# Within-season variations in the social environment : from intra-specific sexual selection to pre-mating isolation

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"I don't know the question, but sex is definitely the answer."

Woody Allen

# Abstract

Spatial and temporal variations in the social environment are predicted to modulate the pattern of inter-sexual interactions within populations through changes in the operational sex ratio and phenotypic composition. Research exploring how the social environment plays a key role in shaping variation in sexual selection usually compares spatially isolated populations or the same populations between breeding seasons. However, small changes in demographics can happen during a breeding season and may also alter selection. Moreover, studies mostly focus on single-species populations with similar life histories, limiting the generalisation of the role of environmental complexity on sexual selection. Driven by this context, this thesis aims to further our understanding of three broad questions (1) How do changes in social context throughout a breeding season influence sexual selection? (2) How do different levels of reproductive synchrony within and between sexes affect sexual selection? and (3) Can the intra-specific process of sexual selection lead to interspecific sexual isolation in sympatric species with synchronized breeding events? To achieve this, I used lampreys as a biological model, as they constitute a highly polygynandrous system in which the duration of individual mating activity is short relative to the length of the breeding season. By developing a model that decomposes the effect of individual traits on the two processes leading to mating success (i.e. number of mating attempts, probability of successful mating), I first showed that the advantage conferred by body size depends on the competitive environment faced by individuals during a breeding season, and their timing of activity (1). Through an experiment study and an Agent-Based-Model, we then highlighted that the level of synchrony within and between sexes modifies the strength and direction of sexual selection, inducing a potential adaptative response in individuals' reproductive timing (2). Finally, I show that considering the complexity of the social environment, e.g. by incorporating the effect of conspecifics with distinct life histories, may explain the emergence of alternative mating strategies through sexual selection such as sneaking in lampreys and shed light on the potential mechanism behind sympatric speciation (3). Overall, this thesis illustrates the role that variation in competitive structure may play on how sexual selection operates both within and between populations and advocates that the complexity and dynamics of the social environment should be more often considered when studying mating system dynamics.

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Chapter 1

# General introduction

## 1.1 Sexual selection theory

### 1.1.1 How to define sexual selection

The theory of sexual selection was first formulated by Darwin (1871, 1859) while attempting to understand a remarkable class of male traits, including bright colours, songs, displays, horns, and other weapons, that defied explanation by conventional natural selection to enhance survival or fecundity. Darwin (1871) suggested that these traits, which are sometimes maladaptive to survival, are instead favoured by competition over mates. Darwin's definition of sexual selection, although not directly stated in *the Descent of man*, is broadly similar to the one later used by Andersson (1994): *"Sexual selection arises from differences in reproductive success caused by competition for access to mates"*. However, this definition, which remains the most widely used by researchers studying sexual selection (see Shuker and Kvarnemo, 2021), focuses only on pre-copulatory sexual selection and excludes post-copulatory processes. Although access to mates is a necessary step towards access to gametes (at least in internal fertilisers or external fertilisers where copulation is necessary), mechanisms occurring after mating (i.e. after pairing) may also increase or limit fertilisation success, ultimately constituting a fully-fledged fitness component. Many researchers have therefore recently advocated broadening Anderson's definition to include post-copulatory processes by defining sexual selection as, for instance, "*selection generated by differential access to opposite-sex mates and gametes*" (Kokko et al., 2006). Recently, Shuker and Kvarnemo (2021) defined sexual selection,

in terms of "*any selection that arises from fitness differences associated with nonrandom success in the competition for access to gametes for fertilisation*". Although very similar to the previous definition, this new one emphasises that variations in access to mates or gametes may exist even under a random-mating pattern (i.e. in absence of sexual selection, see 1.1.3.1). Since Andersson (1994) work, most scientists, including the ones mentioned above, approved the use of sex- and sex-role-neutral definitions of sexual selection. Although anisogamy (i.e. the size difference in gametes) does mean that ova are more likely to be a limiting resource than sperm, both males and females may display traits that are under sexual selection. Moreover, two sexes are not even required for sexual selection to occur; competition over mates that differ in quality may also occur in hermaphrodite species (Ghiselin, 1969; Anthes et al., 2010; Pélissié et al., 2012). This implies that sexual dimorphism (i.e. morphological differences between the sexes) is not a prerequisite for sexual selection to occur.

#### Defining sexual selection in light of natural selection theory

The relationship between natural and sexual selection has been long debated; differences of opinion abound on whether or not sexual selection is a subset of natural selection. In *The Origin of Species*, Darwin made a clear distinction between natural selection and sexual selection. This distinction was drawn because traits that are favoured by sexual selection are sometimes opposed by natural selection (see above). In such conceptualization, natural selection is considered in terms of *viability selection*: for instance, as a sexual ornament gets bigger, natural selection through predation or competition for resources occurs to prevent further elaboration. Traditional sexual selection modelling (e.g. Andersson, 1994) also considers sexual selection as being balanced by natural selection. Endler (1986) was among the first theorists to provide valuable insight into how the relationship between natural and sexual selection could be summarised. Indeed, he defined natural selection in two distinct ways:

- ***Broad-sense natural selection***: natural selection includes all possible components of fitness, making sexual selection a subset of natural selection. This definition is the definition used by Endler (1986) in his book.

- ***Narrow-sense natural selection***: natural selection only comprises viability and fecundity selection and is therefore separated from sexual selection. This is in accordance with the Darwinian definition of natural selection.

Kokko (2021) and Shuker and Kvarnemo (2021) recently proposed that *"natural selection is about being able to enter and remain in the fertilisation game, and sexual selection is about performance once in the game"*. However, partitioning fitness into different subsets can be challenging in an empirical study, especially when fitness components align and confound with each other, for instance in the case of the "endurance rivalry" mechanism (see Box 1.2). Here, this challenge will be overcome as we will use *semalparous* species as a case study (see 1.3) i.e. species that reproduce once in their lifetime. Any trait that generates different access to opposite-sex mates will therefore be attributed to sexual selection and not natural selection.

### Defining sexual selection in light of mating systems theory

Mating system theory constitutes a great deal of empirical and theoretical work in evolutionary biology since the end of the seventies (e.g. Emlen and Oring, 1977; Shuster, 2009). The term "mating system" refers to the way populations are structured in relation to mating (Emlen and Oring, 1977; Davies, 1991). Historically, the classification of mating patterns emerged to better describe and document the diversity of sexual behaviours in animals. The most important criterion for summarizing a species or a population's mating system is the number of mates that each sex has during either one breeding season or over a lifetime. There are several categories of mating systems based solely on the number of mates (Table 1.1). Monogamy is employed when a single male and a single female reproduce exclusively with one another during ei-

ther a single reproductive season (i.e. *partial monogamy*) or over a lifetime (i.e. *sequential monogamy*). When males mate with more than one female, the mating system is described as *polygynous* while the term *polyandrous* is employed when females mate with more than one male. If both sexes mate with multiple partners, the mating system may be defined as either: *polygamous* or more occasionally as *promiscuous*. In the latter case, the term is employed in different contexts: when mating with multiple partners occurs in an indiscriminate way i.e. in a random pattern without any selection-based process, or sometimes in case of absence of any social ties between the mating partners. More rarely, the terms *polygynandry* and *polyandrogyny* can be employed to describe a polygamous mating system for which there is higher variability in male than female mating success or the reverse.

**Table 1.1.** Classical categories of mating systems. Adapted from Emlen and Oring (1977) and Shuster (2009).

| Mating system | Definition |
|---|---|
| *Monogamy* | Each sex has a single mate for either a breeding season or its entire lifetime |
| *Polygyny* | Males have more than one female mate during one breeding season or over their lifetime while females have one single mate |
| *Polyandry* | Females have more than one male mate during one breeding season or over their life time while males have one single mate |
| *Polygamy* | Both sexes have more than one mate |
| *Polygynandry* | Male mating success is more variable than female mating success |
| *Polyandrogyny* | Female mating success is more variable than male mating success |

The mating system being a descriptive summary of interactions between individuals, one primary goal of research in this area is to understand the factors that lead to variations in mating systems. However, understanding selection operating on individuals is a prerequisite to explaining why a species presents a specific mating system. The distribution of matings indeed depends on how individuals are selected to mate with more (or fewer) partners. In this regard, there is a clear link between theories of mating systems and sexual selection. For instance, let's consider a population in which intense male-male competition for access to females leads to pre-copulatory sexual selection in favour of large body size and strong fighting ability in males. In such a case, the evolution of polygyny may likely occur due to the process of pre-copulatory intrasexual selection in males. Yet, mating systems may reciprocally impact how behavioural adaptations evolve in a feedback process. If polyandry increases in this population, a stronger post-copulatory sexual selection in males to ensure fertilisation will emerge. If a trade-off exists between pre- and post-copulatory performance, the strength of pre-copulatory sexual selection will weaken, as will the investment in traits enhancing male mating success. Mating systems are therefore both the foundation and the outcome of selection on individuals.

Shuker (2010) advocated not to confound sexual selection with mating systems theory. While mating system theory can be used to predict and hypothesize the strength and direction of sexual selection, it cannot be relied upon to determine whether or not sexual selection actually occurs. Indeed, although mating systems theory allows us to estimate what opportunities a particular type of system may have on competition for mates, calculating the variation in success in competition for mates and gametes (see 1.1.3.1) remains necessary to actually test the process of sexual selection.

**Box 1.1.** What are the benefits of polyandry?

Early work on mating systems classification appeared long before behaviour tracking devices and genetic parentage analysis. A comprehensive knowledge of sexual interactions between adults of a population was therefore lacking. Owing mainly to anisogamy, the potential of female multiple mating (i.e. polyandry) was underestimated. While males were assumed to benefit from each additional mating, females, on the opposite, were assumed to gain no fitness by mating with an extra male. Once paternity testing had been developed and revealed high levels of polyandry, researchers aimed to identify the benefits of female multiple mating. Several explanations of potential benefits of female polyandry have been proposed (Halliday and Arnold, 1987; Yasui, 1997, 1998) and would be discussed consecutively:

- **Direct benefits**: The *direct* or *environmental benefit hypothesis* supposes that mating with multiple males generates a greater supply of sperm, provides females with food resources, defence against sexual harassment from other males and predators, or parental care of offspring.
- **Indirect benefits**: On the other hand, another explanation would be that polyandry is a way to increase female fitness by conferring genetic benefits. For instance, females may acquire genes which enhance the viability or competitiveness of their off offspring (*good gene hypothesis*), obtain male genes that are compatible with their own genes (*genetic compatibility hypothesis*) or increase genetic diversity within their offspring, which may increase the possibility that some offspring within a clutch can survive in a fluctuating environment (*genetic diversity hypothesis*) (Yasui, 1998).

Environmental benefits are easily understood and accepted by every researcher; however, genetic benefits have many theoretical difficulties and remain controversial (Yasui, 1998). A hypothetical female strategy to deal with such uncertainty is 'genetic bet-hedging' (Parker, 1992; Stockley et al., 1997*b*; Schneider and Elgar, 1998; Yasui, 1998). In the context of evolutionary biology, bet-hedging is a risk-spreading strategy that causes a decrease in average fitness but results in benefits that accumulate over generations due to a decrease in fitness variation. Consequently, a 'bet-hedger' genotype is supposed to reduce the probability of extinction across generations. When females' ability to discriminate male genotypes through mate choice is imperfect, having eggs fertilised by more than one male may reduce sampling error in mate quality (*bet-hedging under the good genes hypothesis*) or mate compatibility (*bet-hedging under the genetic compatibility hypothesis*). Alternatively, polyandry may be advantageous for females in a fluctuating environment as they cannot predict the good genes required by the next generation (*bet-hedging under the genetic diversity hypothesis*).

### 1.1.2 Mechanisms of competition over mates and gametes

Competition over mates and gametes can take many different forms, occurring **before** and/or **after mating**, and can promote a variety of morphological or behavioural traits (Table 1.2). Mechanisms of competition are generally classified into two categories: (1) intra-sexual selection in which members of one sex compete to access mates of the other sex and (2) inter-sexual selection in which individuals of one sex display phenotypic characters that make them more attractive to members of the opposite sex. *Scramble competition* is the first pre-copulatory mechanism that may allow individuals to have higher access to potential mates (Davies, 1991).

**Table 1.2.** Mechanisms of competition over mates and gametes. Adapted from Shuker and Kvarnemo (2021) and based on Andersson (1994).

| Mechanisms | Traits favoured in competing sex | Process |
|---|---|---|
| **Before mating** | | |
| *Scramble competition* | Ability to quickly locate mates (e.g. through developed hearing and olfactory senses) | Intra-sexual competition |
| *Contest competition* | Ability to outcompete competitors before mating through direct combat (e.g. body size, weapons), or ability to avoid such competition through alternative reproductive tactics | Intra-sexual competition |
| *Mate choice* | Competition to be chosen through behavioural or morphological traits that the the opposite sex finds attractive (e.g. ornaments, indicators of "good" genes), or resources that the other sex needs (e.g. parental care) or ability of avoiding mate choice (e.g. forced copulations) | Inter-sexual selection |
| **After mating** | | |
| *Gamete competition* | Ability to outcompete competitors through gamete competition after mating (e.g. large number of sperm or eggs), or ability to avoid that gamete competition after mating (e.g. mating plugs, mate guarding) | Intra-sexual competition |
| *Cryptic mate choice* | Competition to be chosen after mating through traits that the opposite sex prefers (indicators of "good" or "compatible" genes) | Inter-sexual selection |
| **Other** | | |
| *Endurance rivalry* | Ability to endure prolonged reproductive activity (e.g. condition, lifespan) | Intra-sexual competition |

Scramble competition occurs when all individuals are "scrambling" to locate and acquire as fast as they can the limiting resource, i.e. in the context of sexual selection, the members of the opposite sex. *Contest competition* is probably the most famous form of competition over mates and has been the centre of a large of empirical and theoretical studies (e.g. reviewed by Andersson, 1994). The term *contest* is used when rivals display to or fight each other in competition over mates or resources needed to attract mates. Fights over mates generally select for strength, often achieved by large size and for weapons such as horns. *Mate choice* refers to the process by which individuals select and prefer certain mates based on specific traits. *Gamete competition* is another mechanism that may be considered as the post-copulatory equivalent of contest competition. *Sperm competition* in males not only leads to the selection of larger testes and increased sperm production but also influences ejaculate composition and sperm morphology (reviewed by Simmons and Fitzpatrick, 2012). Research experiments on a sex-role reversed pipefish also demonstrated that females experience *egg competition* and can modify the amount and size of eggs produced depending on the level of female-female competition (Berglund, 1991). *Cryptic mate choice* is any process after mating by which individuals of one sex deferentially allocate resources to members of the other sex with respect to their phenotype. In females, this manifests through the facilitation of sperm displacement or preferential sperm use from the most attractive males (e.g. Eberhard, 1996), whereas in males, the focus lies on the quantity or quality of sperm they transfer to females during mating (e.g. Engqvist and Sauer, 2001). The last mechanism of competition over mates and gametes is *endurance rivalry*, i.e. the ability to remain reproductively available for a long time.

**Box 1.2.** What about endurance rivalry?

As explained in 1.1.1, it may be challenging to disentangle the respective role of natural and sexual selection in the case of *endurance rivalry* as longevity and reproductive success are likely to be positively correlated. In accordance with energy allocation theory (Fisher, 1930; Williams, 1966), we may also consider that there is a trade-off between somatic investment (i.e. in longevity via investment in tissues maintenance for instance) and reproductive investment (i.e. gametic investment and competition for mates). In this case, an individual that has invested less energy in the reproductive function would live longer but might have a lower reproductive success. In her commentary to Shuker and Kvarnemo (2021), Kokko (2021) provided a concrete example of how the relative role of natural and sexual selection in endurance rivalry may depend on the temporal scale at which we consider mating opportunities. If we consider a male behavioural trait that confers greater access to females but which, as a counterpart, implies a higher metabolic expenditure limiting the average number of partners encountered during a breeding season, one can easily accept that there is stabilizing sexual selection on this trait. However, if we now consider that the energetic costs of this trait are not immediate (i.e. there are no detrimental effects during the current breeding season) but influence the probability of a male surviving to the next breeding season; we may still consider this trait to be under stabilizing sexual selection, or rather that it is under directional sexual selection and is counteracted by narrow-sense natural selection acting on survival. This example nicely reflects how the temporal scales at which we consider reproductive opportunities can limit our perception of the evolutionary processes underlying a trait fitness. Studying semelparous species for which the overall reproductive success is easier to access would provide a better understanding of the role of sexual selection in *endurance rivalry* (see 1.3 and Chapter 2). Moreover, the relation between endurance rivalry and reproductive investment will be addressed in **Chapter 3**.

### 1.1.3 Measuring the strength of sexual selection

Numerous metrics have been developed to predict and/or quantify the strength of sexual selection. These can be classified into two main categories: variance- and population-based approaches, or trait-based approaches. I will present here four measures commonly used in studies on sexual selection, which I addressed as part of my thesis.

#### 1.1.3.1 Traditional measurement

**Operational sex ratio**

Emlen and Oring (1977) postulated that the strength of sexual selection mainly depends on mate monopolisation, i.e. the capacity of certain individuals of a given sex to control and dominate access to potential mating partners at the expense of other individuals of the same sex. The theory is that mate monopolisation by the most common sex is easier as the operational sex ratio (OSR, the ratio of males to females available at a given time and in a given location for mating, Fig. 1.1) becomes either more male- or female-biased. More precisely, a biased OSR is predicted to lead to stronger competition for mates of the most common sex (intrasexual selection) and higher choosiness for mates of the rare sex (intersexual selection), resulting in a higher monopolisation of mates by the most common sex. The OSR has been therefore widely used as a proxy of sexual selection since then. However, recent works highlighted that the positive relationship between the OSR and sexual selection may not be as ubiquitous as considered. Klug et al. (2010*a*) indeed showed through a straightforward theoretical example that potential competition is not the same as mate monopolisation. More precisely, an increased number of rivals (i.e. a more biased OSR) does not necessarily facilitate mate monopolisation. A few empirical studies showed that mate monopolisation indeed becomes more difficult when the number of potential rivals increases, as investing in intrasexual aggression may be very costly (Mills and Reynolds, 2003; Fitze and Le Galliard, 2008).

For instance, in common lizards (*Lacerta vivipara*), a switch from a female- to male-biased OSR led to a marked decrease in sexual selection on male body size (Fitze and Le Galliard, 2008). Authors suggested that in a population with a biased OSR, the most common sex may invest in alternative behaviours rather than engage in direct contest competition (e.g. in mate guarding, sneaking matings, or parental care) to maximise fitness. In this context, Weir et al. (2011) investigated the effect of OSR, not only on pre-copulatory sexual selection (i.e. on traits that directly influence mate monopolisation such as aggression or courtship behaviours) but also on additional forms of mate competition, notably gamete competition and mate guarding. Using a meta-analytic approach, the authors highlighted that a male-biased OSR is positively related to male-male aggression, but that the effect size decreases when the OSR becomes highly biased due to the increased costs of competition as rivals become more numerous. The OSR had no overall effect on sperm competition intensity, although it followed a similar trend to that observed in male-male competition. However, the OSR did have a negative effect on the courtship rate and a positive effect on mate guarding. This work highlighted that changes in mating behaviours occur in response to OSR, the nature depending on the type of mating behaviour studied.

Recently, two meta-analytical studies reconsidered the relationship between OSR and mate monopolisation by investigating the effect of OSR on the opportunity for sexual selection $I_s$ defined as the variance in mating success divided by the squared mean mating success of a given sex (see section 1.1.3.1). While Moura and Peixoto (2013) did not find a relationship between OSR and male $I_s$, Janicke and Morrow (2018), on the contrary, highlighted that male $I_s$ increases linearly with OSR. The latter study, which may be considered more robust considering the higher sample size used and the statistical method used (phylogenetic non-independence), is in line with Emlen and Oring (1977) classical theory that the OSR is an important parameter driving the opportunity and direction of pre-copulatory sexual

selection. On the contrary, they did not detect a relationship between OSR and female $I_s$ as variance in female mating success was low. This result suggests that females exhibit mate monopolisation to a lesser extent than males and may benefit less in investing in pre-copulatory intrasexual competition than in sharing mating partners.

To conclude, although the relationship between OSR and mate monopolisation is not exclusively positive, individuals of one sex are still likely to compete intensely for mates and gametes when the OSR is strongly biased towards that sex. Under such circumstances, selection likely favours behavioural or morphological traits leading to success in this competition, operating either before or after mating, with the extent depending on the sex and the mating system under study (Shuster and Wade, 2003). The relationship between OSR and the potential strength of sexual selection will be discussed in **Chapter** 2 and in the general discussion (**Chapter** 5).

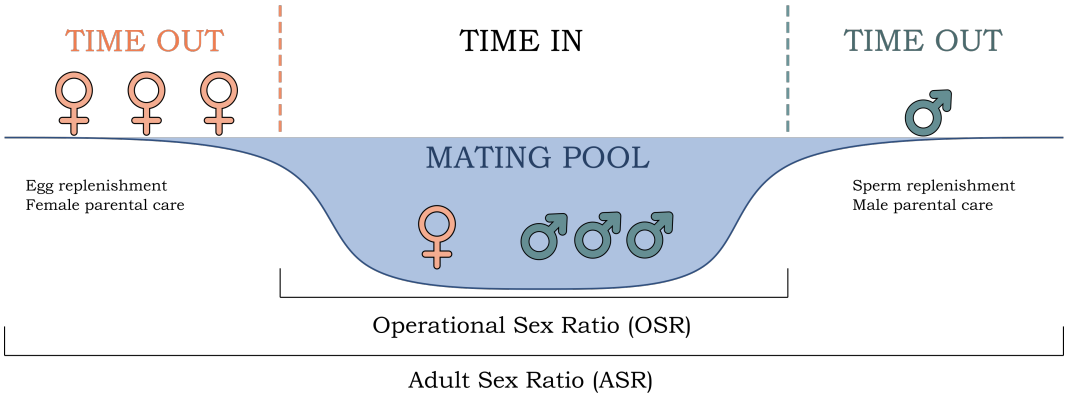


**Figure 1.1.** Conceptual representation of the operational sex ratio (OSR, the ratio of males to females available at a given time and in a given location for mating) and the adult sex ratio (ASR, the ratio of adult males to adult females) developed by Clutton-Brock and Parker (1992). Sexually available individuals form the "mating pool". As females are more likely to provide parental care than males (Kokko and Jennions, 2008; Royle et al., 2012) and are sexually active for shorter time periods, the length of the "time out" is generally higher in females, leading to an overall male-biased OSR, which eventually translates into stronger sexual selection in males (Trivers, 1974).

