0) fflush(file);
                }
                fprintf(file,"\r\n");
        }
}

void write_adult_status(int g){
        //recorded after dispersal in adults
        write_vector(io.sim_disp,adult.disp,adult.n,g);
        write_vector(io.sim_trait,adult.trait,adult.n,g);
        write_vector(io.sim_pref,adult.pref,adult.n,g);
        write_vector_char(io.sim_copy,adult.copy,adult.n,g);
        write_vector_char(io.sim_sex,adult.sex,adult.n,g);
        write_matrix_ushort(io.sim_coord,adult.coord,adult.n,g);
}

void write_local_adult_status(int g){
        //records local data to output files
        unsigned int l,id;
        unsigned short m,f,i;
        double mean_disp, mean_trait, mean_pref, mean_copy;
        fprintf(io.sim_local_n,"#\t%d\r\n",g);
        fprintf(io.sim_local_sex,"#\t%d\r\n",g);
        fprintf(io.sim_local_disp,"#\t%d\r\n",g);
        fprintf(io.sim_local_trait,"#\t%d\r\n",g);
        fprintf(io.sim_local_pref,"#\t%d\r\n",g);
        fprintf(io.sim_local_copy,"#\t%d\r\n",g);
        for(l=0;l<(XA+XG+XF)*YSIZE;l++){
                mean_disp=0, mean_trait=0, mean_pref=0, mean_copy=0;
                m=gsl_vector_ushort_get(patch.m,l);
                f=gsl_vector_ushort_get(patch.f,l);
                fprintf(io.sim_local_n,"%d\t",m+f);
                fprintf(io.sim_local_sex,"%f\t",m+f==0?-
                        1:(double)m/(double)(m+f));
                for(i=0;i<m;i++){
                        id=gsl_matrix_uint_get(patch.m_id,l,i);
                        mean_disp+=gsl_vector_get(adult.disp,id);
                        mean_trait+=gsl_vector_get(adult.trait,id);
                        mean_pref+=gsl_vector_get(adult.pref,id);
                        mean_copy+=gsl_vector_char_get(adult.copy,id);

                }
                for(i=0;i<f;i++){
                        id=gsl_matrix_uint_get(patch.f_id,l,i);
                        mean_disp+=gsl_vector_get(adult.disp,id);
                        mean_trait+=gsl_vector_get(adult.trait,id);
                        mean_pref+=gsl_vector_get(adult.pref,id);
                        mean_copy+=gsl_vector_char_get(adult.copy,id);
                }
                fprintf(io.sim_local_disp,"%0.4f\t",m+f==0?-1:mean_disp/(m+f));
                fprintf(io.sim_local_trait,"%0.4f\t",m+f==0?-
                        1:mean_trait/(m+f));
                fprintf(io.sim_local_pref,"%0.4f\t",m+f==0?-1:mean_pref/(m+f));
                fprintf(io.sim_local_copy,"%0.4f\t",m+f==0?-1:mean_copy/(m+f));
        }
        fprintf(io.sim_local_n,"\r\n");
        fprintf(io.sim_local_sex,"\r\n");
```

```
	fprintf(io.sim_local_disp,"\r\n");
	fprintf(io.sim_local_trait,"\r\n");
	fprintf(io.sim_local_pref,"\r\n");
	fprintf(io.sim_local_copy,"\r\n");
}