### Opportunity for sexual selection

The opportunity for sexual selection ($I_s$), defined as the ratio of variance in mating success and the squared mean mating success of a given sex (Wade and Arnold, 1980) is the most frequently used measure to estimate the strength of sexual selection. Being unit-less, this measure is particularly useful in meta-analytical studies, allowing us to compare classes of individuals (e.g. males vs females) and species. The strength of sexual selection within a sex is expected to increase as $I_s$ increases: the greater the variance in mating success, the stronger the selection could be. However, although $I_s$ is a metric providing an upper bound estimate of the strength of selection on mating success (Wade, 1979; Arnold and Wade, 1984) and does not reflect actual strength of sexual selection, $I_s$ is often used as such (see Box 2, Klug et al., 2010*a*). Through theoretical models, Klug et al. (2010*a*) highlighted that $I_s$ can lead to erroneous conclusions on the actual strength of sexual selection as $I_s$ is sensitive to both nonrandom (i.e. selection) and random (i.e. chance) variance in mating success and can reach high values even when sexual selection is absent, especially when matings are scarce. This is caused by the positive relationship between $I_s$ and OSR: as the OSR becomes more biased, the mean mating success of the most common sex decreases. As encouraged by Klug et al. (2010*a*) or Sutherland (1985) before them, a few empirical works (Janicke and Morrow, 2018; Moura and Peixoto, 2013) have since used bias-corrected $I_s$ by calculating the expected $I_s$ values under a random model (i.e. a null model) considering the density and the OSR observed in the population under study. Thus, although some caution is required in $I_s$ calculations, the metric remains useful to assess the maximum possible strength of selection, especially in situations where it is difficult to quantify the strength of sexual selection in relation to phenotypic traits (i.e. using selection gradient, see section 1.1.3.1) e.g. in species with weak or no sexual dimorphism.

### Selection gradients

In addition to adopting variance- and population-based approaches to estimate the strength of sexual selection, Lande and Arnold (1983) suggested using direct, trait-based measures of sexual selection called "selection gradients" ($\beta$). This measure, defined as the covariance between relative fitness and a trait, is a powerful tool to measure the actual strength of sexual selection operating on phenotypic traits. Selection on such traits can be expressed as $\beta_z$, the slope of the regression of relative fitness $F$ on a given trait $z$:

$$F = \beta_z * z + \alpha \tag{1.1}$$

where $\alpha$ represents the intercept of the regression.

Selection gradients might also be called "selection differential" ($s'$) when fitness is measured as reproductive success (Lande and Arnold, 1983; Jones, 2009) or "mating differential" ($m'$) when fitness is measured as mating success (Jones, 2009). Therefore, $m'$ quantifies success in pre-copulatory sexual selection while $s'$ shows the direction of sexual selection after one generation. However, the potential for using selection gradients is sometimes limited, as researchers may fail to identify and measure traits that are the target of selection and ultimately underestimate the overall strength of sexual selection in a particular mating system. Krakauer et al. (2011) therefore recommended first defining the potential for sexual selection to operate (see section 1.1.3.1 on $I_s$) and then determining whether it correlates with actual selection on targeted phenotypic traits.

### Bateman gradient

The Bateman gradient ($\beta_{SS}$) is a specific type of selection gradient measuring the relationship between reproductive success and mating success of a given sex (Bateman, 1948). Mathematically, it is the slope of the linear regression of reproductive success on mating success. The Bateman gradient is often used as a proxy for the strength of pre-copulatory sexual selection as it provides a measure for the fitness gain of having an additional mate. More precisely, (Jones, 2009) highlighted that the process of pre-copulatory sexual selection may be partitioned into two parts, on one hand, the "mating differential" ($m'$) (see previous section) that generate covariance between trait values and mating success, and on the other hand $\beta_{SS}$ that convert this mating differential into actual selection on the traits. Thus, a non-zero Bateman gradient is required for pre-copulatory sexual selection to operate on these same traits. The concept of the Bateman gradient gained more momentum when Arnold and Duvall (1994) reviewed empirical studies highlighting: (1) a greater variance in both mating and reproductive success in males than females and (2) a stronger relationship between reproductive success and mating success in males than females, i.e. a steeper Bateman gradient in males than in females. This widespread pattern implies that selection to increase mating success (i.e. pre-copulatory sexual selection) is likely stronger in males than females. Interestingly, the Bateman gradient is steeper for females than males in sex role-reversed species (e.g. species with greater female-than-male competition and greater male-than-female care), highlighting how this parameter is reliable for predicting sex-specific differences in the strength of pre-copulatory sexual selection.

#### 1.1.3.2 Methodological biases in the measurement of sexual selection

**Decomposing fitness**

Although the concept of mating success is at the core of each of the measurements listed above (i.e. $I_s$, $m'$ and $\beta_{SS}$), definitions for individual mating success are numerous. With the rise of molecular analysis for parental assignation, individual mating success has been mainly defined as the number of mates with whom a focal individual copulated and produced offspring. Since parentage analyses are generally performed at the end of the breeding season, such a definition of mating success enables to investigate the overall fitness benefits of a reproductive strategy. However, this approach does not allow us to disentangle the relative importance of pre- versus post-copulatory processes (Henshaw et al., 2018, 2016; Anthes et al., 2017). For instance, if one individual appears to have produced no offspring based on parentage analysis, its mating success would be 0. This zero value may indeed represent no mating success but it may alternatively constitute (1) a mating event that never produced offspring due to post-copulatory mechanisms (gamete competition and/or cryptic mate choice), (2) a mating event that produced offspring who died before sampling or (3) a mating event that produced offspring who failed to be sampled. Jones and Avise (2001); Pélissié et al. (2014); Pischedda and Rice (2012) therefore advocated separating components that depend on mating activity (i.e. mate acquisition and number of matings achieved) from post-copulatory components (e.g. fertilisation, good genes effects) to have an insight of selection processes occurring before mating. With this approach, pre-copulatory success includes variance in the number of mates as well as variance in the number of matings, allowing selection on any trait that affects both mate acquisition and matings frequency to be considered. Such an approach therefore requires mating success to be deducted from behavioural observations, which may pose other issues than those arising from genetic parentage analysis. For instance, Klug et al. (2010*b*) revealed the implications of variation in who is included in the measure of mating suc-

cess in animals that require resources for reproduction (e.g. nests). Authors highlighted that excluding non-mating males that are absent from breeding aggregations underestimates the opportunity for sexual selection. This raises again the difficulty of defining the boundary between sexual selection and natural selection when it comes to competition for resources (see 1.1.1). Such problems arising in the wild may be avoided by using experimental approaches that allow to consider all sexually receptive individuals in the measure of mating success.

#### Scales at which estimates are calculated

Fluctuations in narrow-sense natural selection have long been recognised as environmental conditions, which serve as the selective forces, vary over time and space (Endler, 1986; Grant and Grant, 2002). In the context of sexual selection, traditional selection analysis studies suggest, in contrast, that the competitive context and selection pressures are homogeneous across populations. By calculating single population estimates, mechanisms of sexual selection (intra-sexual selection and intra-sexual competition) are suggested to induce directional and constant selection pressures on phenotypic traits. However, these two processes of selection are relative processes because of the context dependence of the many factors involved in sexual selection. For instance, the density of individuals, sex ratios, and presence of heterospecifics may vary in time and space, affecting the genetic and phenotypic composition of populations and so the social structure in which individuals interact. Thus, selection analyses that are repeated over space and time (and thus in a certain context) are necessary to measure lifetime fitness and have an accurate picture of the overall selection on phenotypic traits.

## 1.2 Temporal variations in the social environment

Several studies have examined how sexual selection varies with spatial and temporal fluctuations in the social environment. As my thesis work focuses on the temporal aspects, these will be extensively presented in the next section, while the spatial aspects will be summarised in a box (1.3).

### 1.2.1 Temporal fluctuations in sexual receptivity

#### Inter-annual fluctuations

Several studies have acknowledged the importance of considering the effects of long-term environmental variations on sexual selection in iteroparous species. In a population of adders (*Vipera berus*), seven years of fieldwork showed that inter-annual variations in the OSR have considerable effects on the intensity of sexual selection for large body size in males. Indeed, large body size strongly enhanced male reproductive success when the OSR was male-biased (Madsen and Shine, 1993). In the superb fairywrens *Malurus cyaneus*, Cockburn et al. (2008) highlighted a systematic directional sexual selection for early moult in males. However, sexual selection strength was highly variable from year-to-year, suggesting that studies that are not temporally replicated may misrepresent the pattern of sexual selection in the wild. Through a database of temporal replicates of selection from studies of long-lived animals, Siepielski et al. (2009) also showed that populations can undergo varying levels of sexual selection strength over time, which can be attributed to demographic or environmental changes occurring between breeding cycles. However, our understanding of the variation in sexual selection throughout a breeding season, driven by smaller-scale fluctuations in environmental factors such as the OSR, remains limited and will be discussed in the next section.

**Box 1.3.** Spatial variation in resources and mate's distribution

The spatial distribution of resources needed for reproduction, e.g. food or nesting sites, is expected to affect the mating dynamics of a population. If resources are uniformly distributed in space, it becomes challenging for the most attractive or competitive individuals to respectively attract or get access to potential mates. Under these circumstances, mate guarding is expected to increase and the potential for polygamy is expected to be low (Emlen and Oring, 1977). On the opposite, if the resources needed for reproduction are clustered in space, expectations diverge. On one hand, Emlen and Oring (1977) assumes that competitive and/or attractive individuals may monopolise resources and the mates that need those resources for reproduction. Alternatively, some theoretical works suggest that the level of competition becomes so high that it becomes difficult for individuals to monopolise those resources and mates, ultimately diminishing the potential for pre-copulatory sexual selection to occur (Klug et al., 2010*a*).

Several studies investigated sexual selection repeatedly across different geographical locations and the ecological factors that were demonstrated or suggested to influence changes. Local density has been the first demographic factor shown as responsible for spatially varying selection on male traits. For instance, in arthropods (McLain, 1982, 1992), male-male competition tends to increase at low-density levels, resulting in a greater selection on male body length. Similarly, Lehtonen and Lindström (2008) observed that females were larger under low than high nest density in the convict cichlid *Archocentrus nigrofasciatus*. Jirotkul (1999) also found that male guppies reduced their investment in courtship behaviours as population density increased, demonstrating that density may also induce variation in mating tactics. Differences in sex ratio between spatially separated populations have also been shown to be correlated to changes in the strength and direction of selection. A few studies highlighted that the intensity of selection in males was higher when the ASR (Pröhl, 2002) and the OSR (Kasumovic et al., 2008) was more male-biased, aligning with classical theory (see 1.1.3.1).

### Within-season fluctuations

The availability of sexually receptive individuals can also change over the season due to factors like differential maturation rates, parental care, gamete stock depletion, or mortality (see Fig. 1.3), leading to fluctuations in the OSR and variations in social structure. The gap in our understanding of the potential within-season variation in sexual selection can be explained by the preponderance of cross-sectional data over longitudinal data in estimating mating success. In most empirical studies, individuals are sampled at one particular point in time and individuals are not followed repeatedly during the breeding season. Shuster (2009) showed that single-interval estimates of the intensity of competition (i.e. OSR) tend to overestimate the overall intensity of selection throughout the breeding season. As the OSR does not differentiate between individuals who successfully mate and those that do not, the covariance among time periods in individual mating success cannot be estimated. Consequently, assessing how consistently certain individuals are accumulating mating events over time is not possible. For instance, if male mating success does not remain constant over an entire breeding season (i.e. if the covariance between time intervals is low), the overall variance among males would decrease. Thus, summing up single estimates of OSR over the season might lead to inaccurate conclusions on the expected variation in mating success as it does not consider such covariance.

Anthes et al. (2017) also demonstrated that sampling over an insufficient period of time may induce a decrease in mean mating success, resulting in an overestimation of the opportunity for sexual selection. Indeed, as a higher number of individuals risk not being sampled, the number of individuals considered as "unmated" increases. In a recent meta-analysis study, Carleial et al. (2023) investigated the temporal dynamics in the opportunity for sexual selection over a breeding season across seven species and demonstrated that daily instantaneous measures consistently overestimated the overall

variance in mating success. Thus, single estimates must be used with some caution as the underlying assumption behind this approach is that (1) small demographic changes throughout the breeding season would not impact individual mating success and therefore that (2) the fitness of a given trait character at an instantaneous sample period can be extrapolated to the whole breeding season. On the opposite, a longitudinal approach enables taking into consideration the potential within-season variation in individual mating success and gives more accurate estimates of the strength of sexual selection. However, having full knowledge of the mating sequences occurring might be difficult, as observing all interactions among individuals within a population is time-consuming, especially in long-lived iteroparous species. The appropriate temporal scale to adopt may depend on the biological model under study (iteroparous vs semelparous, short vs long breeding season).

Recently, researchers started to investigate the extent to which within-season fluctuations in demographics may cause variation in selection. For example, Kasumovic et al. (2008) demonstrated within-season variations in OSR and density in different periods of the breeding season in golden orb-web spiders (*Nephila plumipes*), resulting in significant differences in the strength and direction of sexual selection on male body size. Similarly, Wacker et al. (2014) highlighted changes in sexual selection within a season in male two-spotted gobies (*Gobiusculus flavescens*) that coincided with changes in the OSR. Nevertheless, in this study, the estimation of selection strength relies on a limited set of cross-sectional data rather than on a longitudinal approach.

Overall, these findings emphasize the correlation between selection strength and the time frame over which it is assessed, suggesting that averaging values over long-term periods (whether it is over a single season or a lifetime) may lead to misrepresentation or underesti-

mation of the impact of selection on phenotypic evolution. I will discuss in the next section the environmental factors that may lead to spatial and temporal fluctuations in the social environment, with a particular emphasis on the ones that may impact the temporal dynamics of mating opportunities and ultimately sexual selection (summarised in Fig. 1.3).

**Box 1.4.** Sexual networks theory

In recent years, the scientific study of sexual networks has received much attention in the field of animal behaviour. The interest in this approach grew significantly as several studies started acknowledging that spatial and temporal variations in the social environment can influence the overall strength and direction of sexual selection (see 1.2). Sexual networks are composed of nodes representing individuals (males and females) and the connections between these individuals (edges) may characterise any intra- and intersexual interactions. These interactions can be quantified at both the individual and group levels. Group-level metrics capture potential variations between groups regarding network structure i.e. the overall patterns of interactions (e.g. *network density*, *assortativity*, *nestedness*), while individual individual-level metrics quantify the position of each individual within their social network environment (e.g. *connectivity*, *centrality*) (see review by Pinter-Wollman et al., 2014). In a few taxa, studies have highlighted a strong correlation between an individual's position within its social network and its own fitness. For instance, in the cooperatively breeding cichlid *Neolamprologus pulcher*, Dey et al. (2013) showed that higher-ranked individuals had more conflict with one another compared with lower-ranked individuals (i.e. higher *connectivity*), highlighting that the position of an individual within their network can impact its vulnerability to experience aggression. As the fitness consequences of social behaviours are likely to vary depending on group-level properties such as density and sex ratios, selection on a particular social phenotype (i.e. a social network position) may be highly variable across time and space. In forked fungus beetles *Bolitotherus cornutus*, Formica et al. (2021) recently showed that an individual's position in a social network (based on spatial proximity) experiences different fitness consequences within different spatial contexts. Indeed, selection on individual males' *connectivity* and *centrality* was stronger in populations with male-biased ASR and in larger populations. The fitness effects of having a particular position in the network at a particular time of the breeding season might also depend on the current competitive environment. For instance, the percentage of successful matings may depend on the individual's position in its competitive network, i.e. the more competitors an individual has, the lower its probability of mating successfully. Sexual networks theory was the basis of my modelling approach developed in **Chapter** 2.

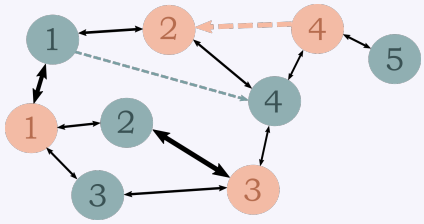


**Figure 1.2.** Intra- and intersexual weighted network with both males (blue nodes) and females (orange nodes). An edge between a male and a female node represents mating between these two individuals (black). An edge between two males or females represents a competitive interaction and is directional (orange or blue). Edge thickness represents the relative edge weight strength i.e. number of matings or aggressions

### 1.2.2 Factors influencing the pattern of reproduction

#### 1.2.2.1 Within-season variations in ecological factors

Temporal clustering of reproduction, i.e. reproductive synchrony, is a widespread phenomenon in seasonal environments, as breeding only during optimal seasons of the year can maximise reproductive success, offspring survival and subsequent recruitment. The cyclic variations in environmental factors, such as temperature, photoperiod, and food availability therefore play pivotal roles in shaping the timing of reproductive events (e.g. Bradshaw and Holzapfel, 2007). As most fishes are poikilotherms, temperature highly influences their reproductive synchrony, by altering the timing of gamete development and maturation as well as spawning (reviewed by Munro et al., 1990). The effects of temperature can vary depending on the time of year when spawning occurs, with elevated spring temperatures being required to trigger maturation in spring-spawning species, while cold temperatures initiate the onset of reproduction in autumn spawners (reviewed by Stacey, 1984; Munro et al., 1990; Pankhurst and Munday, 2011; Pankhurst and King, 2010). In some salmonids, photoperiod determines the initiation of sexual maturation, which may take place at sea, months before migration back to rivers, but the timing of spawning itself is more affected by temperature (e.g. Davies and Bromage, 2002).

As global temperatures increase due to climate change, both marine (Pörtner et al., 2019) and freshwater (Liu et al., 2020) ecosystems are projected to experience increasing warmth, accompanied by a greater occurrence and duration of extreme events like heatwaves. In this context, extensive research has been conducted to gain a better understanding of how significant increases in water temperature affect fish reproduction, especially regarding the timing of reproductive events (e.g. sexual maturation, spawning). For instance, Sandströ et al. (1997) highlighted that the breeding season of the European perch *Perca fluviatilis L.* was

earlier and longer when individuals were exposed to warm effluent water. The causes of the extended spawning period were not provided; however, asynchronous gonad development could have led to various individual responses in reproductive timing. On the other hand, high summer temperatures were correlated with a delay in fall spawning in salmonids populations (Warren et al., 2012; Gillet, 1991). Changes in water temperature therefore seem to influence inter-individual variations in the onset of spawning, ultimately resulting in variations in reproductive synchrony. Moreover, temperature-induced and sex-specific differences in the timing of maturation (Tréhin et al., 2021) may also cause biased adult sex ratios or operational sex ratios at the beginning of the breeding season.

Apart from environmental factors, the presence of heterospecifics or morphs with distinct life histories (e.g. migratory versus resident forms in salmonids) during the breeding season may also impact mating dynamics. Indeed, the spatio-temporal disjunction in breeding between species or between morphs with distinct life histories does not occur in many taxa. For instance, mixed breeding grounds have been observed in birds (e.g. Mönkkönen et al., 1999) and fish (e.g. Lasne et al., 2010), where nest building is common. One hypothesis is that the emission of similar-sex pheromones may induce synchronous spawning of neighbouring individuals and attract closely related populations or species on the same spawning grounds. Although heterospecifics or conspecifics with distinct life histories may directly alter demography, influence intrasexual competition and engage in sexual interactions, they are rarely considered as part of the social environment (McDonald et al., 2019).

#### 1.2.2.2 Individual decisions / Life history traits

Numerous factors can cause variations in the temporal and spatial distribution of sexually available individuals during a breeding season, which will be discussed consecutively below.

- ***Reproductive timing***: although reproductive timing is driven by changes in climatic seasonality, notably through temperature and photoperiod effect on maturation rate and spawning itself (see 1.2.2.1), it may also be caused by adaptive strategies that individuals adopt to maximize their reproductive success (Ims, 1990; Koizumi and Shimatani, 2016; Gochfeld, 1980). For instance, the ability to use visual cues from the environment (e.g. density) may be sexually selected to strategically adjust rates of sexual development or trigger mating behaviour (Jovani and Grimm, 2008; Koizumi and Shimatani, 2016). Thus, social and behavioural factors may alter the temporal distribution of breeding events by synchronizing or de-synchronizing breeding activity. However, many important aspects of reproductive synchrony are not yet fully understood, such as the relative importance of internal and external factors (Koizumi and Shimatani, 2016).

- ***Parental care***: parental care may explain why an individual's sexual receptivity varies through a breeding season. When parents provide care to their offspring, they are generally unavailable for mating (although the trade-off between parental investment and mating does not always exist, see review by Stiver and Alonzo, 2009). As females generally provide more parental care than males, OSR tends to be overall male-biased.

- ***Post-mating refractory period***: refers to a temporary period following mating during which an individual is unable or less willing to engage in further sexual behaviour. This period is often observed in species where gamete production is subject to physiological constraints (e.g. sperm replenishment) that reduce mating frequency (**?**). In species with internal fertilisation, males may also use mechanisms to prevent re-mating in females, either by creating a physical barrier such as a mating plug or by causing a decrease in female sexual receptivity through the transfer of sperm and/or seminal fluid proteins (reviewed by Chapman, 2001; Avila et al., 2011; Gillott, 2003).

- ***Dispersal***: dispersal, i.e. defined in the context of reproduction as movements between

suitable breeding habitats to optimize individual reproductive success, also affects the social environment and thus mate availability. Because the benefits of dispersal depend on local mate competition, it is likely that optimal dispersal strategies will differ between the sexes, and also vary in response to different sex ratios (Clobert et al., 2001). The interdependence between sex ratios and sex-specific dispersal may induce important fluctuations in the social environment throughout a breeding season.