void write_column_adult_status(int g){
	//records local data to output files
	unsigned int x,i,n;
	double sex,mean_disp,mean_trait,mean_pref,mean_copy;
	fprintf(io.sim_col_n,"%d",g);
	fprintf(io.sim_col_sex,"%d",g);
	fprintf(io.sim_col_disp,"%d",g);
	fprintf(io.sim_col_trait,"%d",g);
	fprintf(io.sim_col_pref,"%d",g);
	fprintf(io.sim_col_copy,"%d",g);
	for(x=0;x<XA+XG+XF;x++){
		mean_disp=0,mean_trait=0,mean_pref=0,mean_copy=0,sex=0,n=0;
		for(i=0;i<adult.n;i++){
			if(gsl_matrix_ushort_get(adult.coord,0,i)==x){
				n++;
				if(gsl_vector_char_get(adult.sex,i)==1) sex++;
				mean_disp+=gsl_vector_get(adult.disp,i);
				mean_trait+=gsl_vector_get(adult.trait,i);
				mean_pref+=gsl_vector_get(adult.pref,i);
				mean_copy+=gsl_vector_char_get(adult.copy,i);
			}
		}
		fprintf(io.sim_col_n,"\t%u",n);
		if(n>0){
			fprintf(io.sim_col_sex,"\t%f",sex/n);
			fprintf(io.sim_col_disp,"\t%f",mean_disp/n);
			fprintf(io.sim_col_trait,"\t%f",mean_trait/n);
			fprintf(io.sim_col_pref,"\t%f",mean_pref/n);
			fprintf(io.sim_col_copy,"\t%f",mean_copy/n);
		}else{
			fprintf(io.sim_col_sex,"\t-1");
			fprintf(io.sim_col_disp,"\t-1");
			fprintf(io.sim_col_trait,"\t-1");
			fprintf(io.sim_col_pref,"\t-1");
			fprintf(io.sim_col_copy,"\t-1");
		}
	}
	fprintf(io.sim_col_n,"\r\n");
	fprintf(io.sim_col_sex,"\r\n");
	fprintf(io.sim_col_disp,"\r\n");
	fprintf(io.sim_col_trait,"\r\n");
	fprintf(io.sim_col_pref,"\r\n");
	fprintf(io.sim_col_copy,"\r\n");
}

void write_summary(int g){
	//records all population files
	unsigned int i;
	double mean_disp=0,mean_trait=0,mean_pref=0,mean_copy=0,mean_sex=0;
	fprintf(io.sim_sum,"%d\t%lu",g,adult.n);
	for(i=0;i<adult.n;i++){
		mean_disp+=gsl_vector_get(adult.disp,i);
```

```
                mean_trait+=gsl_vector_get(adult.trait,i);
                mean_pref+=gsl_vector_get(adult.pref,i);
                mean_copy+=gsl_vector_char_get(adult.copy,i);
                mean_sex+=gsl_vector_char_get(adult.sex,i);
        }
        if(adult.n!=0) fprintf(io.sim_sum,"\t%f\t%f\t%f\t%f\t%f",
                mean_disp/adult.n,mean_trait/adult.n,mean_pref/adult.n,
                mean_copy/adult.n,mean_sex/adult.n);
        else fprintf(io.sim_sum,"\t-1\t-1\t-1\t-1\t-1");
        fprintf(io.sim_sum,"\t%d",other.xpos);
        fprintf(io.sim_sum,"\r\n");
}

void write_population(int g,char x){
        //records all population files
        //x is 1 if invading column, 0  if not, 2 if forced writing
        int wl=WRITELOCAL, wm=WRITEMAIN, wc=WRITECOLUMN;
        if(x==2){
                if(wl!=0)write_local_adult_status(g);
                if(wm!=0)write_adult_status(g);
                if(wc!=0)write_column_adult_status(g);
        }else if(x==1){
                if(wl<0)write_local_adult_status(g);
                if(wm<0)write_adult_status(g);
                if(wc<0)write_column_adult_status(g);
        }else{
                if(wl!=0) if(g%wl==0 && wl!=-1)write_local_adult_status(g);
                if(wm!=0) if(g%wm==0 && wm!=-1)write_adult_status(g);
                if(wc!=0) if(g%wc==0 && wc!=-1)write_column_adult_status(g);
        }
        write_summary(g);
}

void write_invasion(int g){
        //writes generation for x breach
        fprintf(io.sim_end,"\t%d",g);
}

void write_end_invasion(int g){
        //writes generation end break
        int x=other.xpos;
        while(x<XA+XG+XF-1){
                write_invasion(-1);
                x++;
        }
        if(other.end==-1){
                write_invasion(-1);
        }else{
                write_invasion(g-GENEND);
        }
        write_invasion(g);
        fprintf(io.sim_end,"\r\n");
}

void close_all_files(){
        fclose(io.sim_env);fclose(io.sim_sum);fclose(io.sim_end);
        if(WRITEMAIN!=0){
                fclose(io.sim_disp);fclose(io.sim_trait);fclose(io.sim_pref);
```

```
                fclose(io.sim_copy);fclose(io.sim_sex);fclose(io.sim_coord);