- ***Timing of mortality***: sexual differences in mortality rate is often important during the spawning season. The factors that induce sex-specific mortality can be diverse, including vulnerability to predation or pathogens. For instance, the level of *G. anomala* parasitism in three-spined sticklebacks *Gasterosteus aculeatus* was higher in males than females, resulting in a female-biased ASR at the end of the breeding season (Arnold et al., 2003).

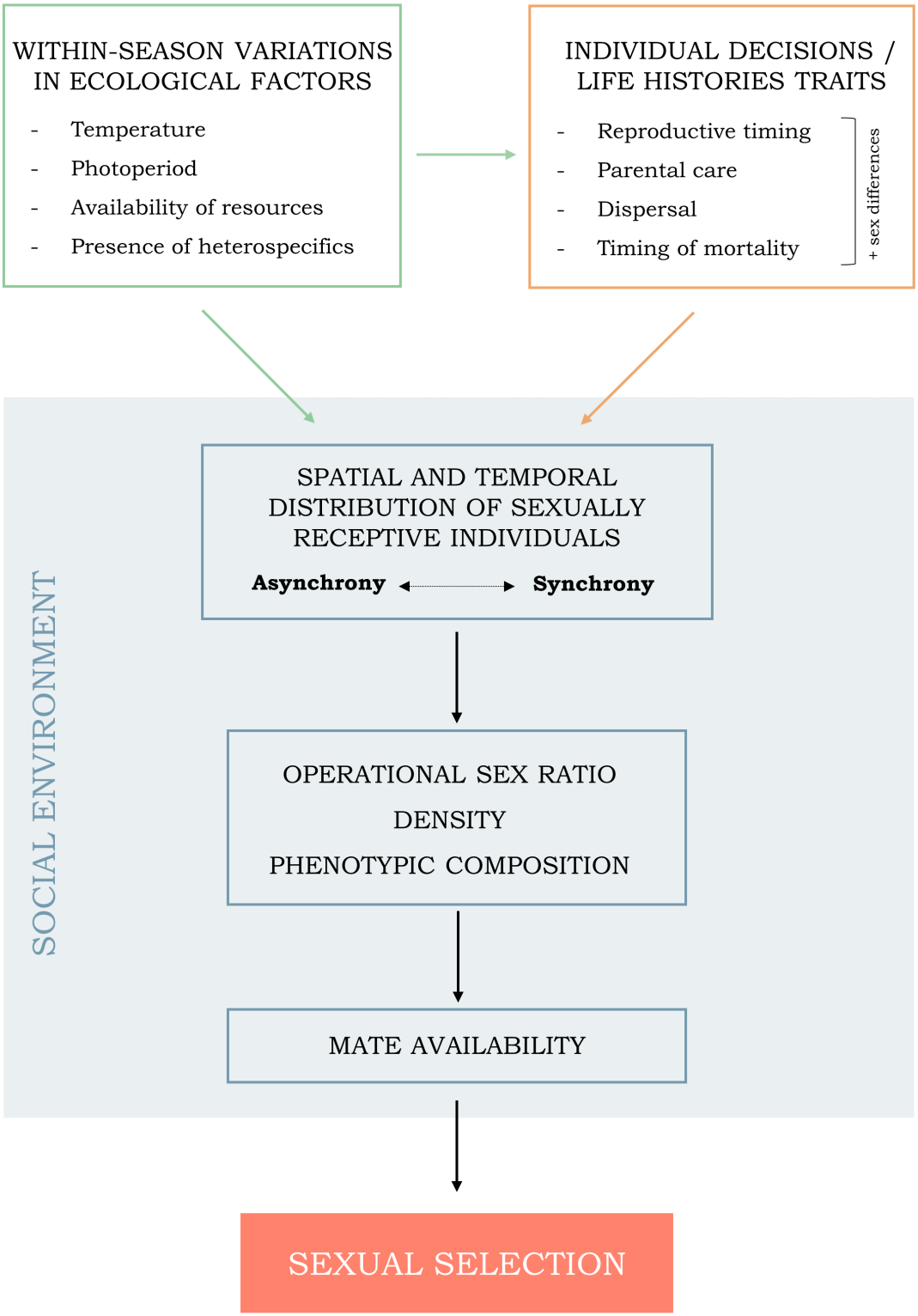


**Figure 1.3.** Abiotic (environmental) and biotic (ecological) factors that may affect mating system dynamics and ultimately the strength and direction of sexual selection.

## 1.3 Lampreys as a biological model

Building upon the preceding sections, this part will provide an insight into the ecology of lampreys and outline the reasons I used them as a case study throughout my thesis project to investigate how temporal fluctuations in the social environment during a breeding season affect sexual selection.

### 1.3.1 General ecology

The lampreys, together with hagfishes, are the only living members of the most primitive group of vertebrates: the Agnatha. Lampreys can be categorised into three distinct monophyletic groups, each recognized as distinct families (Fig. 1.4). Among these groups, two are found exclusively in the southern hemisphere (*Geotriidae* and *Mordaciidae*), while the third, which serves as the focus of my thesis, is limited to the northern hemisphere (*Petromyzontidae*). The lamprey life cycle is predominantly spent as a burrowing larva known as an *ammocoete*, which is a small filter-feeding stage (from 1 to 15 cm in length) that resides in mud and sand beds along riverbanks for several years. During an extensive period of metamorphosis, marked by major morphological and physiological changes, mainly in the digestive tract and visual perception, the ammocoete continues its nocturnal behaviour, burying itself in sediment or hiding under cover. After this complete metamorphosis, lampreys adopt distinct life history paths. Out of the currently known 41 lamprey species, 23 called "brook lampreys" stop feeding and directly reach sexual maturity at the end of the metamorphosis. Although sometimes describes as "non-migratory", adult brook lampreys still initiate upstream migration to reach suitable spawning habitats in rivers. For instance, several *Lampetra planeri* populations cover distances of less than 2 km in the few weeks preceding spawning while some others engage in longer migrations, extending over six months and exceeding distances of 5 km (Hume, 2011). The remaining 18 species adopt a parasitic life history, attaching to host species

(mainly fishes) through their oral disc to feed on blood and tissues. Unlike non-parasitic lampreys, they are referred to as juveniles during this period of their life cycle, as they have not yet reached sexual maturity after metamorphosis. This juvenile parasitic phase can last from a few months to several years, after which the adult lamprey reaches sexual maturity and undertakes a long migration back to the freshwater environment to reproduce. Given the feeding phase of parasitic lampreys after metamorphosis, a large size difference is observed at the adult stage; for instance, *L. planeri* is about 10-15 cm long while *L. fluviatilis* is 20-30 cm long (Docker, 2015). All lamprey species are semelparous i.e. they reproduce once in their lifetime and die (Larsen, 1980).

### 1.3.2 Stem-satellite species complexes

Lamprey phylogeny exhibits a recurring pattern characterised by the existence of species complexes, the members of which are commonly referred to as either paired species or stem-satellite species (Vladykov and Kott, 1979; Docker, 2019). Within each complex, there are one or more closely related species that are believed to have evolved from an anadromous parasitic species (Zanandrea, 1959; Hardisty and Potter, 1971; Yamazaki et al., 2001). Most of these derived species both stay in freshwater as adults and cease to feed while others exhibit freshwater residency but remain parasitic. Despite ecological and phenotypic differences in juveniles and adults, the members of a complex are often morphologically indistinguishable during the larval stage (Zanandrea, 1959). Is it admitted that non-parasitic lampreys have undergone recent evolutionary divergence in response to environmental changes and resource availability (Evans and Limburg, 2019). Indeed, non-parasitic lampreys might have emerged as a strategy to enhance their reproductive output by minimizing the risky adult phase in the sea and extending the larval period. However, the specific cause and rate of such significant adaptation remain unclear (Salewski, 2003; Docker, 2019). In several stem-satellite species

complexes, speciation occurred over a long period of geographical isolation (i.e. allopatric speciation) but the divergence times happened either (1) hundreds of years ago as a response to anthropogenic influences, (2) thousands of years ago triggered by major glacial events or (3) hundreds of thousands of years in reaction to geological change (Yamazaki et al., 2011; Docker, 2015). In certain cases, non-parasitic lamprey populations appeared to evolve repeatedly from sympatric parasitic populations (i.e. sympatric speciation). Although many taxonomists consider life history (and more precisely feeding type) to be specific to each species, the existence of stem-satellite species complexes living in sympatry with no or few genetic differentiation between members of them challenges this theory (Docker, 2019; Rougemont et al., 2015). For instance, Rougemont et al. (2015) suggested that the non-parasitic *L. planeri* does not represent a single evolutionary lineage but rather represents an alternative life-history strategy of the parasitic *L. fluviatilis*, thus forming a single polymorphic species.

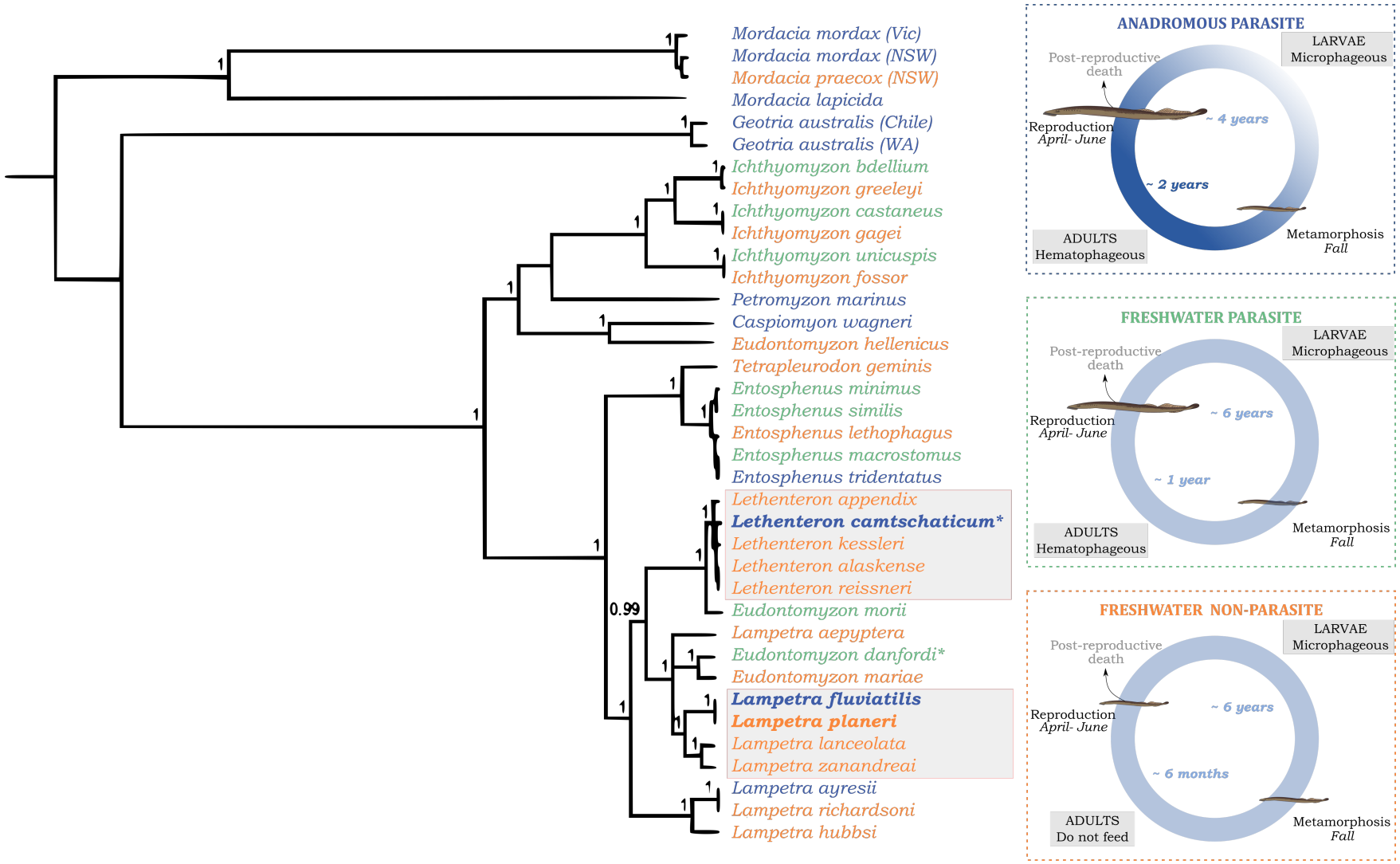


**Figure 1.4.** Phylogenetic relationships between 35 out of 41 lamprey species recognized by Potter et al. (2015), derived from cytochrome b sequence data and the three alternative life cycles. Bayesian posterior probabilities are given for those nodes where values are more than 0.95. Geotria and Mordacia occur in the Southern Hemisphere (Vic, Victoria; NSW, New South Wales; WA, Western Australia) while all other genera are found in the Northern Hemisphere. 11 lamprey species are anadromous (dark blue), 8 are freshwater-resident parasitic (green) and 18 are freshwater non-parasitic "brook lamprey" species (orange). Grey boxes reflect two stem-satellites species complexes. The asterisk designates *Lethenteron camstschaticum* which is usually considered as an anadromous parasite only although a non-parasitic dwarf form was found in Japan (Iwata and Hamada, 1986; Yamazaki et al., 1998). Species in bold are those I studied as part of my thesis.

### 1.3.3 The spawning behaviour

Spawning occurs in the upper regions of rivers in spring or early summer, depending on location and species. Lampreys aggregate in pairs or larger groups to create nests formed in gravel and pebbles where they deposit their gametes. Both male and female lampreys are usually present during the construction phase of the nests although some authors proposed that males initiate nest building, as they generally arrive first in the spawning grounds (Applegate, 1950; Hagelin and Steffner, 1958; Hagelin, 1959; Maitland, 1980). Initially, a patch of stones and gravel is cleared of silt by the vigorous beating of an individual's tail which leads to the formation of a depression in the gravel. Lampreys then remove pebbles with their mouth and move them downstream, further contributing to the formation of the nest.

The spawning act starts when the female attaches herself to a large stone located at the front of the nest, aligning her body with the water current. The male approaches the female from behind and glides along her body until he reaches the head region with its oral disc. Subsequently, the male attaches to the female and extends the lower portion of his body across the female, forming a loose coil around her trunk. This tail loop is then tightened, and both the male and female vigorously vibrate and wag their tails for a few seconds. As a result, the ova and milt are expelled into the nest, which quickly becomes covered in sand and small gravel, providing a surface for the fertilised eggs to adhere to. Previous studies have highlighted the function of the nest in enhancing the survivorship of eggs as depression in the gravel allows for egg covering, which protects them from predation (Manion and Hanson, 1980). As there is no refractory period following mating, both the male and female return to nest-building activities or directly re-mate. It is quite common to observe multiple males attach to different positions on a single female and vibrate at the same time (Malmqvist, 1983; Yamazaki and Koizumi, 2017)

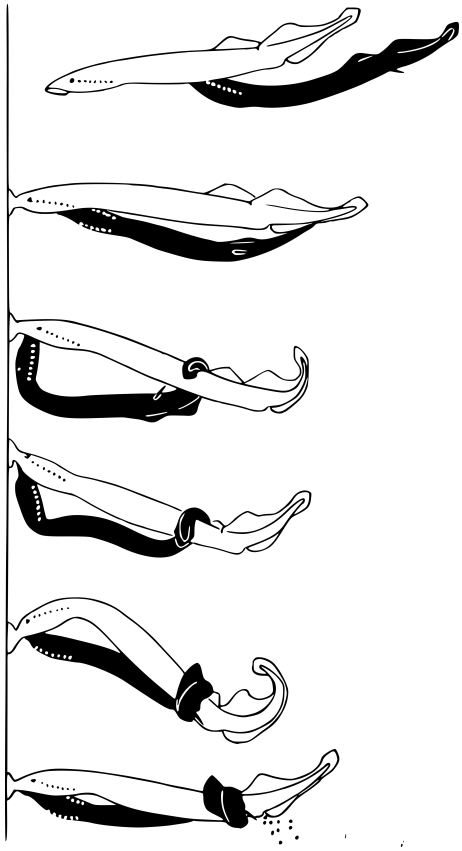

**Figure 1.5.** The mating act in lampreys (from Sterba, 1962)

Evidence of alternative male reproductive behaviours has been documented in *Lethenteron appendix* (Cochran et al., 2008) and in *L. planeri* (Malmqvist, 1983). During egg release, an unattached male, known as the "sneaker," swiftly circles around the cloaca of a spawning pair in an attempt to achieve egg fertilisation (Malmqvist, 1983).

### 1.3.4 Within-season fluctuations in lamprey's social environment

Although numerous studies indicate that most lamprey species display a polygynandrous mating system, limited information is available on the population structure of adult lampreys during the breeding season and the factors that may impact its dynamic. Early works indicate that males of several lamprey species reach the spawning ground first and begin nest building while females arrive later (Applegate, 1950; Hagelin and Steffner, 1958; Hagelin,

1959; Malmqvist, 1983), inducing a male-biased sex ratio at the start of the breeding season. In *L. planeri*, *Lethenteron reissneri* and *L. appendix* populations, males also appeared to dominate on spawning grounds later in the season (Hardisty, 1961; Seagle and Nagel, 1982; Takayama, 2002). Jang and Lucas (2005) observed as well a preponderance of males during the spawning phase but a domination by females during the nest-building phase, contrasting the above-mentioned previous studies. However, although sex ratios obtained over a restricted portion of time may be biased, no study to date has monitored a full spawning period except the study conducted by Jang and Lucas (2005). Pletcher (1963) and Jang and Lucas (2005) suggested that fluctuations in the OSR throughout the breeding season might be a result of sex differences in life histories traits and/or individual decisions (see 1.2.2.2) e.g. sex differences in the timing of maturation and lifespan (Dhamelincourt et al., 2021; Gardner et al., 2012). However, a comprehensive investigation of this issue is still required.

The number of lampreys on a nest can also be highly variable within, as well as among species. In Europe for instance, sea lamprey is considered mostly monogamous, although more than two individuals can be regularly observed on a nest (Applegate, 1950; Manion and Hanson, 1980; Dhamelincourt et al., 2021) while *L. planeri* and *Lampetra fluviatilis* are known as highly polygynandrous and spawn in nests hosting clusters of two to 70 individuals (Jang and Lucas, 2005; Lasne et al., 2010). Information is lacking regarding the potential fluctuations of density during a breeding season. On a single spawning site (area of 450 $m^2$) in the River Derwent, England, the daily number of nests occupied by river lamprey varied between 27 and 102 over a 15 days spawning season while the mean number of lampreys per nest varied between 12 and 24 (Jang and Lucas, 2005). Overall, the number of individuals observed each day varied between 336 and 1804 (mean $\pm$ SD = 1199 $\pm$ 104 individuals/day). The temporal pattern of abundance was not explicitly presented in their study, however.

Within-season variations in phenotypic composition may also be observed due to the occurrence of interspecific spawning associations between paired species living in sympatry. Such communal spawning has been observed between *Lethenteron camtschaticum* and *L. reissneri* in Russia (Kucheryavyi et al., 2007) or *L. planeri* and *L. fluviatilis* throughout Europe (Huggins and Thompson, 1970; Lasne et al., 2010). However, spawning times do not entirely overlap between anadromous and resident species occurring in sympatry. In Europe for instance, *L. planeri* typically spawns from February to April while *L. fluviatilis*, on the other hand, generally reproduces slightly later, with their breeding season ranging from April to June, with peak activity occurring in May (Renaud, 2011). Such staggered spawning between species with large size differences may result in a preponderance of small individuals in earlier months and an increased abundance of large ones later in the season, although this remains to be explored. In the following section, I will discuss environmental factors that may induce spatial and temporal variations in the social environment through changes in the OSR and phenotypic composition.

### Seasonal variations in ecological factors

One of the factors determining the onset of spawning in lampreys is water temperature. As mentioned above, there is a difference in spawning time within the same species according to latitude and climatic factors. For instance, the spawning season of *L. fluviatilis* occurs between February and April on the upper Rhine River whereas it takes place from May to early July in the lower Neva River, Russian Federation (Maitland, 1980; Renaud, 2011). Applegate (1950) and Hardisty and Potter (1971) highlighted a clear relationship between changes in water temperature and the density of individuals at spawning sites in *L. planeri* and *P. marinus*. A decline in the numbers of individuals on the sites was indeed related to a slight drop in temperature below the critical spawning temperatures of the species (i.e. the temperature at which spawning is generally initiated: 10-11°C in *L. planeri* and 15°C in *P.*

*marinus*). Furthermore, by comparing the temperature data and the dates of peak spawning activity of a small population of *L. planeri* during four years, Hardisty and Potter (1971) showed the duration of the breeding season was related to temperature trends in March and early April but also to the density of the population. The season was typically short in years with consistently high temperatures and low population densities. Conversely, during years of higher relative abundance and variable temperatures, lampreys were observed on the spawning grounds for an extended duration. As temperature and density merge into one another, it is difficult to disentangle the relative role of each parameter. In the Pacific lamprey *Entosphenus tridentatus*, Clemens et al. (2009) demonstrated that maturation timing is more rapid under warm water temperatures, which raises questions about the potential impact this may have on reproductive fitness. To my knowledge, no study has yet investigated the effect of photoperiod on gonadal development, sexual maturation, or reproduction in lampreys.

Apart from temperature, the presence of pheromones plays a significant role in directing adult lampreys towards rivers that are suitable for spawning. A few studies have shown that adult lampreys were preferentially attracted to water containing ammocoetes and that the response was stronger when the number of ammocoetes was higher (Sorensen et al., 2005; Li et al., 2002). Interestingly, pheromones composition is not species-specific and induces the same behavioural response in a wide range of petromyzontids species (Fine et al., 2004), suggesting that they have been evolutionarily conserved. This may explain the occurrence of interspecific communal spawning between closely related species. If pheromones produced by a given species are attractive to other species, the spatial and temporal separation between sympatric interspecific populations may be limited. Moreover, there is some indication that non-parasitic lampreys may select larger and deeper nests of parasitic species to reduce the energetic costs of building nests, reduce predation risk and boost their reproductive success

by mating with larger individuals (Cochran et al., 2008). The occurrence of interspecific nest associations complicates the social structure in which individuals may interact as it induces strong variations in the phenotypic composition of sexually receptive individuals. Considering this more complex environment is particularly relevant in lampreys as sexual interactions between species may change the evolutionary outcomes only predicted in single species systems.