        }
        if(WRITELOCAL!=0){
                fclose(io.sim_local_disp);fclose(io.sim_local_trait);
                fclose(io.sim_local_pref);fclose(io.sim_local_copy);
                fclose(io.sim_local_sex);
        }
        if(WRITECOLUMN!=0){
                fclose(io.sim_col_disp);fclose(io.sim_col_trait);
                fclose(io.sim_col_pref);fclose(io.sim_col_copy);
                fclose(io.sim_col_sex);
        }
}

void main_info_all(){
        //creates files and writes log and environment files
        create_folder();
        printf("\r\nMCC simulation written by Manuel Sapage");
        sim_t=present_time();
        create_log();
        print_input(stdout);
        print_input(io.sim_log);
        fclose(io.sim_log);
        create_all_files();
        write_matrix(io.sim_env,other.env_mat,XA+XG+XF,YSIZE,-1);
}

#endif
```

Supporting File: dynamics.h

```
#ifndef DYNAMICS_H_INCLUDED
#define DYNAMICS_H_INCLUDED

void place_individual(int g){
        //checks the individuals coordinates and places them in the right
        patch
        gsl_vector_ushort_set_zero(patch.m);
        gsl_vector_ushort_set_zero(patch.f);
        unsigned int i,l,count_end=0;
        for(i=0;i<adult.n;i++){
                l=gsl_matrix_ushort_get(adult.coord,0,i)+
                        gsl_matrix_ushort_get(adult.coord,1,i)*(XA+XG+XF);
                if(gsl_matrix_ushort_get(adult.coord,0,i)>=XA+XG) count_end++;
                if(gsl_vector_char_get(adult.sex,i)==1){ //male

        gsl_matrix_uint_set(patch.m_id,l,gsl_vector_ushort_get(patch.m,l),i);

        gsl_vector_ushort_set(patch.m,l,gsl_vector_ushort_get(patch.m,l)+1);
                }else{ //female

        gsl_matrix_uint_set(patch.f_id,l,gsl_vector_ushort_get(patch.f,l),i);

        gsl_vector_ushort_set(patch.f,l,gsl_vector_ushort_get(patch.f,l)+1);
                }
```

```
       }
       printf(", n in new environment= %d",count_end);
       if(count_end>=other.limit && other.end==-1) other.end=g+GENEND;
}

void set_values(unsigned int l){
       //sets social information to 0 and retrieves female innate preference
       unsigned int i,id,copiers=0;
       unsigned short x,y;
       double value=0;
       x=l%(XA+XG+XF); //conversion from l to x
       y=floor(l/(XA+XG+XF)); //conversion from l to y
       for(i=0;i<gsl_vector_ushort_get(patch.m,l);i++){
              id=gsl_matrix_uint_get(patch.m_id,l,i);
              if(COPYTYPE==1)gsl_vector_set(patch.social_trt_v,i,0);
              gsl_vector_ushort_set(patch.m_select,i,0);
              value+=exp(-CSUR*pow(gsl_vector_get(adult.trait,id)-
                     gsl_matrix_get(other.env_mat,x,y),2));
       }
       for(i=0;i<gsl_vector_ushort_get(patch.f,l);i++){
              id=gsl_matrix_uint_get(patch.f_id,l,i);
              gsl_vector_set(patch.pref_v,i,gsl_vector_get(adult.pref,id));
       }
       patch_off.n=0;
}

unsigned int breeding_number(unsigned int f_id,unsigned int m_id){
       //computes the number of offspring for each mated female
       gsl_ran_poisson(r,ROFF);
}

void inheritance(unsigned int f_id,unsigned int m_id, unsigned int j,
gsl_vector *local,
       gsl_vector *adult){
       //selects offspring genotype for continuous traits
       gsl_vector_set(local,j,gsl_vector_get(adult,gsl_rng_uniform(r)<0.5?f_i
d:m_id));
}

void mutation(unsigned int i, double mut, double sd, gsl_vector *local){
       //computes mutation values for continuous traits
       if(gsl_rng_uniform(r)<mut){

       gsl_vector_set(local,i,gsl_vector_get(local,i)+gsl_ran_gaussian(r,sd))
;
              if(gsl_vector_get(local,i)>1)gsl_vector_set(local,i,1);
              else if(gsl_vector_get(local,i)<0)gsl_vector_set(local,i,0);
       }
}

void inheritance_char(unsigned int f_id,unsigned int m_id, unsigned int j,
       gsl_vector_char *local, gsl_vector_char *adult){
       //selects offspring genotype for binary traits
       gsl_vector_char_set(local,j,
              gsl_vector_char_get(adult,gsl_rng_uniform(r)<0.5?f_id:m_id));
}