### 1.3.5 The role of sexual selection in sympatric speciation of lampreys

Although many researchers highlighted that non-parasitic lampreys are derived from parasitic lampreys, the mechanisms leading to divergence and reproductive isolation remain overlooked. The primary mechanism thought to play a role in the coexistence of parasitic and non-parasitic lamprey species living in sympatry is *size-assortative mating*, i.e. the tendency for individuals with a similar size to be more likely to mate with one another than would be expected under a random mating pattern (Hardisty and Potter, 1971; Beamish and Neville, 1992; Malmqvist, 1983). Due to the high size difference between adults of non-parasitic forms and parasitic forms (around 10-15 versus 20-40 cm), size-assortative has been hypothesized to act as a pre-mating barrier to gene flow between diverging populations. More specifically, it is believed that assortative mating occurs via mate choice and that individuals tend to *prefer* mates of similar size. However, the only experimental study investigating it was inconclusive due to the lack of adequate statistical analysis (Beamish and Neville, 1992).

Moreover, it remains uncertain whether the evolution of non-parasitic lampreys follows a step-wise pattern (from anadromous parasitic to dwarf freshwater residents, and finally to distinct non-parasitic species) due to the limited availability of systems that contain different life history strategies (Docker, 2019). In Japan, Iwata and Hamada (1986) and Yamazaki

et al. (1998) reported the presence of dwarf freshwater forms of the parasitic Arctic lamprey *L. camtschaticum*. The total length of the dwarf individuals was similar to those of individuals at metamorphosis and considerably shorter than that of mature anadromous individuals. Despite the large size difference due to their divergence in life history, the two types are morphologically identical at the opposite of the satellite brook lampreys that occur in sympatry (*L. reissneri* and *Lethenteron kessleri*, Yamazaki and Goto, 2000). The occurrence of sexually mature specimens of two different phenotypes, each representing an alternative life history strategy that belongs to a single species, provides a unique opportunity to test the potential of size-assortative mating as a pre-mating barrier to gene flow between diverging populations. The study of closely related species that have already diverged provides valuable insights into the barriers to hybridisation. However, the investigation of different life forms within the same species is even more compelling as it offers a deeper understanding of the initial steps of the reproductive isolation process and the role of sexual selection in it.

## 1.4 Thesis overview

### 1.4.1 Thesis objectives

Through this general introduction, I identified gaps emphasizing **(1)** biases in the way pre-copulatory sexual selection metrics are calculated, **(2)** a lack of knowledge on the influence of within-season fluctuations in demography on sexual selection, **(3)** the need to take into account complexity of social structure in sexual selection studies by incorporating the effect of heterospecifics or conspecifics with alternative life histories, **(4)**, especially for species such as lampreys for which mixed spawning grounds, involving highly contrasted phenotypes, are common. The general objective of this thesis work is therefore to investigate the effects of within-season variations in the social environment on the strength and direction of pre-copulatory sexual selection in lampreys and more precisely to better understand how social factors (OSR, phenotypic distribution) can shape the evolution of traits and behavioural responses. More specifically, this thesis aims to further our understanding of three broad questions:

**(1) How do changes in social context throughout a breeding season influence pre-copulatory sexual selection?** *(Chapter 2)*

**(2) How do variations in reproductive timing within and between sexes affect sexual selection?** *(Chapter 3)*

**(3) Can the intra-specific process of sexual selection lead to sexual isolation in sympatric species with synchronized breeding events?** *(Chapter 4)*

### 1.4.2 Manuscript organisation

This **Chapter 1** exposed the context of the thesis, introducing concepts related to the measurement of sexual selection, the potential sources of temporal fluctuation in the social environment of reproduction, and the relevance of lampreys as a biological system to explore these concepts. **Chapter** 2 firstly explores how changes in social context throughout a breeding season influence pre-copulatory sexual selection on morphological and behavioural traits in an experimental group of river lamprey *L. fluviatilis*. More precisely, I developed a model that decomposes the effect of individual traits on the two processes leading to mating success (i.e. number of mating attempts, probability of successful mating) to shed light on the part of the mating process that is affected by individual and social characteristics. **Chapter** 3 uses an agent-based model to explore how the degree of reproductive synchrony between and among sexes modifies the strength and direction of sexual selection. The output of this simulation approach was compared to the results of an experimental study on the European brook lamprey *L. planeri*. In an experimental group of Arctic lamprey (*L. camstschaticum*), **Chapter** 4 investigates how complexifying the social environment by incorporating the effect of conspecifics with distinct life history may explain the occurrence of alternative mating behaviours such as sneaking in lampreys and proposes insights on the potential mechanism behind sympatric speciation. While **Chapter** 2**,** 3 and 4 provide answers to the three main questions set out in the previous box, **Chapter** 5 presents a general discussion synthesizing my main research findings, the encountered obstacles but above all the research areas that require further investigation. **Appendix** A represents a parallel work I conducted during my thesis, mainly in collaboration with another PhD student, on the role of the substrate on the spawning preference and egg retention of river lamprey. **Appendix** B constitutes a collaborative work resulting from a scientific network gathering researchers and students, of which I was a member, working on demo-genetic agent-based models. This chapter provides useful

information for understanding the importance of explicitly modelling sexual interactions (as I did in **Chapter** 3) to explore the evolution of traits considering the dynamic aspects of mating opportunities.

Chapter 2

# The importance of considering temporal variations in mating opportunities

This section corresponds to an article accepted for publication in ***Animal behaviour***. The data used comes from an experiment conducted by Anne Michaud as part of her master's internship.

## Contents

## Considering temporal variations in mating opportunities: consequences on sexual selection estimates

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### Abstract

The strength of pre-copulatory sexual selection may vary within a breeding season depending on fluctuations in the social environment faced by active individuals. Here, we investigate within-season variations in pre-copulatory sexual selection in the river lamprey (*Lampetra fluviatilis*). We determined individual lifetime mating success in a group of 20 females and 15 males through constant video recording in an experimental aquarium. Among each sex, we calculated the potential strength of sexual selection and selection on identified traits (body size and temporal spawning patterns) at two different time scales: a fine-grained scale in which we considered mating events at daily time steps and a global scale in which we pooled

all mating events that occurred during the breeding season. We found a predictable change in the operational sex ratio that corresponded with a change in the opportunity for sexual selection in males. Selection on both male and female body size was stronger when active competitors were larger. In addition, the timing (onset and span) of both the male's and the female's reproductive activity affected the number of matings performed over the season with a strength dependent on individual body size. Overall, our study documented that river lampreys experience within-season changes in pre-copulatory sexual selection. Such temporal dynamics are important to consider, and we advocate for longitudinal observation of mating behaviour to complement traditional time-integrated estimation of mating success based on genetic parentage analysis or cross-sectional analysis.

**Keywords:** intra-sexual competition, mate choice, operational sex ratio, opportunity for sexual selection, selection gradient.

## 2.1 Introduction

Phenotypic variation found in natural populations is predicted by the strength and direction of selection pressures acting on heritable traits (Fisher, 1930; Lande and Arnold, 1983). Among these, sexual selection is any selection that is generated by differential access to opposite-sex mates and/or gametes (Andersson, 1994; Kokko et al., 2006; Shuker and Kvarnemo, 2021). In many animal taxa, the intensity of sexual selection varies among spatially isolated populations (e.g. McLain, 1982), demonstrating how ecological variables, such as population density (Pröhl, 2002) or habitat complexity (Myhre et al., 2013), may cause variations in sexual selection. Recently, a few studies have also shown that in long-lived animals, populations may experience different levels of sexual selection strength over time (e.g. reviewed by Siepielski et al., 2009), due to demographic or environmental changes between breeding cycles. These studies highlighted that selection strength can be correlated with the time period over which it is measured, and averaging values over long-term periods may misrepresent or underestimate the effect of selection on phenotypic evolution.

However, less is known about variation in sexual selection over the course of a breeding season and how it may also be driven by smaller-scale changes in environmental or social variables such as operational sex ratio (OSR, i.e. the ratio of sexually receptive males to females; Emlen and Oring, 1977) within a season. In populations with a biased OSR, the mate-limited sex is expected to compete more strongly for access to mates, and therefore to face stronger sexual selection (Emlen and Oring, 1977). The availability of sexually receptive individuals may change throughout the season, potentially affecting selection on phenotype. Indeed, the rate at which males and females become sexually receptive (e.g. due to differential maturation rates) or become sexually unavailable (due to parental care, gamete stock depletion or death; Kokko and Jennions, 2008) generates

fluctuations in OSR and heterogeneity in social structure. For instance, Kasumovic et al. (2008) showed within-season variation in OSR and density at different times of the breeding season in the golden orb-web spider (*Nephila plumipes*), leading to significant variation in the strength and direction of sexual selection on male body size between those sampling periods. Similarly, Wacker et al. (2014) highlighted within-season change in sexual selection in male two-spotted gobies (*Gobiusculus flavescens*), that aligns with a change in the OSR.

Nevertheless, most empirical studies, including those mentioned above, estimate mating success via cross-sectional analysis. In this approach, the population is sampled at one or a few particular points in time and individuals are not followed repeatedly during the breeding season. Thus, if mating success varies over the season, single estimates or cross-sectional estimates calculated from a few short time intervals may significantly over- or underestimate overall success. This is particularly true for species that mate several times and for which the duration of individual mating activity is short relative to the length of the breeding season. Although a few studies on hermaphrodites have already inferred mating success via intensive observations of individually tagged individuals (Anthes et al., 2010; Pélissié et al., 2012), none to our knowledge have used longitudinal behavioural data to examine how the selection operates when the social context changes. By ignoring the temporal variations in mating opportunities during a breeding season, traditional selection analysis assumes that small changes in demographics do not alter selection (Kasumovic et al., 2008; Wacker et al., 2014).

In the present study, we estimated pre-copulatory sexual selection throughout the breeding season of the European river lamprey (*Lampetra fluviatilis*) in an experimental setting. This biological model is relevant for studying within-season variation in sexual selection

as the OSR changes between breeding phases, from a majority of females during the nest-building phase, to a prevalence of males during the spawning phase, followed by a return to an excess of females at the end of the season (Jang and Lucas, 2005). Individuals mate frequently (up to 20 matings/h) with different partners on the same nest or on several nests successively, thus constituting a highly polygynandrous system (Docker, 2019). The brevity of the lamprey breeding season (a few weeks; Hardisty and Potter, 1971) as well as their semelparous reproductive strategy (Docker, 2019) makes it possible to observe in a relatively short time the overall mating success of all individuals studied. This point is essential, as it is net selection over an individual's lifetime that ultimately determines the overall response to selection on phenotypic traits (Blanckenhorn, 2000). To investigate potential changes in sexual selection, we calculated sexual selection metrics at a fine-grained scale that segments mating events at daily time steps. We then estimated overall sexual selection by pooling all mating events that occurred during the breeding season. The potential strength for sexual selection was first estimated by using a fitness variance-based approach (i.e. the opportunity for sexual selection $Is$, Crow, 1989; Wade, 1979) and a population-based approach (i.e. OSR, Emlen and Oring, 1977). Although these measures do not reflect the actual strength of selection acting on specific traits, they are essential to consider when the targets of selection are poorly known as in lampreys. We then used direct, trait-based measures of sexual selection (i.e. sexual selection gradients through two Bayesian models) to quantify actual mechanisms of selection on identified traits (body size and temporal spawning pattern). As mating success is usually estimated via genetic data, analysis of sexual selection treats male and female mating success independently and ignores the fact that the success of a male-female sexual interaction can be attributed to the phenotypes of both individuals in a specific demographic context. Using constant behavioural data allowed us to incorporate this aspect as well as disentangle pre-copulatory components of mating success and investigate the traits that affect each of them.

In our study, we considered mating success as a sequence of two interdependent pairwise processes: the number of mating attempts and the probability of successful mating. A first Bayesian model, considering mating interactions at daily time steps, therefore aimed to define how daily variation in social environment (i.e. OSR, size of current competitors) impacted the two processes leading to mating success (i.e. number of mating attempts, rate of successful mating). First, we expected larger males and larger females to mate more successfully as body size generally influences success during intrasexual mate competition (Hunt et al., 2009; Malmqvist, 1983). We also suspected that probability of mating successfully would be higher in pairs of similar size as Hardisty and Potter (1971) predicted that size-assortative mating may occur in lampreys. Then, we predicted interactive effects between individual phenotype and social environment. For instance, we expected that the potentially positive effect of individual body size would be stronger in a more competitive environment. At the scale of the whole breeding season, a second Bayesian model aimed at investigating whether processes leading to mating success were impacted by temporal characteristics of mating activities that may be under selection. We expected that individuals starting early in the season and distributing their mating effort over a long period may experience a higher number of mating attempts. Finally, the interaction between body size and temporal distribution of mating activity was tested, since the fitness benefit of adopting a given temporal distribution may depend on individual phenotype. For example, smaller individuals may compensate for a lower competitive ability by concentrating their mating activity in a shorter time.

## 2.2 Methods

### 2.2.1 Study species

The river lamprey is an externally fertilising fish that spawns in nests hosting groups of two to 50 individuals (Jang and Lucas, 2005; Lasne et al., 2010) and whose mating act consists of a fixed sequence of recognizable behaviours: female positioning, male mounting (i.e. attaching his mouth to the female's head), tail wrapping and squeezing (Docker, 2019), followed by simultaneous release of gametes, when the pair quivers for approximately 2 s. Such distinctive behaviours allow us to visually discriminate the focal individuals during copulations. This parasitic species is suited for experimental behavioural studies as it can reproduce in captivity (Hagelin, 1959) and tolerates the close presence of observers (Lasne et al., 2010; Yamazaki and Koizumi, 2017).

### 2.2.2 Field collection and maintenance

Individuals were collected in early spring 2019 (between 15 and 26 March) as river lampreys spawn between April and June (Hardisty and Potter, 1971). Thirty-five individuals (20 females, 15 males) were captured during their upstream migration on the Garonne river (south-west France) by professional fishermen, and transferred to the INRAE experimental facilities (ECP, *https://doi.org/10.15454/1.5572402068944548E12*) in Saint-Pée-sur-Nivelle, France. Lampreys were acclimated for 1-3 weeks (according to the fishing date) in tanks supplied with Nivelle river water to avoid behavioural changes due to physical and chemical properties of the water during the experiment. Although the chemical composition of Garonne and Nivelle rivers probably differ, our set-up mimicked a situation in which river lampreys migrate from the main stem of a watershed to a small tributary with a different water chemistry. Each individual was tagged with a unique combination of three spots of UV-fluorescent visible implant

elastomer (yellow, orange, red or blue) injected in the posterior dorsal fin to allow individual recognition under both white light and UV light (Silver et al., 2009). We measured two morphological traits: total body length (±0.5 mm) and total mass (±0.5 g). The two traits may be targeted by sexual selection (Malmqvist, 1983) and their combination is an indicator of fish condition (i.e. their quality and fecundity). Biometry and tagging were performed after fish were placed in an anaesthesia tank containing benzocaine solution (0.3ml/litre) for 5 min.

### 2.2.3 Experimental set-up

The experiment took place in a 4 $m^3$ (10 x 1 m and 0.4 m water depth) longitudinal section of a large 25 m3 circular flume, supplied with water from the Nivelle river in a semi-open circuit, with water replacement of 6 litres/min. To mimic natural spawning conditions, current speed was set to 0.3 m/s, spawning substrate and shelters (tiles, woody debris) were provided, and water temperature (known to affect spawning activity, Hardisty and Potter, 1971) was monitored daily and followed that of the river (between 14 and 18°C). To facilitate observation, spawning substrate was limited to two 0.48 m2 (0.6 x 0.8 m) boxes placed 5 m from each other, and filled (0.1 m depth) with a mixture of sand, gravels and pebbles corresponding to the spawning habitat selected by river lampreys in natural environments (Jang and Lucas, 2005). The aquarium was lit with white neon bulbs following the natural photoperiod (12:12 h with 30 min of dawn and dusk), but as river lampreys are active 24 h per day during the spawning period (Sjoberg, 1977), we placed a UV light above the substrate boxes to identify individuals at night. Two video cameras (Basler acA1920-40gc) continuously recorded lampreys' activity in each spawning patch throughout the experiment. The flume section was inspected three times a day (morning, noon, evening) to ensure that no spawning occurred outside the spawning substrate, and to collect dead individuals). All individuals were placed in the experimental tank on 3 April and the experiment ended on 3 May, after the death of the last individual.

### 2.2.4 Mating characterisation

All video footage was analysed with BORIS software (Friard and Gamba, 2016) to note the exact timing of each behaviour and the identity of the individuals involved. Numerous attempts to copulate were interrupted before the male could squeeze the female's abdomen. We therefore discriminated successful matings acts (i.e. those ending with squeezing and quivering) from failed mating attempts. Each successful mating act usually involved one male and one female but sometimes two or more males copulated simultaneously with the same female, as highlighted by previous studies (Case, 1970; Docker, 2015; Huggins and Thompson, 1970; Malmqvist, 1983). In that case, the identity of each male involved was noted, so that the female was considered to have successfully mated with each of them.

### 2.2.5 Definition of mating success

Considering lampreys' mating system, (external fertilisation, high polygynandry, very frequent matings), the classic genetic view of mating success (i.e. number of different individuals with which the focal individual produced at least one offspring) may show little inter-individual variation, while a behavioural view that quantifies the number of mating events may represent more accurately the link between an individual's phenotype, its social environment and its ability to secure matings. Thus, we first calculated $MS_P$, defined as the number of *partners* with which the focal individual successfully mated to fit the genetic definition of mating success. Then, we calculated $MS_M$ as the number of *successful mating acts* performed by the focal individual with all its mates to match the behavioural definition of mating success.

### 2.2.6 Estimation of potential strength of sexual selection

We first characterised the potential strength of sexual selection by calculating the opportunity for sexual selection ($Is$) at the scale of the whole season. We measured $Is$ for each sex as

the variance in mating success (i.e. both as the number of mates, $MS_P$, and the number of matings, $MS_M$) divided by the square of the mean mating success (Wade, 1979; Wade and Arnold, 1980). Recent research showed that $Is$ is connected to OSR, even in the absence of sexual selection as a result of a decreased mean mating success of the dominant sex (Jennions et al., 2012; Klug et al., 2010*a*; Krakauer et al., 2011). To consider this source of bias, we therefore evaluated the expected $Is$ under random mating given the observed OSR and mean mating success, as recommended by Janicke and Morrow, 2018. For this purpose, we randomly distributed the total number of mating acts among all individuals in each sex. We iterated this distribution 10000 times in R and we subtracted the median $Is$ of these simulations from the observed $Is$. The number obtained was defined as the bias-corrected $Is$ (hereafter $Is_{bc}$). We also report 95% confidence intervals for all estimates of $Is_{bc}$ obtained from the simulations. When simulating $MS_P$, care was taken to ensure that no individual was assigned a higher mating success than the actual total number of individuals of the opposite sex. Sex-specific differences in variances were also assessed using Levene's F test.

We then split the breeding season into 22 daily periods, which allowed us to assess both among-days variation in the social environment and a large number of mating events within each day. In the same way as above, we analysed potential variation in the strength of sexual selection by calculating $Is_{bc}$ each day. We then calculated OSR for each day as the ratio of sexually receptive males to females. Individuals were considered sexually receptive from their first mating attempt until their death, as there is no post-mating refractory period in male and female lampreys (L. Daupagne, personal observation). We also calculated what we called the functional sex ratio (FSR) on each day as the ratio of sexually active males to females (i.e. individuals that actually attempted to copulate on that day). We then calculated correlations between $Is_{bc}$ and OSR using a Spearman' rank correlation test. Indeed, as stated by Emlen and

Oring, 1977, a biased OSR should induce a greater variance in mating success of the dominant sex due to a higher degree of mate monopolisation, and therefore a greater $Is_{bc}$.

### 2.2.7 Quantitative estimation of sexual selection on identified traits

Instead of the classic multiple regression approach (e.g. Lande and Arnold, 1983), which separately models the mating success (number of mates) of either males or females as a linear combination of individual phenotypic traits and possibly social environment (Okasha, 2004), we considered each mating act as a statistical unit, following the approach of Gauthey et al., 2017. In our first Bayesian model, we considered parameters reflecting changes in the social environment each day that may affect sexual selection estimates: 1) individual body size of both interacting partners, (2) size difference between partners, (3) OSR, (4) average competitors' size relative to the size of the focal individual, and (5) the time since the start of the individual's reproductive period. Competitors were defined as individuals of the same sex as the focal individual and were sexually receptive on the focal day (i.e. those contributing to the OSR). The last parameter (5) may reflect variation in mating effort over an individual's reproductive period. We first checked for correlation between morphological traits (body size and body mass) with a Spearman' rank correlation test. As they was a significant correlation ($p$ = 0.76), only total body size was included in our analysis. From daily behavioural observations, we constructed two different matrices confronting all possible pairs of individuals of each sex each day: a first three-dimensional array of the total number of mating attempts between each male $m$ and female $f$ on day $t$ ($A_{(m,f,t)}$), and a second three-dimensional array of the total number of successful matings ($C_{(m,f,t)}$) between each male $m$ and female $f$ on day $t$. The number of mating attempts was modelled by a Poisson distribution and the number of successful matings was modelled by a binomial distribution.

$$\begin{aligned} A_{m,f,t} &\sim Poisson(T_{m,f,t}) \\ C_{m,f,t} &\sim binomial(A_{m,f,t}, \theta_{m,f,t}) \end{aligned} \tag{2.1}$$

We tested the effects of body size of the focal male and female ($S_m$ and $S_f$, respectively), the absolute difference in partner size ($abs(S_m - S_f)$), the average competitors' size relative to the size of the focal individual on day $t$ (($CSM_t - S_m$) and ($CSF_t - S_f$)), the OSR on day $t$ ($OSR_t$) and time (days) since the start of the individual's reproductive period ($RP_{m,t} - RP_{f,t}$) on the number of mating attempts ($T_{m,f,t}$, Eq. 2.2) and on the probability that a mating attempt was successful ($\theta_{m,f,t}$, Eq. 2.3). Because our goal was to test whether selection on an individual trait depended on the social context, we also included interaction terms as follows:

$$\begin{aligned} T_{m,f,t} = \exp(&\alpha_1 + \beta_1 S_m + \beta_2 S_f + \beta_3 abs(S_m - S_f) + \beta_4 OSR_t + \beta_5 (S_m * OSR_t) \\ &+\beta_6 (S_f * OSR_t) + \beta_7 (CSM_t - S_m) + \beta_8 (CSF_t - S_f) + \beta_9 RP_{m,t} \\ &+\beta_{10} RP_{f,t} + r_{1,m} + r_{1,f}) \end{aligned} \tag{2.2}$$

$$\begin{aligned} \theta_{m,f,t} = inv.logit(&\alpha_2 + \beta_{11} S_m + \beta_{12} S_f + \beta_{13} abs(S_m - S_f) + \beta_{14} OSR_t \\ &+\beta_{15} (S_m * OSR_t) + \beta_{16} (S_f * OSR_t) + \beta_{17} (CSM_t - S_m) \\ &+\beta_{18} (CSF_t - S_f) + \beta_{19} RP_{m,t} + \beta_{20} RP_{f,t} + r_{2,m} + r_{2,f}) \end{aligned} \tag{2.3}$$

where $r_{.,m}$ and $r_{.,f}$ are random male and female effects (individuals' effects) to better account for uncontrolled sources of variation.

Then, we constructed a second Bayesian model to test how mating success could be affected by two variables pertaining to the temporal distribution of mating effort: date of first mating attempt and delay between first and last mating attempt (i.e. duration of mating activity). From behavioural observations, we constructed two different matrices confronting all possible pairs of individuals of each sex: a first matrix of the total number of mating attempts over the whole breeding season ($A_{m,f}$) and a second matrix of the total number of successful matings ($C_{m,f}$). The number of mating attempts between a pair was modelled by a Poisson distribution while the number of successful matings was modelled by a binomial distribution.

$$\begin{aligned} A_{m,f} &\sim Poisson(T_{m,f}) \\ C_{m,f} &\sim binomial(A_{m,f}, \theta_{m,f}) \end{aligned} \tag{2.4}$$

We tested the effects of body size of focal male and female (respectively $S_m$ and $S_f$), absolute difference in partner size ($abs(S_m - S_f)$), mating activity first date ($I_m$ and $I_f$) and duration of mating activity ($D_m$ and $D_f$) on both the number of mating attempts ($T_{m,f}$, Eq. 2.5) and on the probability of mating success ($\theta_{m,f}$, Eq. 2.6) as follows:

$$\begin{aligned} T_{m,f} \sim \exp(&\alpha_1 + \beta_1 S_m + \beta_2 S_f + \beta_3 abs(S_m - S_f) + \beta_4 I_m + \beta_5 I_f + \beta_6 D_m + \beta_7 D_f \\ &+\beta_8 (S_m * I_m) + \beta_9 (S_f * I_f) + \beta_{10} (S_m * D_m) + \beta_{11} (S_f * D_f) \\ &+r_{1,m} + r_{1,f}) \end{aligned} \tag{2.5}$$

$$\begin{aligned} \theta_{m,f} \sim inv.logit(&\alpha_2 + \beta_{12} S_m + \beta_{13} S_f + \beta_{14} abs(S_m - S_f) + \beta_{15} I_m + \beta_{16} I_f \\ &+\beta_{17} D_m + \beta_{18} D_f + \beta_{19} (S_m * I_m) + \beta_{20} (S_f * I_f) \\ &+\beta_{21} (S_m * D_m) + \beta_{22} (S_f * D_f) + r_{1,m} + r_{1,f}) \end{aligned} \tag{2.6}$$

where $r_{.,m}$ and $r_{.,f}$ are random male and female effects to better account for uncontrolled sources of variation.

### 2.2.8 Statistical analysis

All classical statistical analyses were performed using R software version 4.0.4 (R Core Team, 2022). Average values presented throughout the paper correspond to the mean. The two statistical models in this study were fitted under a Bayesian framework that allows the handling of a large number of predictor variables using HMC sampling applied by STAN through the R package RStan (Carpenter et al., 2017). For each model, three independent chains were run to save 5000 iterations after a warmup of 1000 iterations and with a thinning of 5. In each chain, we used a non-informative Cauchy distribution for all parameters ($C(0, 5)$, Gelman et al., 2008. Chain convergence was visually checked and parameter convergence was assessed with the Gelman and Rubin's convergence diagnostic (gelman.diag function, Brooks and Gelman, 1998; Gelman and Rubin, 1992. Each parameter was considered as significant if 0 was not included in its highest density interval at 95% ($HDI_{95\%}$). Information on the validation of the models is provided in the Appendix (Fig. 2.A.7, 2.A.10 and Tab. 2.A.1, 2.A.2).

### 2.2.9 Ethical note

The use of experimental animals complied with the French environmental and animal welfare laws, guidelines and policies as evidenced by the authorization issued by the ethical committee for birds and fishes in the French region Nouvelle Aquitaine (authorization #2019021009248986). The potential harm to the animals is very limited and mainly concerns exposure to electricity during fishing, tagging under anaesthesia and keeping the individuals in an aquarium during reproduction. Lampreys are semelparous and die shortly after reproduction. Thus, the condition of the individuals deteriorates very rapidly during reproduction,

even in the natural environment. We did not observe any pre-mating mortality (the dead individuals had all participated in reproduction and contained no or very few gametes).

## 2.3 Results

### 2.3.1 General description of the mating system

Body size and weight did not differ between the sexes: males measured on average (±SD, minimum:maximum) 282.9 mm (±21.7, 237:315) while females measured on average 284.2 mm (±16.9, 250:316). The mating season, calculated as the time between the first and last day on which matings were observed, lasted 22 days. The first mating attempts occurred on 9 April while the last one occurred on 30 April. Differences existed in terms of temporal distribution of mating effort: females took part in the spawning during a much shorter period than males in terms of number of days between the first and last mating attempt (Fig. 2.1), on average 6.5 days in females and 14 days in males (ANOVA: $F_{1,33}$ = 42.88, $P$ < 0.001). The females started to mate on average later than males (ANOVA: $F_{1,33}$ = 4.74, $P$ = 0.03) and more gradually. Differences also appeared in terms of number of days between the last mating attempt observed and the day of death: females died much faster than males (Fig. 2.1), on average 1.5 days in females and 3.5 in males (Kruskal-Wallis test: $H_{11}$ = 9.16, $P$ < 0.001). This sex-specific temporal distribution of mating effort led to fluctuations in size distribution of active individuals (Appendix Fig. 2.A.1). A total of 8582 mating attempts were observed, among which 6815 were successful matings. The mating system clearly can be qualified as polygynandrous, as the 15 males successfully mated on average (±SD, minimum:maximum) 454.33 (±355.82, 17:1088) times with on average 14.73 (±2.91, 9:20) females, and the 20 females mated on average 340.75 (±222.52, 8:897) times with on average 11.05 (±3.22, 4:15) males. The number of successful matings was correlated with the number of mates for males (Spearman rank correlation: $r_s$ = 0.7, $N$ = 15, $P$ < 0.005) but not for the females ($r_s$ = 0.29, $N$ = 20, $P$ = 0.21).

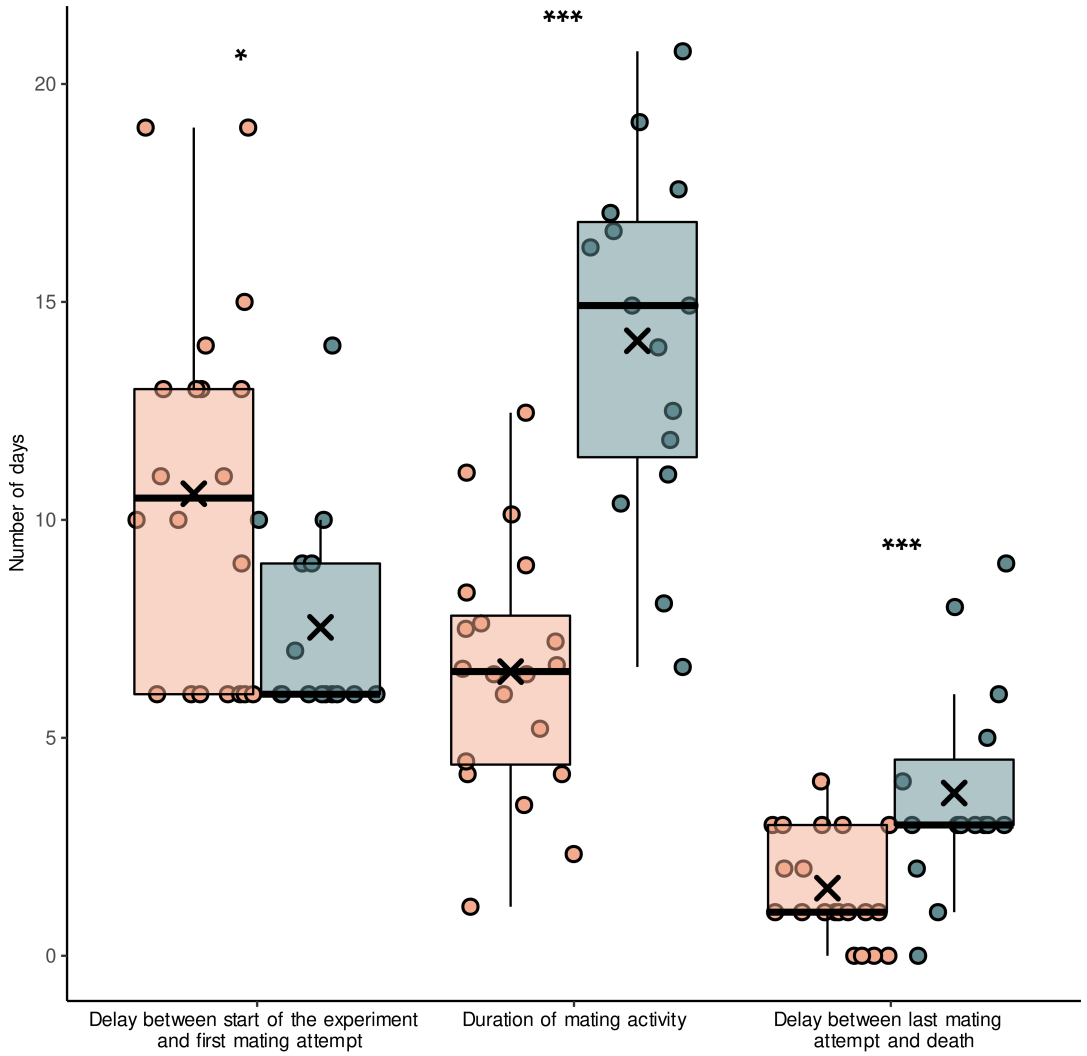


**Figure 2.1.** Delay between the start of the experiment and the first mating attempt, duration of mating activity and delay between the last mating attempt and death (days) in 15 *Lampetra fluviatilis* males (blue) and 20 *L. fluviatilis* females (orange). The box plots show the median (horizontal line), mean (cross) and $25^{th}$ and $75^{th}$ percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are the jittered data points. Tests: one-way ANOVA/Kruskal-Wallis. *: $P < 0.05$, ***: $P < 0.005$.

### 2.3.2 Estimation of potential strength of sexual selection

#### 2.3.2.1 At daily time steps

The OSR and FSR were on average (±SD, minimum:maximum) 1.97 (±0.90, 1.08:3. 67) and 1.7 (±0.69, 0.75:3), respectively (Appendix Fig. 2.A.2). The indices were highly correlated (Spearman rank correlation, $r_s$ = 0.76, $N$ = 20, $P$ < 0.001), so only OSR was used in further analysis. The $Is_{bc}$ with $MS_P$ was on average (±SD, minimum:maximum) 0.38 (±0.59, -0.49:1.85) per day in males and 0.54 (±0.52, -0.33:1.48) per day in females (Appendix Fig. 2.A.3, a). $Is_{bc}$ with $MS_M$ was on average (±SD, min:max) respectively 1.92 (±1.24, 0.46:5.57) per day in males and 2.07 (±1.05, 0.93:5.96) per day in females (Appendix Fig. 2.A.3, b). A Spearman rank correlation was computed to assess the relationship between $Is_{bc}$ and OSR in each sex (Appendix Fig. 2.A.4). There was a positive correlation between the two variables in males when $Is_{bc}$ was calculated with MSB (rs = 0.53, N = 20, P = 0.01) but not with $MS_P$ ($r_s$ = -0.12, $N$ = 20, $P$ = 0.60). There was no significant correlation in females with $Is_{bc}$ calculated with either $MS_M$ ($r_s$ = 0.38, $N$ = 20, $P$ = 0.07) or MSG ($r_s$ = 0.15, $N$ = 20, $P$ = 0.49).

#### 2.3.2.2 At the scale of the whole breeding season

The $Is_{bc}$ with $MS_P$ was slightly lower for males than for females while the $Is_{bc}$ with $MS_M$ was higher for males (Table 2.1). Variances in relative mating success were not significantly different as a function of sex, either for $MS_P$ or $MS_M$ ($F$ = 2.08, $P$ = 0.16 and $F$ = 0.76, $P$ = 0.39 respectively, Table 2.1).

**Table 2.1.** Estimates of mating success and the potential strength of sexual selection in *Lampetra fluviatilis* males and females at the scale of the whole breeding season. Number of individuals ($N$), mean mating success, standard deviation (SD), observed opportunity of sexual selection ($ObsIs$), and bias-corrected $Is$ ($Is_{bc}$) are presented with mating success calculated either as the number of mates ($MS_P$) or the number of mating acts ($MS_MB$). Differences in variances for mating success were estimated via Levene's test.

| | **Males** | | | | | **Females** | | | | | **Levene's test** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $N$ | $Mean$ | $SD$ | Obs$Is$ | $Is_{bc}$ | $N$ | $Mean$ | $SD$ | Obs$Is$ | $Is_{bc}$ | F | Df | P |
| $MS_P$ | 15 | 14.7 | 2.9 | 0.03 | -0.01 | 20 | 11 | 3.2 | 0.08 | 0.03 | 2.08 | 1 | 0.16 |
| $MS_M$ | 15 | 454 | 356 | 0.61 | 0.60 | 20 | 341 | 223 | 0.43 | 0.41 | 0.76 | 1 | 0.39 |

### 2.3.3 Quantitative measure of sexual selection

#### 2.3.3.1 At daily time steps: variation in the social environment

Female body size had a negative effect on the number of mating attempts but a positive effect on the probability of mating success, while male body size had a positive effect on the number of mating attempts but a negative effect on the probability of success (Fig. 2.2a). Difference in partner size had a negative effect on both the number of mating attempts and the probability of mating success (Fig. 2.2b). The OSR had a negative effect on the number of mating attempts but had no effect on the probability of success (Fig. 2.2c). In both sexes, the interaction between body size and OSR had a positive effect on the number of mating attempts (Fig. 2.2d,2.3a,c). In males, the interaction had a negative effect on the probability of mating success (Fig. 2.3d) while the interaction had a positive effect in females (Fig. 2.2d, 2.3b). In males, the average size difference between the focal individual and its competitors had a positive effect on the number of mating attempts but a negative effect on the probability of mating success while in females, it had a negative effect on the number of mating attempts but a positive effect on the probability of success (Fig. 2.2e). Finally, in males, the time (days) since the start of the individual's reproductive period had a negative effect on the number of mating attempts, while in females, it had a positive effect on the number of mating attempts but a negative effect on the probability of success.

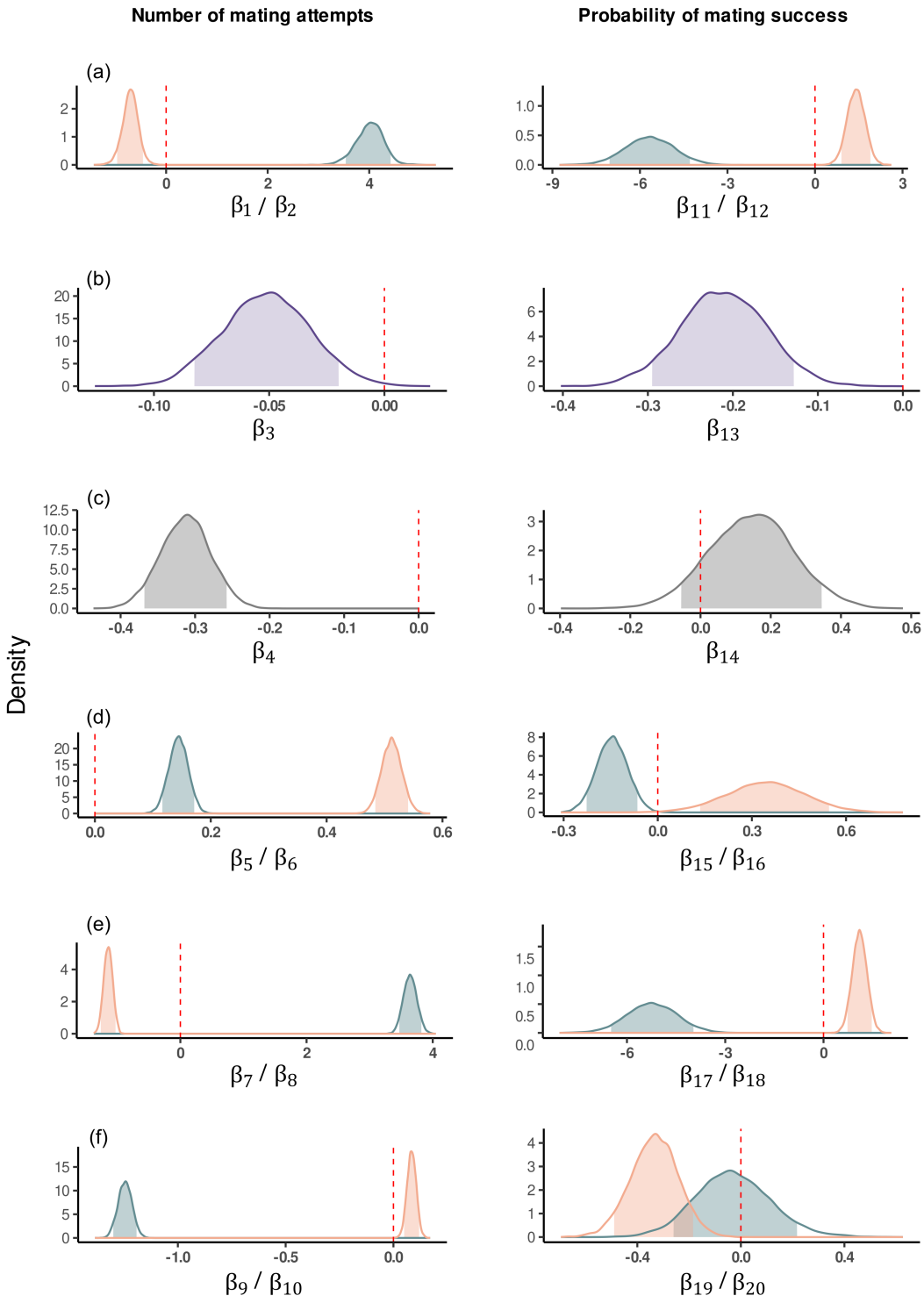


**Figure 2.2.** Posterior distribution for the parameters of the model inferring the effect of (a) individual body size, (b) difference in partner size, (c) operational sex ratio (OSR), (d) interaction between individual body size and OSR, (e) difference in competitors' size and individual body size and (f) time since the start of an individual's reproductive period in males (blue) and females (orange) on the number of mating attempts and on the probability of mating success. Labels on the x-axes refer to parameters presented in Eq. 2.2 and 2.3. Density plots show the distribution of the parameter values sampled from 12000 iterations. The coloured portions inside the density plots represent the 95% credible intervals. The dashed red vertical lines correspond to a null effect.