void mutation_char(unsigned int i, double mut, gsl_vector_char *local){
```

```
    //computes mutation values for binary traits
    if(gsl_rng_uniform(r)<mut){

    gsl_vector_char_set(local,i,gsl_vector_char_get(local,i)==0?1:0);
    }
}

void breeding(unsigned int f_id,unsigned int m_id,unsigned int l){
    //simulates breeding in patch l
    unsigned int i,n=breeding_number(f_id,m_id);
    for(i=patch_off.n;i<patch_off.n+n;i++){
        //this i is sometimes j as index depending if it is a vector or
        //matrix only
        //sets trait, other values will be set inherited after survival
        //for efficiency
        inheritance(f_id,m_id,i,patch_off.trait,adult.trait);
        mutation(i,MU_TRAIT,SD_TRAIT,patch_off.trait);
        gsl_vector_uint_set(patch_off.f_id,i,f_id);
        gsl_vector_uint_set(patch_off.m_id,i,m_id);
    }
    patch_off.n+=n;
}

void survived_inheritance(unsigned int i,unsigned short x, unsigned short
y){
    //inherits traits after offspring surviving
    if(offspring.n+1>=(XA+XG+XF)*YSIZE*K*ROFF)
        error_statement("Population larger allocated memory");
    unsigned int f_id=gsl_vector_uint_get(patch_off.f_id,i);
    unsigned int m_id=gsl_vector_uint_get(patch_off.m_id,i);
    gsl_vector_set(offspring.trait,offspring.n,gsl_vector_get(patch_off.tr
ait,i));
    gsl_vector_char_set(offspring.sex,offspring.n,gsl_rng_uniform(r)<0.5?1
:0);
    inheritance(f_id,m_id,offspring.n,offspring.pref,adult.pref);
    mutation(offspring.n,MU_PREF,SD_PREF,offspring.pref);
    inheritance(f_id,m_id,offspring.n,offspring.disp,adult.disp);
    mutation(offspring.n,MU_DISP,SD_DISP,offspring.disp);
    inheritance_char(f_id,m_id,offspring.n,offspring.copy,adult.copy);
    mutation_char(offspring.n,MU_COPY,offspring.copy);
    gsl_matrix_ushort_set(offspring.coord,0,offspring.n,x);
    gsl_matrix_ushort_set(offspring.coord,1,offspring.n,y);
    offspring.n++;
}

void patch_survival(unsigned int l,int g){
    //simulates offspring survival
    unsigned int i,k;
    size_t a[patch_off.n];
    unsigned short x,y,shuffle[patch_off.n];
    double v[patch_off.n],ktemp=0;
    x=l%(XA+XG+XF); //conversion from l to x
    y=floor(l/(XA+XG+XF)); //conversion from l to y
    for(i=0;i<patch_off.n;i++)shuffle[i]=i;
    gsl_ran_shuffle(r,shuffle,patch_off.n,sizeof(unsigned short));
    for(i=0;i<patch_off.n;i++){
        v[i]=gsl_vector_get(patch_off.trait,shuffle[i]);
```

```
                v[i]=exp(-CSUR*pow(v[i]-gsl_matrix_get(other.env_mat,x,y),2));

                ktemp+=v[i];
        }
        k=floor(ktemp);
        if(k>K) k=K;
        gsl_sort_index(a,v,1,patch_off.n);
        for(i=0;i<(patch_off.n>k?k:patch_off.n);i++){
                survived_inheritance(shuffle[a[patch_off.n-i-1]],x,y);
        }
}

unsigned short int female_decision_trait_pref(double f_pref, unsigned int l,
        unsigned short int m){
        //female choice following her preference and patch l for conditional
        //independent traits
        unsigned int i;
        unsigned short x,y;
        long double difference, exp_values[m], chosen, total, max=0;
        total=0;
        for(i=0;i<m;i++){

        difference=gsl_vector_get(adult.trait,gsl_matrix_uint_get(patch.m_id,
                l,i))-f_pref;
                exp_values[i]=exp(-CHOOSY*pow(difference,2));
                if(max<exp_values[i])max=exp_values[i];
                total+=exp_values[i];
        }
        if(max<10E-300) return(m);
        chosen=gsl_rng_uniform(r)*total;
        for(i=0;i<m;){
                chosen-=exp_values[i];
                if(chosen<0) break;
                i++;
        }
        return(i);
}