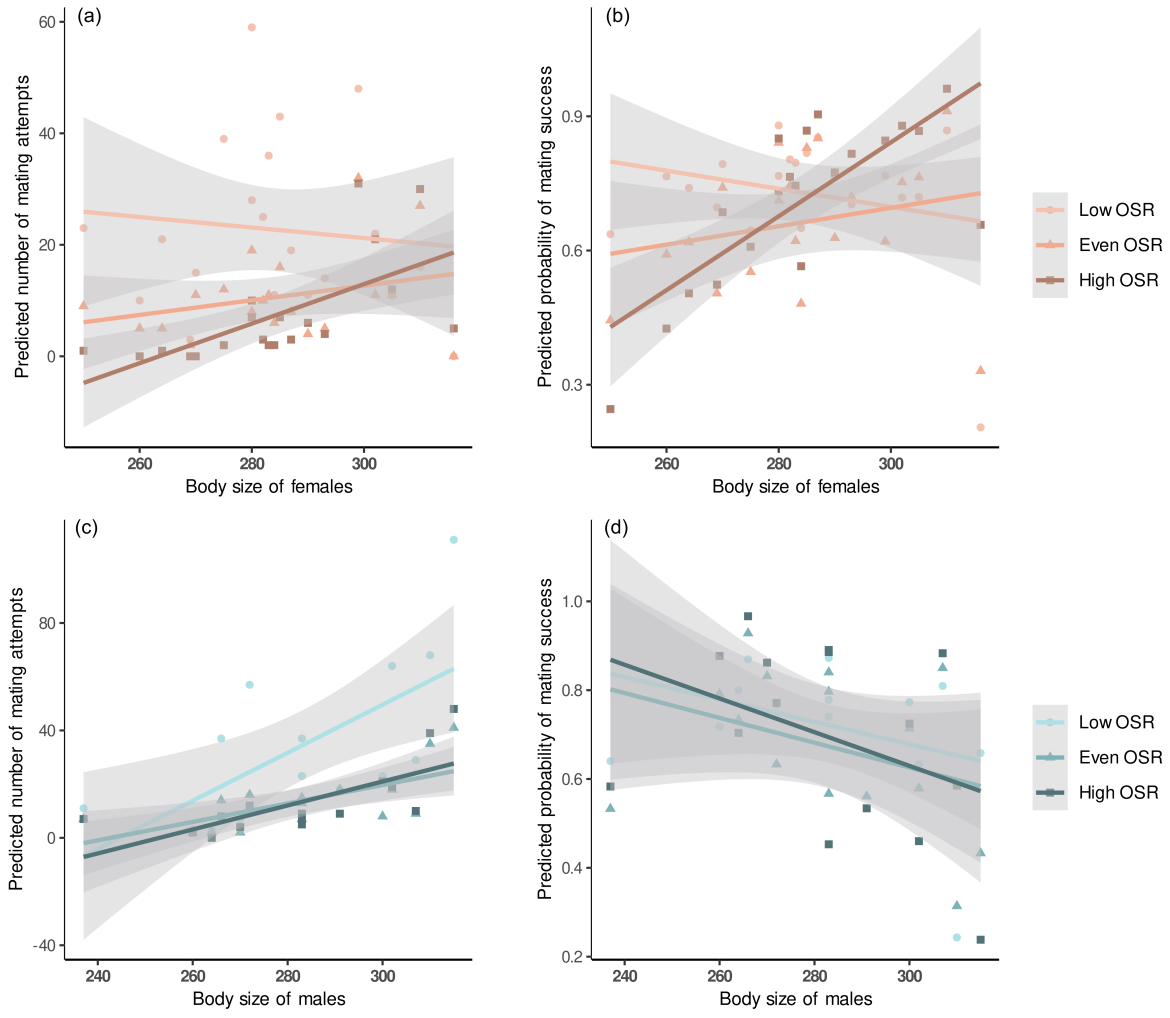


**Figure 2.3.** Predicted number of mating attempts and probability of mating success in males (blue) and females (orange) at low, even and high operational sex ratio (OSR). The grey areas represent the 95% confidence level interval for predictions from each linear model.

#### 2.3.3.2 At the scale of the whole season: temporal spawning patterns

In either sex, body size had overall no effect on either the number of mating attempts or the probability of mating success (Fig.2.4a). The difference in partner size had a negative effect on both the number of mating attempts and the probability of mating success (Fig. 2.4b). The first date of mating activity had a positive effect on the number of attempts and a negative effect on the probability of mating success in females, but it had no effect on both metrics in males (Fig. 2.4c). The total duration of mating activity had no significant effect on either the number of mating attempts or the probability of success in either sex (Fig. 2.4d). The interaction between body size and the first date of mating activity had a negative effect on the number of mating attempts in females and a positive effect on the probability of success, while it had no effect on both metrics in males (Fig. 2.4e). Finally, the interaction between body size and duration of mating activity had no significant effect on either the number of mating attempts or the probability of success in either sex (Fig. 2.4f).

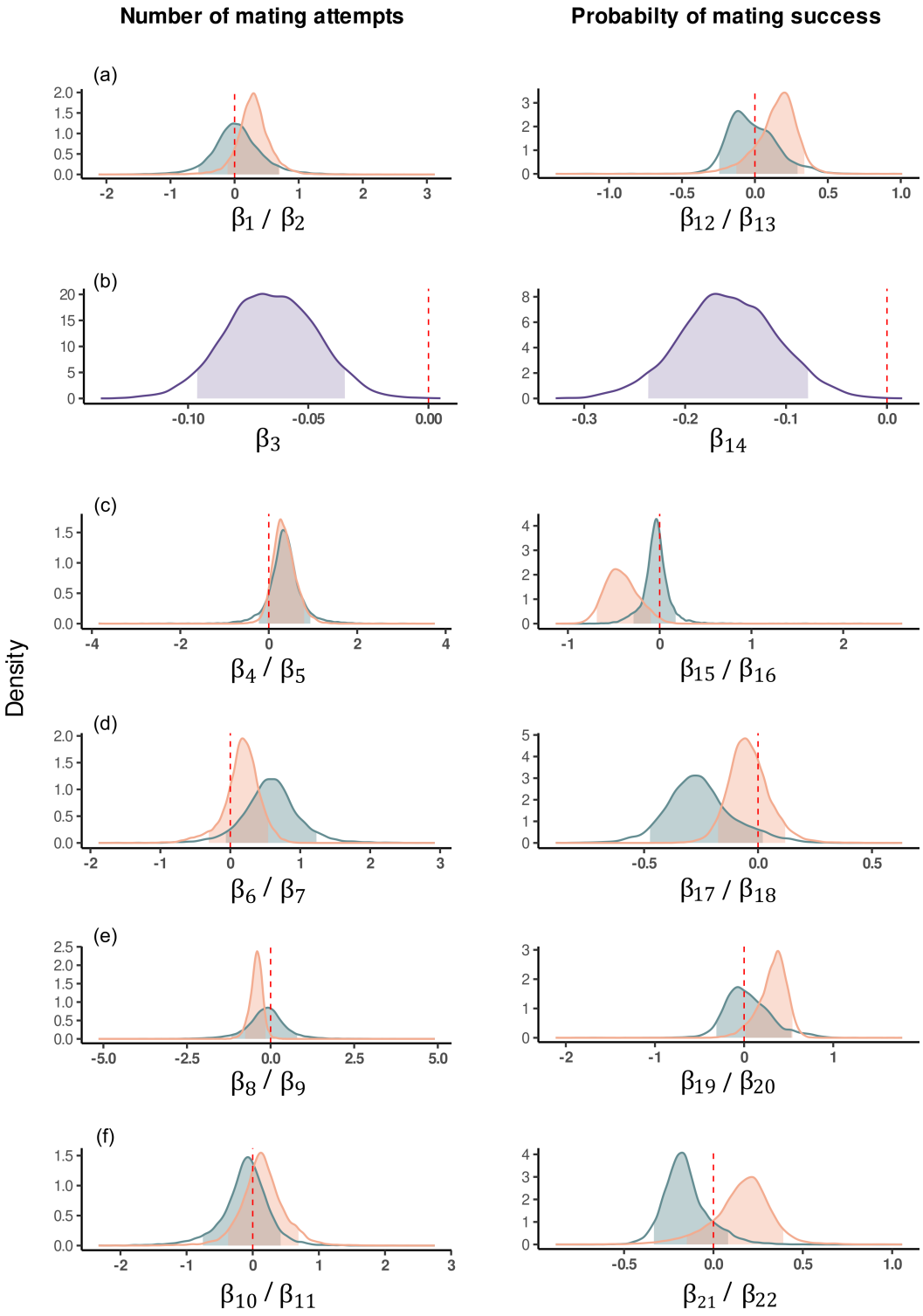


**Figure 2.4.** Posterior distribution for the parameters of the model inferring the effect of (a) individual body size, (b) difference in partner size, (c) first date of mating activity, (d) total duration of mating activity, (e) interaction effect between body size and first date of mating activity and (f) interaction between body size and duration of mating activity in males (blue) and females (orange) on the number of mating attempts and the probability of mating success at the scale of the whole breeding season. Labels on the x-axes refer to parameters presented in Eq. 2.5 and 2.6. Density plots show the distribution of the parameter values sampled from 12000 iterations. The coloured portions inside the density plots represent the 95% credible intervals. The dashed red vertical lines correspond to a null effect.

## 2.4 Discussion

Our results showed that (1) the social environment (OSR, body size distribution of active individuals) fluctuated throughout the breeding season of a group of river lamprey in controlled conditions, (2) the number of matings on a given day depended on individual body size, social environment on that day, and their interaction, and (3) the timing (onset and span) of breeding activity could affect the number of matings performed over the season with a strength dependent on individual body size. We discuss the implications of these findings in terms of both sexual selection in lampreys and broader meaning for sexual selection estimation in polygynandrous external fertilisers.

Despite a female-biased adult sex ratio (0.75) in the breeding group, the OSR was always male-biased and varied throughout the reproductive season (Fig. 2.A.2), because of sex differences in the onset and time span of sexual activity (Fig. 2.1). While most males were active from the beginning of the season and stayed active on average for 15 of the 22 days during which the group spawned, individual females started their activity in a more gradual way and for on average 6.5 days. Such patterns have also been documented in the brook lamprey (*Lampetra planeri*) in an experimental approach (Malmqvist, 1983) and in the sea lamprey (*Petromyzon marinus*) in the field (Dhamelincourt et al., 2021). Although the water recirculation in our experimental set-up may have increased the synchrony of sexual maturation due to an accumulation of sex pheromones throughout the experiment, this result suggests this is not the case or that such an acceleration of maturation also occurs in the wild, for example, when spawning densities upstream are high (Wang et al., 2013). Besides the span of reproductive activity, the time between last mating and death was shorter in females than in males, further suggesting that the rapid senescence triggered by reproduction was more acute in females than in males. This sex difference in the timing of reproduction therefore

led to the observed biased OSR (Fig. 2.A.2), causing fluctuations in the social environment in which sexual selection operates. We then found a positive correlation between OSR and bias-corrected opportunity for sexual selection $Is_{bc}$ with $MS_M$ in males but not females (Fig. 2.A.4, a), as originally suspected by Emlen and Oring (1977) and recently observed by Janicke and Morrow (2018) in a meta-analysis performed on 82 estimates of $Is_{bc}$ in 58 animal species. Additionally, female $Is_{bc}$ with $MS_M$ was insensitive to OSR and remained sufficiently high to equal male $Is_{bc}$ when cumulated over the whole season (Tab. 2.1). This indicates that there was as much scope for sexual selection in females as in males in this polygynandrous system, but that the availability of males was not the factor that constrained the variability of access to mates and matings among females. Outcompeting rivals probably do not bring significant direct or indirect benefits, leading to an overall less pronounced mate monopolisation in females. Interestingly, no correlation between OSR and $Is_{bc}$ with $MS_P$ was found in males (Fig. 2.A.4, b), showing that the chosen quantitative approach to measure mating success does affect the inference of sexual selection. By approximating the number of mating events with the number of mates, the "genetic definition" of mating success cannot detect potential multiple inseminations and thus the degree of mate monopolisation. This first analysis, by using a population and a fitness-based approach, highlighted that changes in the social environment affect both males' access to reproduction in terms of the number of matings achieved and, consequently, the potential strength of sexual selection in this sex.

With a statistical framework that models each mating as a two-step process (attempt and success; Gauthey et al., 2017), we then investigated how these changes in social environment directly modulate the strength of sexual selection on individual phenotypic traits. The distinction between the number of mating attempts and the probability of success sheds light on the part of the mating process that is affected by individual and social characteristics.

We showed that social context affected each part of the process both directly and through interactions with individual phenotype. In our model, larger males appeared to attempt more matings, but smaller males had a higher probability of mating successfully. This pattern was even stronger on days with higher OSR, as large males performed better in terms of mating attempts, but smaller individuals had an even higher probability of mating successfully (Fig. 2.2, 2.3). The first result was in line with our predictions, as we initially expected that larger males would have an overall advantage in intrasexual mate competition and thus have easier access to females, especially at a male-biased OSR. On the other hand, the higher probability of mating success in small males was more surprising as we initially thought that females would overall favour large males. This pattern may reflect either a female preference towards smaller males that can be expressed more freely under high OSR, or the choice of small males to mate with lower-quality females that might accept them more easily, especially when the competition is high (see below). Our model also highlighted that size-assortative mating does occur in lampreys, as suggested by previous work (Malmqvist, 1983), and concerns both processes leading to mating (attempt and success). The higher probability of success in pairs with similar size may be due to a physical constraint imposed by size differences between partners while the higher number of attempts in pairs with similar size may result from a mate choice in relation to one's own size. This latter may explain the higher probability of mating success in small males, especially at a high OSR. If male-male competition is sufficiently costly, the benefits conferred by mating with large females are outweighed, which may ultimately lead low-competitive males (i.e. small males) to attempt to mate with small low-quality females (i.e. small females) that would accept them more easily. The higher probability of mating successfully in small males is therefore the result of a size-assortative mating pattern based on mate choice.

The social context affected the number of matings in females too. High OSR increased both the number of mating attempts and the probability of success for large females. This suggests that under stronger male-male competition, larger females are more often solicited by males and accept mating more readily. Lamprey females parcel their large egg stock (around 26 000 in the anadromous river lamprey; Docker, 2019) in many clutches (on average 341 in this study). Larger females bear more eggs and may therefore mate with more males, which could benefit them directly and indirectly. A direct benefit of female multiple mating in lampreys may be insurance against incomplete fertilisation due to sperm limitation. On the other hand, indirect genetic benefits may include (1) improved viability or competitiveness of their offspring or (2) higher genetic diversity of offspring which may increase the possibility that some individuals can survive in a changing environment (Fox and Rauter, 2003; Garcia-Gonzalez et al., 2015; Yasui, 2001). Finally, compared to their competitors the smaller females seemed to attempt fewer matings but had a higher probability of mating successfully. This suggests that small females are solicited even less by males when competition is high and therefore more readily accept mating.

Given the interactions between individual phenotype and fluctuating social environment, and the sex difference in the temporal distribution of reproductive activity, one could expect to see sexual selection on the timing of reproductive activity, possibly in relation to sex and phenotype. In males, there was a tendency for long-lasting males to perform more mating attempts. This was in accordance with our initial thought that males mating over a long period may maximize the number of mating opportunities by encountering more females during the mating season. Interestingly, long-lasting males also appeared to have a slightly lower probability of mating successfully. This may suggest that such males have more time to seek out matings with high-quality females that have a higher probability of rejecting

them. The duration of an individual's mating season could also be an adjustment to its ability to successfully mate with members of the opposite sex. If one individual repeatedly fails to reproduce, it will remain in the breeding pool for longer to deplete its gamete stock. The starting date had no effect on either the number of mating attempts or the probability of mating success in males. This result was all the more surprising as in polygynandrous species such as lampreys, males arrive at the breeding grounds before females, suggesting an advantage of early males in terms of access to females (Morbey and Ydenberg, 2001). Females are, however, relatively asynchronous (Fig. 2.1) and the OSR was lower from day 8 to day 13 than from day 1 to day 7; males starting early therefore did not have access to a higher number of receptive females. However, we cannot exclude the possibility that this may be an artefact of captivity. The early arrival of females in the wild may be more synchronous or may be selected for reasons other than the mating parameters investigated here.

In females, early onset of mating activity decreased the number of mating attempts but increased the probability of success, and the interactions with body size imply that these effects of early activity were stronger in smaller females. This may suggest that late-arriving females attempt more matings with males active at the end of the season but are more selective towards them. A recent experiment using sea lampreys showed that ovulatory females use spermine, a pheromone that originates in the seminal plasma, to identify males actively releasing sperm (Scott et al., 2019). As late-active males have a higher probability of being sperm-depleted, females are probably more discriminating towards them to prevent costly matings. Small females appeared to be even more selective which is consistent with their lower fecundity. Such results suggest that females are selected to start early, especially if they are small. Interestingly, estimates values ($\beta_5/\beta_{16}$) were similar to those corresponding to the effect of the time since the start of the female's reproductive period in our daily model

($\beta_{10}/\beta_{20}$). This suggests that females that had been mating for a long time and were more likely to have few eggs left, attempted more matings but were more selective to avoid costly matings with low-quality males.

### Conclusion

Overall, our study highlighted the within-season dynamics of pre-copulatory sexual selection in lampreys and how it is directly related to characteristics of the sexual environment. From a methodological perspective, our results illustrate the complexity of measuring sexual selection and the necessity to increase studies using fine-grained behavioural data sets. For most studies, quantification of sexual selection remains generally based on one of a few samplings per season that may therefore lead to biased or even incorrect estimation of sexual selection, depending on which day the metrics are calculated. For instance, if we had only calculated metrics on days when the OSR was high, we would have overestimated the actual strength of sexual selection on female body size. Ongoing methodological advances in telemetry monitoring (Tentelier et al., 2016; Whitford and Klimley, 2019) or video recording systems (Yang et al., 2018), for instance, are overcoming previous difficulties in obtaining such high-resolution behavioural data. From a more theoretical perspective, showing that the benefits of exhibiting specific sexual traits are highly context-dependent has important implications. Based on our results, we can hypothesize that conditional temporal strategies, in which individuals adapt the timing of sexual activity according to their own phenotype, may exist in lampreys. In swordtails (*Xiphophorus helleri*), it has been shown that the age at sexual maturity shifts in developing individuals in accordance with the perceived quality of competitors and potential mates. After maturity, environmental visual cues might also lead to behavioural plasticity (e.g. longer or shorter mating seasons) depending on the competitive challenges faced by individuals.

# 2.A Appendix

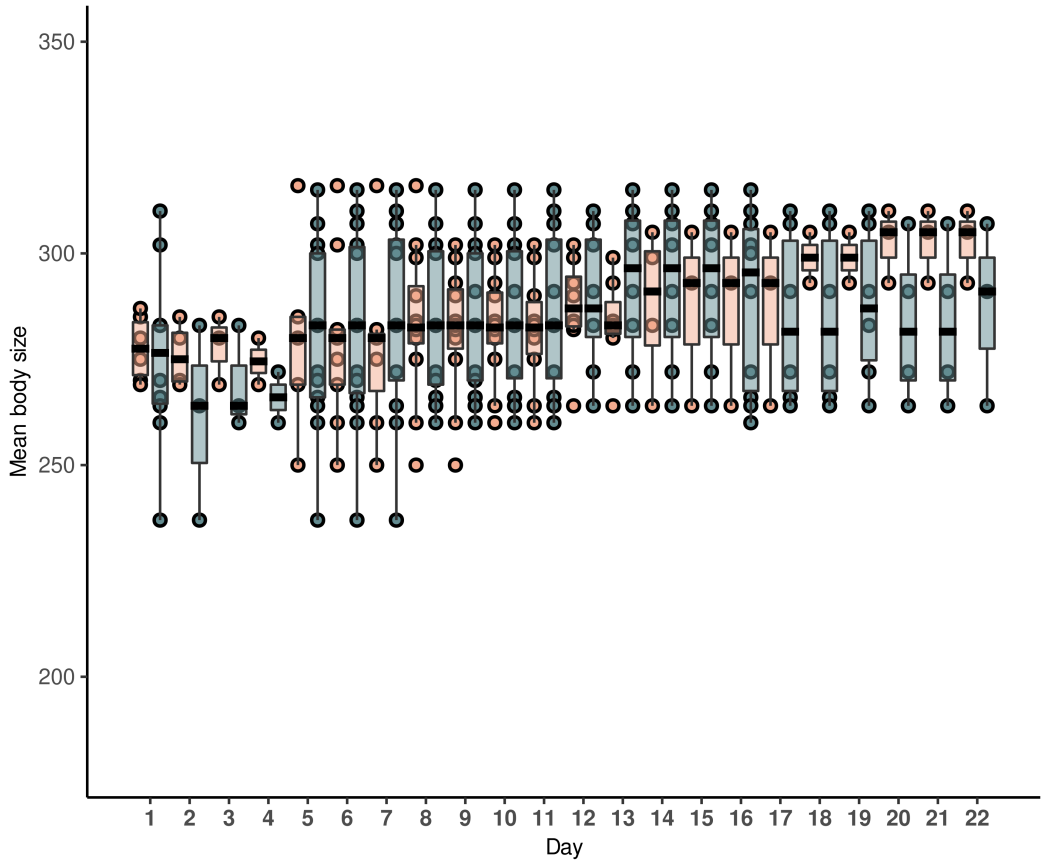


**Figure 2.A.1.** Size distribution (total length in mm) of active individuals each day of the breeding season (males: blue; females: orange). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are the jittered data points.

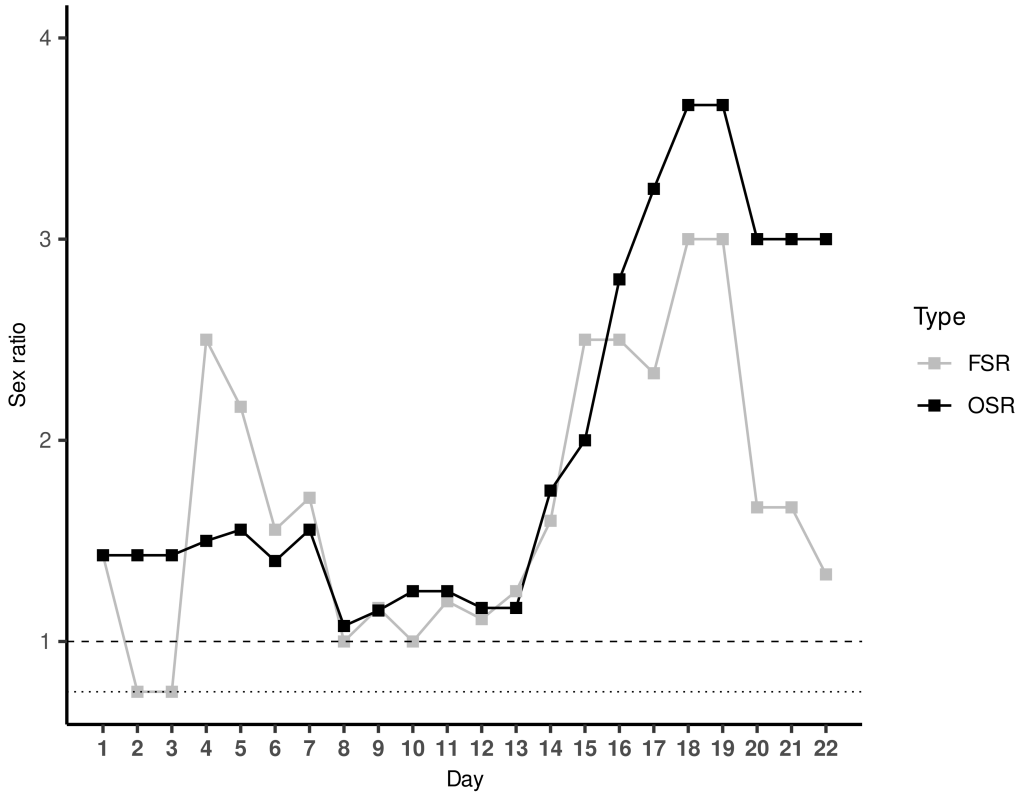


**Figure 2.A.2.** The operational sex ratio (OSR) and the functional sex ratio (FSR) each day of the breeding season. The OSR corresponds to the ratio of males to females that are ready to mate on a given day while FSR corresponds to the ratio of males to females that attempt to mate on a given day. The dashed line corresponds to an unbiased sex ratio (1) while the dotted line represents the adult sex ratio in the breeding group (0.75).

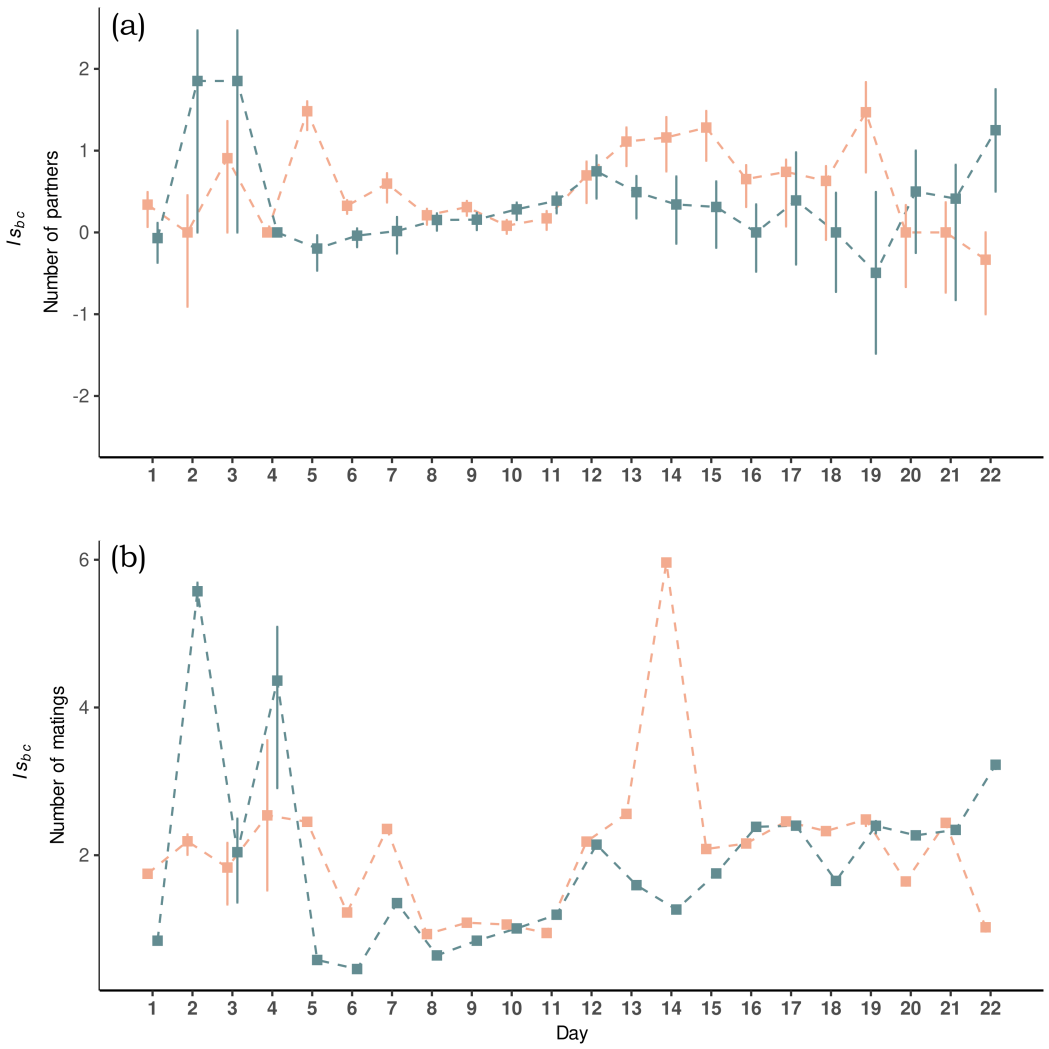


**Figure 2.A.3.** Bias-corrected opportunity for sexual selection ($Is_{bc}$) with 95% confidence intervals are presented (vertical whiskers) with mating success calculated either (a) as the number of partners ($MS_P$) or (b) as the number of matings ($MS_M$) in males (blue) and females (orange) on each day of the breeding season.

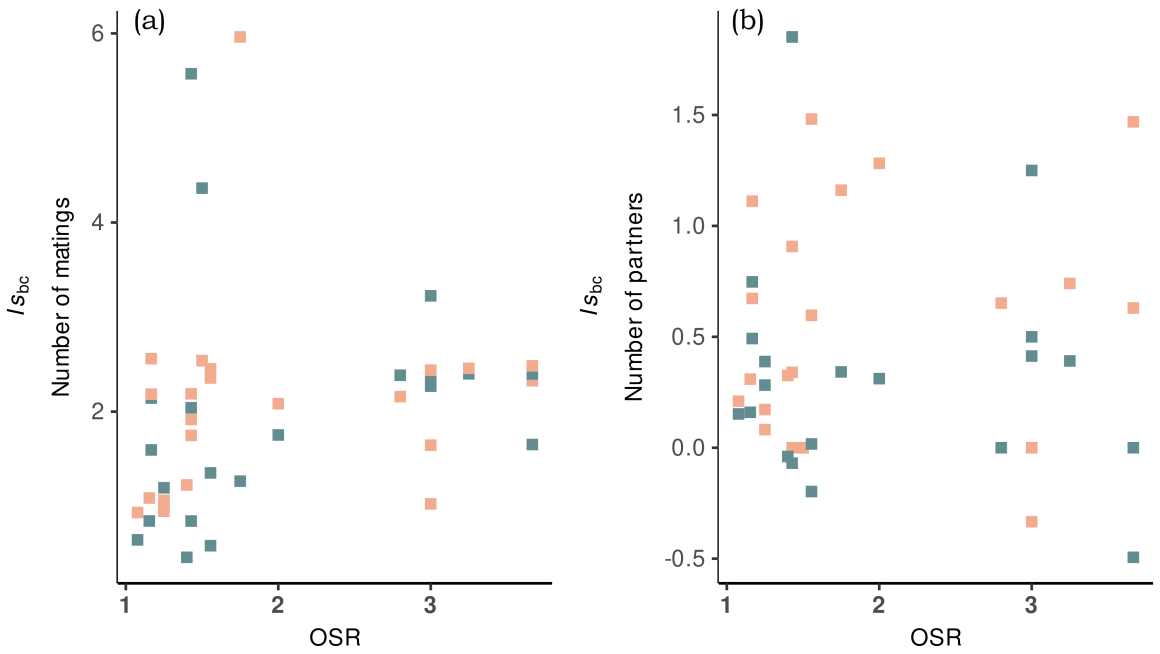


**Figure 2.A.4.** Relationship between the biais corrected opportunity for sexual selection ($Is_{bc}$) and the operational sex ratio (OSR) with mating success calculated either (a) as the number of partners ($MS_P$) or (b) as the number of matings ($MS_M$) in males (blue) and females (orange).

## 2.A.1 Bayesian model: at daily time steps

Random effects were slightly more variable for males than for females for the number of mating attempts (mean of respectively 0.61 and 0.47) while they were more variable for females for the probability of mating success (mean of respectively 0.11 and 0.31) (Fig. 2.A.5). The correlations between random individual effects of two processes were calculated in each sex but none were statistically significant (Fig. 2.A.5).

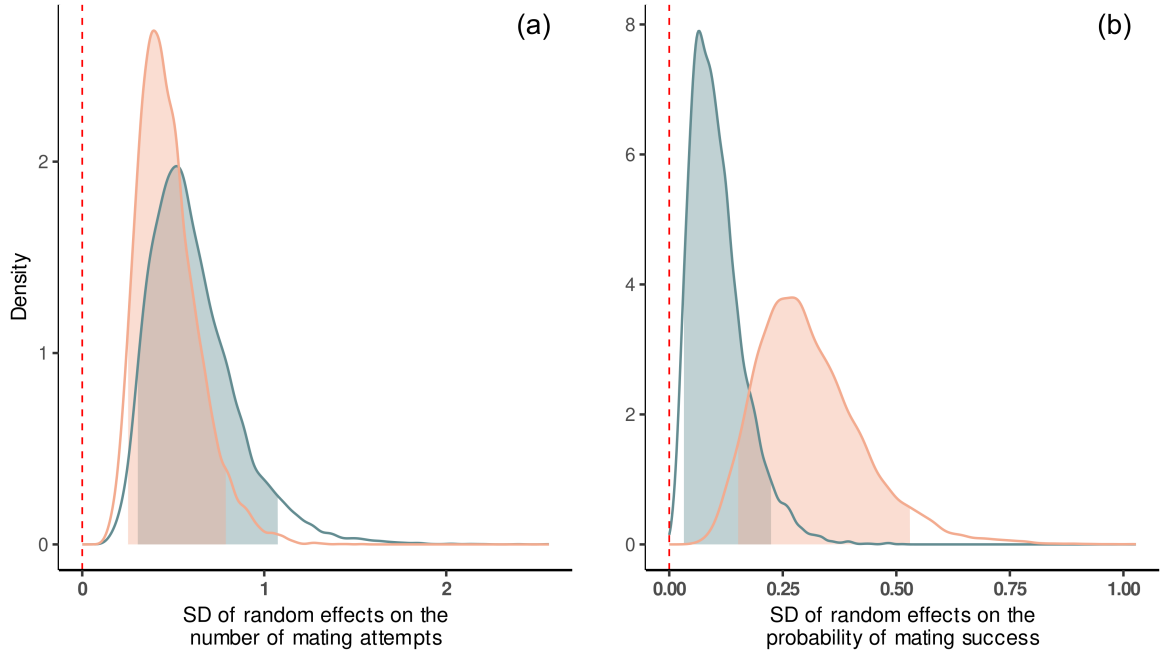


**Figure 2.A.5.** Posterior probability distribution of the standard deviation of random individual effects on (a) the number of mating attempts and (b) the probability of mating success on each day for males (blue) and females (orange). The dashed red vertical lines correspond to a null effect. Density plots show the distribution of the parameter values sampled from 12 000 iterations. The coloured portions inside the density plots represent the 95% credible intervals.

Spearman's rank correlations were computed to assess the pairwise relationship between random individual effects on the number of mating attempts and the probability of success in both sexes. In males, there was no correlation between the number of mating attempts and the probability of mating success (r = -0.09, df = 13, $P$ = 0.75). Similarly, there were no correlation in females (r = 0.26, df = 18, $P$ = 0.27) (Fig. 2.A.6).

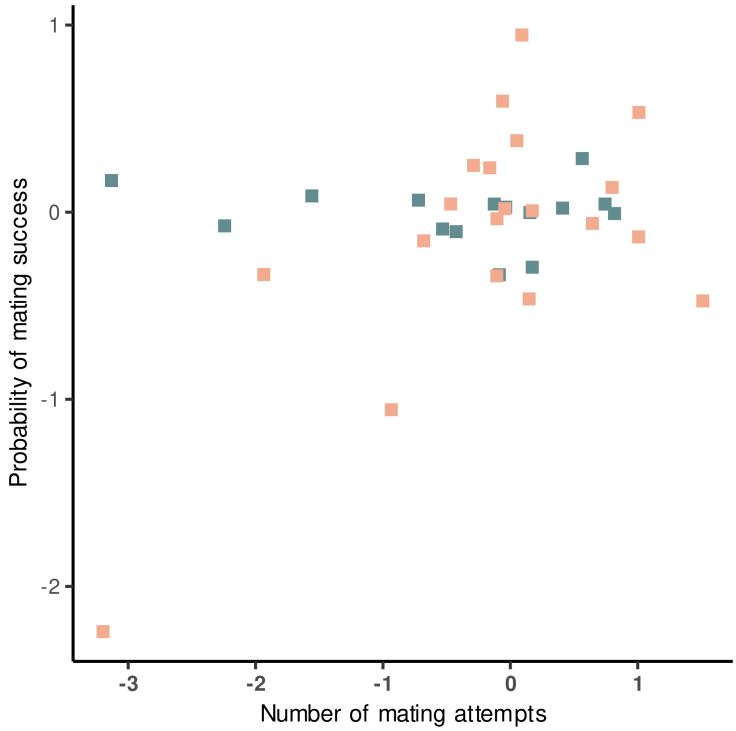


**Figure 2.A.6.** Pairwise relationship between random individual effects on the number of mating attempts and the probability of success for males (blue) and females (orange).

### Model validation

We performed Gelman–Rubin diagnostic to analyse the difference between the three Markov chains. For each parameter, the scale reduction factor $\hat{r}$ was equal to 1, highlighting that all chains have converged (see Tab. 2.A.1 for details). Based on the posterior distribution of all parameters of our model, the number of mating attempts and successful matings was calculated for each individual and these predictions were plotted against the number of mating attempts and successful matings observed in our experiment (Fig. 2.A.7). Spearman's rank correlations were computed to assess the pairwise relationship between the number of mating attempts and successful matings predicted in our model and those observed in our experiment. In both sexes, there were strong positive correlations between the predicted and observed number of mating attempts (r = 0.99, df = 33, $P < 0.001$) (Fig. 2.A.7, a), and the predicted and observed number of successful matings (r = 0.99, df = 33, $P < 0.001$) (Fig. 2.A.7,

b). For most individuals, numbers predicted by the model were equivalent to the number of interactions observed. The model predicted on average (±SD, [HDI95%]) 616 (±482, [46:1388]) mating attempts in males, 462 (±312, [64:890]) mating attempts in females, 477 (±382, [37:1117]) successful matings in males and 358 (±244, [46:758]) successful matings in females.

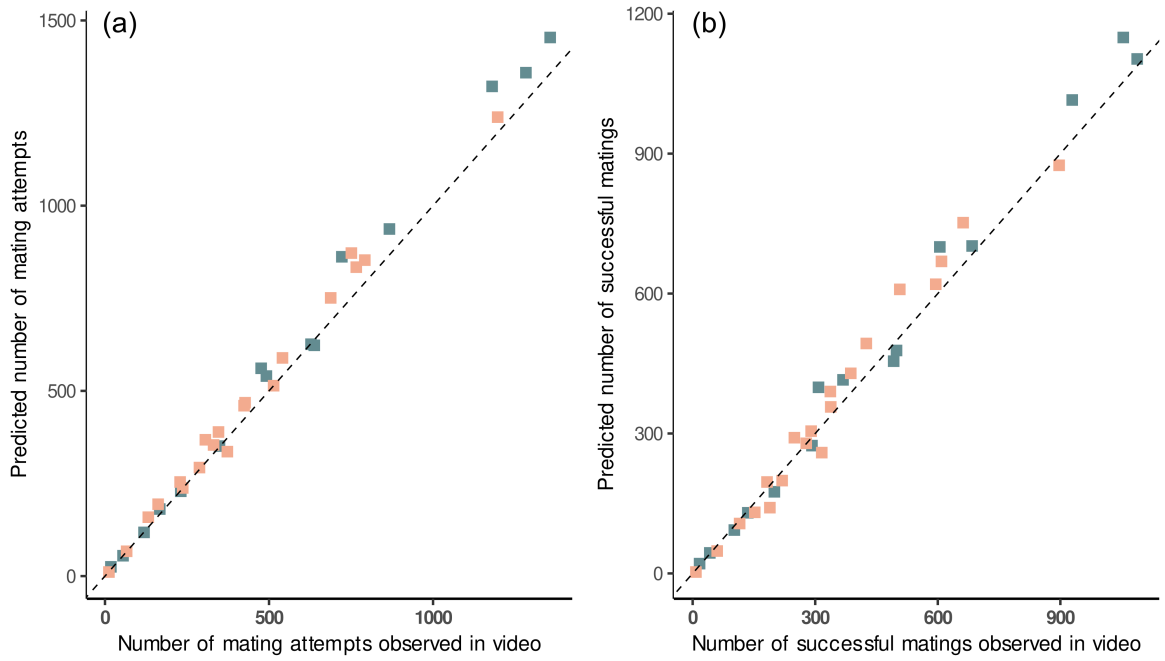


**Figure 2.A.7.** Pairwise relationship between the number of (a) mating attempts and (b) successful matings predicted in our model and those observed in our experiment for males (blue) and females (orange). The dashed line has intercept zero and slope one, which corresponds to a perfect fit between observed and predicted values.

## 2.A.2 Bayesian model: all season

Random effects were slightly more variable for males than for females for the number of mating attempts (mean of respectively 0.67 and 0.41) and were similar for the probability of mating success (mean of respectively 0.13 and 0.12) (Fig. 2.A.8) The correlations between random effects of both processes were calculated in each sex but none were statistically significant (Fig. 2.A.9).

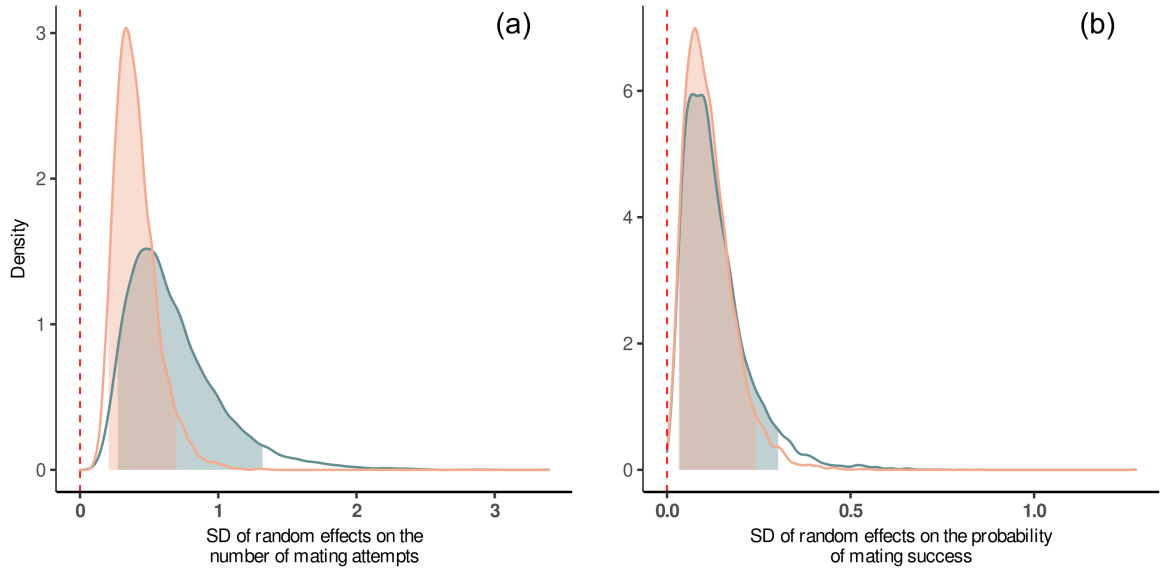


**Figure 2.A.8.** Posterior probability distribution of the standard deviation of random individual effects on (a) the number of mating attempts and (b) the probability of mating success for males (blue) and females (orange). The dashed red vertical line corresponds to a null effect. Density plots show the distribution of the parameter values sampled from 12 000 iterations. The coloured portions inside the density plots represent the 95% credible intervals.

Spearman's rank correlations were computed to assess the pairwise relationship between random individual effects on the number of mating attempts and probability of success in both sexes. In both males and females, there was no correlation between the number of mating attempts and probability of mating success (r = -0.32, df = 13, $P$ = 0.24 for males and r= -0.12, df = 18, $P$ = 0.61 for females) (Fig. 2.A.9).

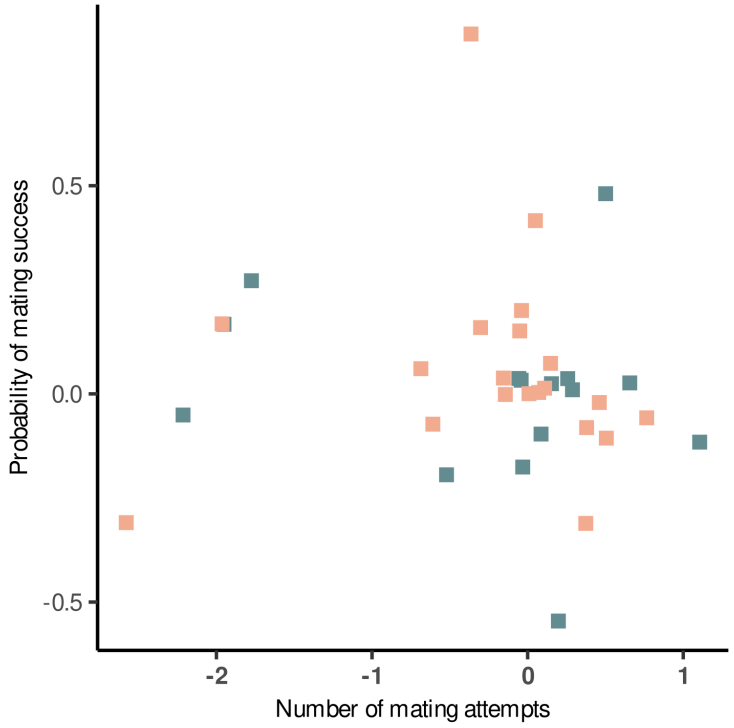


**Figure 2.A.9.** Pairwise relationship between random individual effects on the number of mating attempts and the probability of success for males (blue) and females (orange).