unsigned short int female_decision_perfomance_pref(double f_pref, unsigned
        int l, unsigned short int m){
        //female choice following her preference and patch l for conditional
        //traits
        unsigned int i;
        unsigned short x,y;
        long double difference, exp_values[m], chosen, total,max=0;
        total=0;
        x=l%(XA+XG+XF); //conversion from l to x
        y=floor(l/(XA+XG+XF)); //conversion from l to y
        for(i=0;i<m;i++){
                difference=fabs(gsl_vector_get(adult.trait,
                        gsl_matrix_uint_get(patch. m_id,l,i))-
                        gsl_matrix_get(other.env_mat,x,y))-f_pref;
                exp_values[i]=exp(-CHOOSY*pow(difference,2));
                if(max<exp_values[i])max=exp_values[i];
                total+=exp_values[i];
        }
        if(max<10E-300) return(m);
        chosen=gsl_rng_uniform(r)*total;
```

```
        for(i=0;i<m;){
                chosen-=exp_values[i];
                if(chosen<0) break;
                i++;
        }
        return(i);
}

void set_social_trait_scores(unsigned short int f, unsigned int l){
        //add male scores for female copying TB
        unsigned short int i,j,n=0,time_selected,
                m=gsl_vector_ushort_get(patch.m,l);
        char new_value;
        double add,trait_v,m_trait,pref,temp,value[m],max=0;
        //update values
        for(i=0;i<m;i++){
                time_selected=gsl_vector_ushort_get(patch.m_select,i);
                if(time_selected>0){
                        m_trait=gsl_vector_get(adult.trait,
                                gsl_matrix_uint_get(patch.m_id,l,i));
                        for(j=0;j<m;j++){
                                trait_v=gsl_vector_get(adult.trait,
                                        gsl_matrix_uint_get(patch.m_id,l,j));
                                add=exp(-CHOOSY*pow(m_trait-trait_v,2));
                                gsl_vector_set(patch.social_trt_v,j,
                                        gsl_vector_get(patch.social_trt_v,j)+
                                        add*time_selected);
                        }
                        gsl_vector_ushort_set(patch.m_select,i,0);
                }
        }
        //find maximum value
        for(i=0;i<m;i++){
                if(max<gsl_vector_get(patch.social_trt_v,i))
                max=gsl_vector_get(patch.social_trt_v,i);
        }
        //find individuals with maximum value
        if(max!=0){
                for(i=0;i<m;i++){
                        if(max-gsl_vector_get(patch.social_trt_v,i)<1E-16){
                                temp=gsl_vector_get(adult.trait,
                                        gsl_matrix_uint_get(patch.m_id,l,i));
                                if(n==0){
                                        value[n]=temp;
                                        n++;
                                }else{
                                        new_value=0;
                                        for(j=0;j<n;j++) if(value[j]-temp<1E16)
                                                new_value=1;
                                        if(new_value==0){
                                                value[n]=temp;
                                                n++;
                                        }
                                }
                        }
                }
                for(i=0;i<f;i++){
                        if(gsl_vector_char_get(adult.copy,
```

```
                                gsl_matrix_uint_get(patch.f_id,l,i))==1){
                                        gsl_vector_set(patch.pref_v,i,
                                        value[gsl_rng_uniform_int(r,n)]);
                        }
                }
        }
}

void set_social_perfomance_scores(unsigned short int f, unsigned int l){
        //add male scores for female copying preference for conditional
        //traits
        unsigned short int i,j,n=0,time_selected,
                m=gsl_vector_ushort_get(patch.m,l);
        char new_value;
        double add,trait_v, m_trait,pref,temp,value[m],max=0;
        unsigned short x,y;
        x=l%(XA+XG+XF); //conversion from l to x
        y=floor(l/(XA+XG+XF)); //conversion from l to y
        //update values
        for(i=0;i<m;i++){
                time_selected=gsl_vector_ushort_get(patch.m_select,i);
                if(time_selected>0){
                        m_trait=fabs(gsl_vector_get(adult.trait,
                                gsl_matrix_uint_get(patch.m_id,l,i))-
                                gsl_matrix_get(other.env_mat,x,y));
                        for(j=0;j<m;j++){
                                trait_v=fabs(gsl_vector_get(adult.trait,
                                        gsl_matrix_uint_get(patch.m_id,l,j))-
                                        gsl_matrix_get(other.env_mat,x,y));
                                add=(exp(-CHOOSY*pow(m_trait-trait_v,2)));
                                gsl_vector_set(patch.social_trt_v,j,

                                        gsl_vector_get(patch.social_trt_v,j)+
                                        add*time_selected);
                        }
                        gsl_vector_ushort_set(patch.m_select,i,0);
                }
        }
        //find maximum value
        for(i=0;i<m;i++){
                if(max<gsl_vector_get(patch.social_trt_v,i))
                        max=gsl_vector_get(patch.social_trt_v,i);
        }
        //find individuals with maximum value
        if(max!=0){
                for(i=0;i<m;i++){
                        if(max-gsl_vector_get(patch.social_trt_v,i)<1E-16){
                                temp=fabs(gsl_vector_get(adult.trait,
                                        gsl_matrix_uint_get(patch.m_id,l,i))-
                                        gsl_matrix_get(other.env_mat,x,y));
                                if(n==0){
                                        value[n]=temp;
                                        n++;
                                }else{
                                        new_value=0;
                                        for(j=0;j<n;j++) if(value[j]-temp<1E16)
                                                new_value=1;
                                        if(new_value==0){
```

```
                        value[n]=temp;
                        n++;
                    }
                }
            }
        }
        for(i=0;i<f;i++){
            if(gsl_vector_char_get(adult.copy,
                gsl_matrix_uint_get(patch.f_id,l,i))==1){
                    gsl_vector_set(patch.pref_v,i,
                    value[gsl_rng_uniform_int(r,n)]);
            }
        }
    }
}

unsigned short int find_popular_males(unsigned short int f, unsigned int l){
    unsigned short int i,copied_m,max=0,n=0,
        m=gsl_vector_ushort_get(patch.m,l),value[m];
    //returns number of most popular males (draws), 0 if no male is
    //selected
    //find maximum value
    for(i=0;i<m;i++){
        if(max<gsl_vector_ushort_get(patch.m_select,i))
            max=gsl_vector_ushort_get(patch.m_select,i);
    }
    //find individuals with maximum value
    if(max==0) return(0); //if no individuals were selected
    else{
        for(i=0;i<m;i++){
            if(max-gsl_vector_ushort_get(patch.m_select,i)==0){
                gsl_vector_ushort_set(patch.m_popular,n,i);
                n++;
            }
        }
    }
    return(n);
}

void patch_dynamics(unsigned int l,int g){
    //simulates dynamics in each patch
    unsigned short int i,m,n=0,nc=0,f=gsl_vector_ushort_get(patch.f,l);
    unsigned int f_id;
    double trait_v;
    set_values(l);
    for(i=0;i<f;i++){ //non-copiers choose first
        f_id=gsl_matrix_uint_get(patch.f_id,l,i);
        if(gsl_vector_char_get(adult.copy,f_id)==0){
            if(PREFTYPE==0) m=female_decision_trait_pref(
                gsl_vector_get(patch.pref_v,i),l,
                gsl_vector_ushort_get(patch.m,l));
            else if(PREFTYPE==1) m=female_decision_perfomance_pref(
                gsl_vector_get(patch.pref_v,i),l,
                gsl_vector_ushort_get(patch.m,l));
            if(m<gsl_vector_ushort_get(patch.m,l)){
                gsl_vector_ushort_set(patch.m_select,m,
                    gsl_vector_ushort_get(patch.m_select,m)+1);
                nc++;
```

```
                                breeding(f_id,gsl_matrix_uint_get(patch.m_id,
                                        l,m),l);
                        }
                }
        }
        if(COPYTYPE==1){
                if(PREFTYPE==0) set_social_trait_scores(f,l);
                else if(PREFTYPE==1) set_social_perfomance_scores(f,l);
                else error_statement("PREFTYPE value error");
        }
        else if(COPYTYPE==0)n=find_popular_males(f,l);
        for(i=0;i<f;i++){ //copiers
                f_id=gsl_matrix_uint_get(patch.f_id,l,i);
                if(gsl_vector_char_get(adult.copy,f_id)==1){
                        if(COPYTYPE==2 || COPYTYPE==1 ||nc==0){
                                if(PREFTYPE==0)m=female_decision_trait_pref(
                                        gsl_vector_get(patch.pref_v,i),l,
                                        gsl_vector_ushort_get(patch.m,l));
                                else if(PREFTYPE==1)
                                        m=female_decision_perfomance_pref(
                                                gsl_vector_get(patch.pref_v,i),l,
                                                gsl_vector_ushort_get(patch.m,l));
                        }else if(COPYTYPE==0){ //Individual based-copying
                                m=gsl_vector_ushort_get(patch.m_popular,
                                        gsl_rng_uniform_int(r,n));
                        }
                        if(m<gsl_vector_ushort_get(patch.m,l))
                                breeding(f_id,gsl_matrix_uint_get(patch.m_id,
                                l,m),l);
                }
        }
        if(patch_off.n>0)patch_survival(l,g);
}

void grow_up(){
        //switches offspring and adult structs
        gsl_vector_swap(offspring.disp,adult.disp);
        gsl_vector_swap(offspring.trait,adult.trait);
        gsl_vector_swap(offspring.pref,adult.pref);
        gsl_vector_char_swap(offspring.copy,adult.copy);
        gsl_vector_char_swap(offspring.sex,adult.sex);
        gsl_matrix_ushort_swap(offspring.coord,adult.coord);
        adult.n=offspring.n;
}

void kill_individual(int i){
        //kills individual i (for dispersal mortality)
        int a;
        adult.n--;
        gsl_vector_char_set(adult.sex,i,gsl_vector_char_get(adult.sex,adult.n
                ));
        gsl_vector_set(adult.disp,i,gsl_vector_get(adult.disp,adult.n));
        gsl_vector_set(adult.trait,i,gsl_vector_get(adult.trait,adult.n));
        gsl_vector_set(adult.pref,i,gsl_vector_get(adult.pref,adult.n));
        gsl_vector_char_set(adult.copy,i,gsl_vector_char_get(adult.copy,
                adult.n));
        for(a=0;a<2;a++) gsl_matrix_ushort_set(adult.coord,a,i,
                gsl_matrix_ushort_get(adult.coord,a,adult.n));
```

```
}

unsigned short change_coord_y(unsigned short y, char pos){
        //pos 0 = move down, pos 1 = move up
        if(pos==0) y=(y==0)?YSIZE-1:y-1;
        else y=(y==YSIZE-1)?0:y+1;
        return y;
}

void change_coord(unsigned int i, unsigned short x, unsigned short y,int g){
        char left=0,right=0,neighbours=8;
        if(x==0){
                right=1;
                neighbours-=3;
        }
        if((g<GENWARM && x==XA-1)||(g>=GENWARM && x==XA+XG+XF-1)){
                left=1;
                neighbours-=3;
        }
        char rand=(char)gsl_rng_uniform_int(r,neighbours);
        //adjust dispersal location
        if(neighbours==2){
                y=change_coord_y(y,rand==0?0:1);
        }else if(right==1){
                if(rand!=2) y=change_coord_y(y,rand<2?0:1);
                if(rand>0 && rand<4) x++;
        }else if(left==1){
                if(rand!=2) y=change_coord_y(y,rand<2?0:1);
                if(rand>0 && rand<4) x--;
        }else{
                if(rand!=3 && rand!=7) y=change_coord_y(y,rand<3?0:1);
                if(rand!=1 && rand!=5) (rand>1 && rand<5)? x++:x--;
        }
        gsl_matrix_ushort_set(adult.coord,0,i,x);
        gsl_matrix_ushort_set(adult.coord,1,i,y);
        while(other.xpos<x){
                write_invasion(g+1);
                other.xpos++;
        }
}

void set_location(int i, int g){
        unsigned short x,y;
        x=gsl_matrix_ushort_get(adult.coord,0,i);
        y=gsl_matrix_ushort_get(adult.coord,1,i);
        change_coord(i,x,y,g);
}

int disperse_each(int i, int g){
        double x=gsl_rng_uniform(r);
        if(x<CDISP){ //not survived
                kill_individual(i);
                return 1;
        }else{ //survived
                set_location(i,g);
                return 0;
        }
}
```

```
void disperse_all(int g){
        int i;
        for(i=0;i<adult.n;i++){
                if(gsl_rng_uniform(r)<gsl_vector_get(adult.disp,i)){
                        i-=disperse_each(i,g);
                }
        }
}

void world_dynamics(int g){
        unsigned int l;
        offspring.n=0;
        for(l=0;l<(XA+XG+XF)*YSIZE;l++){

        if(gsl_vector_ushort_get(patch.m,l)!=0&&gsl_vector_ushort_get(patch.f,
l)!=0){
                        patch_dynamics(l,g);
                }
        }
        grow_up();
        disperse_all(g);
}

#endif
```