### Model validation

We performed Gelman–Rubin diagnostic to analyse the difference between the three Markov chains. For each parameter, the scale reduction factor $\hat{r}$ was equal to 1, highlighting that all chains have converged (see Tab. 2.A.2 for details). Based on the posterior distribution of all parameters of our model, the number of mating attempts and successful matings was calculated for each individual and these predictions were plotted against the number of mating attempts and successful matings observed in our experiment (Fig. 2.A.10). Spearman's rank correlations were computed to assess the pairwise relationship between the number of mating attempts and successful matings predicted in our model and those observed in our experiment. In both sexes, there were positive correlations between the predicted and

observed number of mating attempts (r = 0.48, df = 33, $P < 0.05$) (Fig. 2.A.10, a), and the predicted and observed number of mating attempts (r = 0.46, df = 33, $P < 0.05$) (Fig. 2.A.10, b). However, the numbers predicted by the model exceeded the number of observations in most cases. Indeed, the model predicted on average (±SD, [HDI95%]) 1296 (±1242, [66:3360]) mating attempts in males, 972 (±738, [133:2547]) mating attempts in females, 1038 (±996, [53:2662]) successful matings in males and 778 (±615, [121:2134]) successful matings in females.

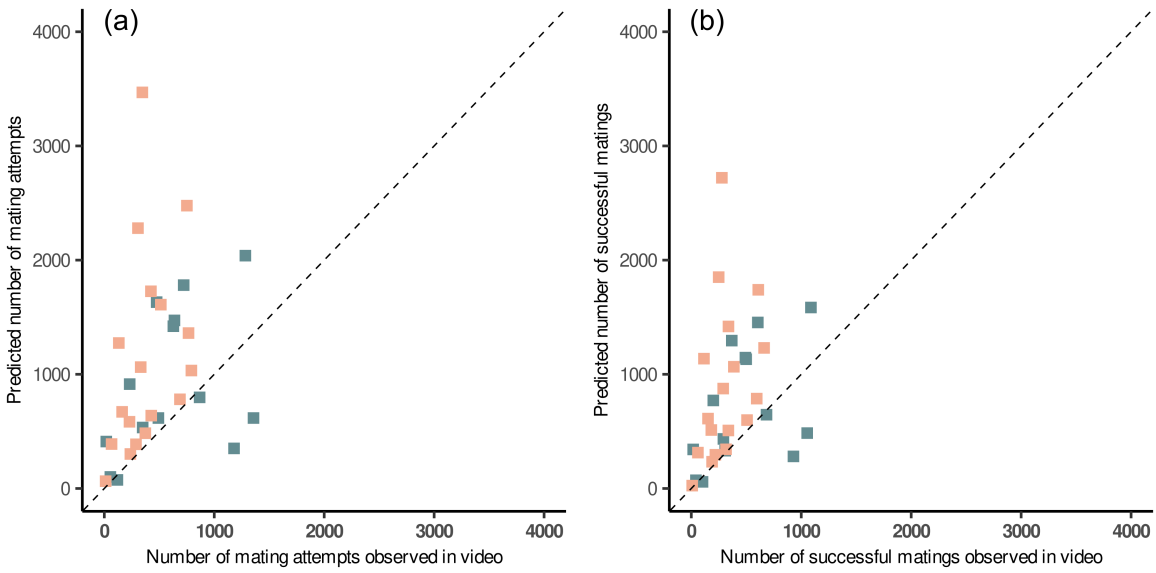


**Figure 2.A.10.** Pairwise relationship between the number of (a) mating attempts and (b) successful matings predicted in our model and those observed in our experiment for males (blue) and females (orange). The dashed line has intercept zero and slope one, which corresponds to a perfect fit between observed and predicted values.

**Table 2.A.1.** Summary of estimated parameters distributions and derived quantities using the posterior draws of the model at daily time steps (see equation 2.2 and 2.3 for details). The summary includes $means$, Monte Carlo standard errors ($se_{mean}$), standard deviations ($sd$), quantiles, effective sample sizes ($n_{eff}$), and split $Rhats$ (i.e. the potential scale reduction derived from all chains after splitting each chain in half and treating the halves as chains). $m_{x,1:15}$ and $f_{x,1;20}$ are random male and female effects. $\sigma_{mx}$ and $\sigma_{fx}$ are the standard deviation of random individual effects for males and females, respectively. $x$ refers to the process concerned, either (1) the number of mating attempts or (2) the probability of successful mating. The summary comprises all chains merged.

| | $mean$ | $se\_mean$ | $sd$ | 2.5% | 25% | 50% | 75% | 97.5% | $n_{eff}$ | $Rhat$ |
|---|---|---|---|---|---|---|---|---|---|---|
| $\alpha_1$ | -0,27 | 0,01 | 0,29 | -0,85 | -0,46 | -0,26 | -0,07 | 0,27 | 2709,74 | 1,00 |
| $\alpha_2$ | 1,67 | 0,00 | 0,18 | 1,32 | 1,54 | 1,66 | 1,78 | 2,02 | 4045,39 | 1,00 |
| $\beta_1$ | 4,01 | 0,00 | 0,27 | 3,43 | 3,83 | 4,02 | 4,19 | 4,50 | 3613,95 | 1,00 |
| $\beta_{11}$ | -5,67 | 0,01 | 0,84 | -7,33 | -6,23 | -5,66 | -5,09 | -4,03 | 5394,95 | 1,00 |
| $\beta_2$ | -0,70 | 0,00 | 0,16 | -1,02 | -0,80 | -0,70 | -0,60 | -0,40 | 4277,59 | 1,00 |
| $\beta_{12}$ | 1,41 | 0,00 | 0,31 | 0,80 | 1,20 | 1,41 | 1,61 | 2,00 | 6126,74 | 1,00 |
| $\beta_3$ | -0,05 | 0,00 | 0,02 | -0,09 | -0,06 | -0,05 | -0,04 | -0,01 | 14990,54 | 1,00 |
| $\beta_{13}$ | -0,21 | 0,00 | 0,05 | -0,31 | -0,25 | -0,21 | -0,18 | -0,11 | 10874,02 | 1,00 |
| $\beta_4$ | -0,31 | 0,00 | 0,03 | -0,38 | -0,34 | -0,31 | -0,29 | -0,25 | 9192,19 | 1,00 |
| $\beta_{14}$ | 0,14 | 0,00 | 0,12 | -0,10 | 0,06 | 0,15 | 0,23 | 0,38 | 8142,88 | 1,00 |
| $\beta_5$ | 0,14 | 0,00 | 0,02 | 0,11 | 0,13 | 0,14 | 0,16 | 0,18 | 15200,28 | 1,00 |
| $\beta_{15}$ | -0,15 | 0,00 | 0,05 | -0,24 | -0,18 | -0,15 | -0,11 | -0,05 | 11360,48 | 1,00 |
| $\beta_6$ | 0,51 | 0,00 | 0,02 | 0,48 | 0,50 | 0,51 | 0,52 | 0,55 | 14614,69 | 1,00 |
| $\beta_{16}$ | 0,34 | 0,00 | 0,12 | 0,09 | 0,26 | 0,34 | 0,43 | 0,59 | 8663,82 | 1,00 |
| $\beta_7$ | 3,64 | 0,00 | 0,11 | 3,44 | 3,57 | 3,64 | 3,71 | 3,85 | 10071,95 | 1,00 |
| $\beta_{17}$ | -5,24 | 0,01 | 0,77 | -6,75 | -5,75 | -5,23 | -4,71 | -3,73 | 5593,68 | 1,00 |
| $\beta_8$ | -1,14 | 0,00 | 0,07 | -1,28 | -1,19 | -1,14 | -1,10 | -1,01 | 8107,89 | 1,00 |
| $\beta_{18}$ | 1,10 | 0,00 | 0,23 | 0,66 | 0,95 | 1,10 | 1,25 | 1,54 | 8150,31 | 1,00 |
| $\beta_9$ | -1,24 | 0,00 | 0,03 | -1,31 | -1,27 | -1,24 | -1,22 | -1,18 | 12297,37 | 1,00 |
| $\beta_{19}$ | -0,03 | 0,00 | 0,15 | -0,31 | -0,13 | -0,04 | 0,06 | 0,27 | 5305,12 | 1,00 |
| $\beta_{10}$ | 0,08 | 0,00 | 0,02 | 0,04 | 0,07 | 0,08 | 0,10 | 0,13 | 13422,73 | 1,00 |
| $\beta_{20}$ | -0,33 | 0,00 | 0,09 | -0,52 | -0,40 | -0,33 | -0,27 | -0,16 | 5288,98 | 1,00 |
| $m[1,1]$ | -0,13 | 0,01 | 0,41 | -1,00 | -0,37 | -0,10 | 0,14 | 0,65 | 2749,25 | 1,00 |
| $m[1,2]$ | -2,24 | 0,01 | 0,38 | -3,03 | -2,48 | -2,23 | -1,99 | -1,51 | 2859,43 | 1,00 |
| $m[1,3]$ | 0,56 | 0,01 | 0,31 | -0,02 | 0,37 | 0,56 | 0,74 | 1,21 | 3484,68 | 1,00 |
| $m[1,4]$ | 0,17 | 0,00 | 0,25 | -0,29 | 0,01 | 0,16 | 0,32 | 0,68 | 2670,22 | 1,00 |
| $m[1,5]$ | -0,04 | 0,00 | 0,23 | -0,47 | -0,19 | -0,05 | 0,10 | 0,46 | 2701,11 | 1,00 |
| $m[1,6]$ | 0,82 | 0,01 | 0,38 | 0,03 | 0,59 | 0,85 | 1,06 | 1,54 | 2678,07 | 1,00 |
| $m[1,7]$ | 0,15 | 0,00 | 0,27 | -0,36 | -0,02 | 0,15 | 0,31 | 0,74 | 3396,21 | 1,00 |
| $m[1,8]$ | -0,53 | 0,01 | 0,65 | -1,93 | -0,92 | -0,46 | -0,11 | 0,66 | 2921,98 | 1,00 |
| $m[1,9]$ | -0,72 | 0,00 | 0,25 | -1,20 | -0,89 | -0,73 | -0,56 | -0,21 | 2756,49 | 1,00 |
| $m[1,10]$ | -0,09 | 0,01 | 0,33 | -0,72 | -0,29 | -0,09 | 0,11 | 0,60 | 3559,05 | 1,00 |
| $m[1,11]$ | 0,74 | 0,01 | 0,31 | 0,11 | 0,54 | 0,76 | 0,94 | 1,35 | 2624,90 | 1,00 |
| $m[1,12]$ | -1,56 | 0,00 | 0,28 | -2,08 | -1,74 | -1,57 | -1,39 | -0,97 | 3501,07 | 1,00 |
| $m[1,13]$ | -3,13 | 0,01 | 0,40 | -3,93 | -3,39 | -3,12 | -2,87 | -2,34 | 3504,31 | 1,00 |
| $m[1,14]$ | 0,41 | 0,00 | 0,25 | -0,05 | 0,25 | 0,40 | 0,56 | 0,93 | 2690,90 | 1,00 |
| $m[1,15]$ | -0,43 | 0,01 | 0,37 | -1,14 | -0,66 | -0,43 | -0,20 | 0,34 | 3570,19 | 1,00 |
| $m[2,1]$ | 0,04 | 0,00 | 0,12 | -0,17 | -0,03 | 0,03 | 0,10 | 0,33 | 9082,51 | 1,00 |
| $m[2,2]$ | -0,07 | 0,00 | 0,18 | -0,55 | -0,14 | -0,04 | 0,03 | 0,23 | 7719,36 | 1,00 |
| $m[2,3]$ | 0,29 | 0,00 | 0,16 | 0,00 | 0,17 | 0,29 | 0,40 | 0,59 | 5528,73 | 1,00 |
| $m[2,4]$ | -0,29 | 0,00 | 0,13 | -0,56 | -0,39 | -0,30 | -0,20 | -0,03 | 7390,86 | 1,00 |
| $m[2,5]$ | 0,03 | 0,00 | 0,12 | -0,19 | -0,04 | 0,01 | 0,08 | 0,31 | 5440,83 | 1,00 |
| $m[2,6]$ | -0,01 | 0,00 | 0,09 | -0,19 | -0,06 | -0,01 | 0,04 | 0,18 | 8353,45 | 1,00 |
| $m[2,7]$ | 0,00 | 0,00 | 0,11 | -0,25 | -0,06 | 0,00 | 0,06 | 0,23 | 5349,27 | 1,00 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| $m[2,8]$ | -0,09 | 0,00 | 0,19 | -0,57 | -0,16 | -0,05 | 0,02 | 0,21 | 5958,56 | 1,00 |
| $m[2,9]$ | 0,06 | 0,00 | 0,13 | -0,15 | -0,01 | 0,04 | 0,12 | 0,40 | 7550,57 | 1,00 |
| $m[2,10]$ | -0,33 | 0,00 | 0,20 | -0,73 | -0,47 | -0,33 | -0,19 | 0,00 | 5007,29 | 1,00 |
| $m[2,11]$ | 0,04 | 0,00 | 0,09 | -0,11 | -0,01 | 0,03 | 0,09 | 0,25 | 5936,38 | 1,00 |
| $m[2,12]$ | 0,09 | 0,00 | 0,17 | -0,17 | -0,01 | 0,05 | 0,16 | 0,51 | 5931,40 | 1,00 |
| $m[2,13]$ | 0,17 | 0,01 | 0,43 | -0,29 | -0,03 | 0,04 | 0,20 | 1,43 | 3096,08 | 1,00 |
| $m[2,14]$ | 0,02 | 0,00 | 0,10 | -0,17 | -0,03 | 0,02 | 0,07 | 0,24 | 8464,50 | 1,00 |
| $m[2,15]$ | -0,10 | 0,00 | 0,16 | -0,49 | -0,18 | -0,07 | 0,00 | 0,14 | 5243,11 | 1,00 |
| $f[1,1]$ | 0,15 | 0,00 | 0,20 | -0,24 | 0,03 | 0,15 | 0,27 | 0,53 | 3962,26 | 1,00 |
| $f[1,2]$ | -0,06 | 0,00 | 0,22 | -0,51 | -0,20 | -0,06 | 0,08 | 0,38 | 4222,17 | 1,00 |
| $f[1,3]$ | -1,94 | 0,00 | 0,19 | -2,33 | -2,06 | -1,93 | -1,80 | -1,56 | 3798,22 | 1,00 |
| $f[1,4]$ | -0,93 | 0,00 | 0,17 | -1,29 | -1,04 | -0,93 | -0,82 | -0,60 | 3110,36 | 1,00 |
| $f[1,5]$ | -0,29 | 0,00 | 0,20 | -0,72 | -0,40 | -0,28 | -0,16 | 0,08 | 2678,65 | 1,00 |
| $f[1,6]$ | -3,20 | 0,00 | 0,37 | -3,98 | -3,43 | -3,18 | -2,95 | -2,50 | 5769,50 | 1,00 |
| $f[1,7]$ | -0,68 | 0,00 | 0,24 | -1,19 | -0,82 | -0,66 | -0,53 | -0,24 | 2882,20 | 1,00 |
| $f[1,8]$ | 0,80 | 0,00 | 0,16 | 0,47 | 0,70 | 0,80 | 0,90 | 1,10 | 2615,98 | 1,00 |
| $f[1,9]$ | 0,09 | 0,00 | 0,18 | -0,27 | -0,02 | 0,09 | 0,20 | 0,44 | 3747,58 | 1,00 |
| $f[1,10]$ | -0,47 | 0,00 | 0,26 | -1,00 | -0,63 | -0,47 | -0,31 | 0,04 | 4370,73 | 1,00 |
| $f[1,11]$ | -0,11 | 0,00 | 0,15 | -0,43 | -0,20 | -0,10 | -0,01 | 0,19 | 2849,17 | 1,00 |
| $f[1,12]$ | -0,16 | 0,00 | 0,17 | -0,53 | -0,27 | -0,15 | -0,05 | 0,16 | 2616,46 | 1,00 |
| $f[1,13]$ | 0,64 | 0,00 | 0,17 | 0,28 | 0,54 | 0,65 | 0,75 | 0,96 | 2546,40 | 1,00 |
| $f[1,14]$ | -0,10 | 0,01 | 0,28 | -0,74 | -0,26 | -0,08 | 0,07 | 0,43 | 3008,33 | 1,00 |
| $f[1,15]$ | -0,04 | 0,01 | 0,35 | -0,82 | -0,23 | -0,02 | 0,17 | 0,63 | 3160,46 | 1,00 |
| $f[1,16]$ | 0,17 | 0,00 | 0,16 | -0,17 | 0,07 | 0,18 | 0,28 | 0,49 | 2642,94 | 1,00 |
| $f[1,17]$ | 0,05 | 0,00 | 0,17 | -0,28 | -0,05 | 0,05 | 0,16 | 0,38 | 3604,78 | 1,00 |
| $f[1,18]$ | 1,51 | 0,00 | 0,15 | 1,21 | 1,42 | 1,51 | 1,61 | 1,81 | 2978,51 | 1,00 |
| $f[1,19]$ | 1,01 | 0,00 | 0,16 | 0,67 | 0,91 | 1,01 | 1,11 | 1,31 | 2551,92 | 1,00 |
| $f[1,20]$ | 1,01 | 0,00 | 0,26 | 0,44 | 0,87 | 1,03 | 1,17 | 1,50 | 2867,43 | 1,00 |
| $f[2,1]$ | -0,46 | 0,01 | 0,34 | -1,15 | -0,70 | -0,44 | -0,20 | 0,11 | 4418,11 | 1,00 |
| $f[2,2]$ | 0,59 | 0,01 | 0,43 | -0,15 | 0,26 | 0,57 | 0,90 | 1,46 | 5040,63 | 1,00 |
| $f[2,3]$ | -0,33 | 0,00 | 0,43 | -1,34 | -0,58 | -0,26 | -0,03 | 0,35 | 8146,70 | 1,00 |
| $f[2,4]$ | -1,06 | 0,01 | 0,44 | -1,89 | -1,36 | -1,07 | -0,76 | -0,18 | 6282,68 | 1,00 |
| $f[2,5]$ | 0,25 | 0,00 | 0,19 | -0,09 | 0,11 | 0,24 | 0,38 | 0,66 | 6713,09 | 1,00 |
| $f[2,6]$ | -2,24 | 0,01 | 0,93 | -3,83 | -2,91 | -2,34 | -1,69 | -0,13 | 7647,47 | 1,00 |
| $f[2,7]$ | -0,15 | 0,00 | 0,31 | -0,87 | -0,32 | -0,11 | 0,04 | 0,40 | 7998,95 | 1,00 |
| $f[2,8]$ | 0,13 | 0,00 | 0,15 | -0,14 | 0,03 | 0,13 | 0,23 | 0,44 | 5148,88 | 1,00 |
| $f[2,9]$ | 0,95 | 0,00 | 0,26 | 0,45 | 0,78 | 0,94 | 1,11 | 1,47 | 5152,17 | 1,00 |
| $f[2,10]$ | 0,04 | 0,00 | 0,30 | -0,57 | -0,13 | 0,03 | 0,21 | 0,69 | 5253,44 | 1,00 |
| $f[2,11]$ | -0,34 | 0,00 | 0,20 | -0,75 | -0,48 | -0,33 | -0,19 | 0,03 | 5706,74 | 1,00 |
| $f[2,12]$ | 0,24 | 0,00 | 0,18 | -0,08 | 0,11 | 0,23 | 0,35 | 0,62 | 7248,62 | 1,00 |
| $f[2,13]$ | -0,06 | 0,00 | 0,14 | -0,34 | -0,15 | -0,06 | 0,03 | 0,21 | 5645,76 | 1,00 |
| $f[2,14]$ | -0,04 | 0,00 | 0,21 | -0,47 | -0,16 | -0,03 | 0,09 | 0,39 | 7717,89 | 1,00 |
| $f[2,15]$ | 0,02 | 0,00 | 0,26 | -0,50 | -0,13 | 0,01 | 0,16 | 0,56 | 6902,25 | 1,00 |
| $f[2,16]$ | 0,01 | 0,00 | 0,15 | -0,29 | -0,09 | 0,01 | 0,10 | 0,31 | 6410,97 | 1,00 |
| $f[2,17]$ | 0,38 | 0,00 | 0,23 | -0,03 | 0,23 | 0,38 | 0,53 | 0,85 | 5075,07 | 1,00 |
| $f[2,18]$ | -0,47 | 0,00 | 0,25 | -0,98 | -0,65 | -0,46 | -0,29 | -0,02 | 4298,78 | 1,00 |
| $f[2,19]$ | -0,13 | 0,00 | 0,15 | -0,43 | -0,23 | -0,13 | -0,03 | 0,15 | 4417,56 | 1,00 |
| $f[2,20]$ | 0,53 | 0,00 | 0,26 | 0,05 | 0,36 | 0,53 | 0,70 | 1,05 | 5749,81 | 1,00 |
| $\sigma_{m[1]}$ | 0,61 | 0,00 | 0,24 | 0,27 | 0,44 | 0,57 | 0,74 | 1,21 | 7824,04 | 1,00 |
| $\sigma_{m[2]}$ | 0,11 | 0,00 | 0,06 | 0,03 | 0,06 | 0,10 | 0,14 | 0,26 | 3114,69 | 1,00 |
| $\sigma_{f[1]}$ | 0,47 | 0,00 | 0,17 | 0,22 | 0,35 | 0,45 | 0,57 | 0,88 | 8685,50 | 1,00 |
| $\sigma_{f[2]}$ | 0,31 | 0,00 | 0,12 | 0,13 | 0,23 | 0,29 | 0,37 | 0,59 | 7895,81 | 1,00 |
| $lp\_\_$ | -19005,63 | 0,15 | 8,02 | -19021,79 | -19010,91 | -19005,34 | -19000,21 | -18990,44 | 2795,17 | 1,00 |

**Table 2.A.2.** Summary of estimated parameters distributions and derived quantities using the posterior draws of the model at the scale of the whole season (see equation 2.5 and 2.6 for details). The summary includes $means$, Monte Carlo standard errors ($se_{mean}$), standard deviations ($sd$), quantiles, effective sample sizes ($n_{eff}$), and split $Rhats$ (i.e. the potential scale reduction derived from all chains after splitting each chain in half and treating the halves as chains). $m_{x,1:15}$ and $f_{x,1;20}$ are random male and female effects. $\sigma_{mx}$ and $\sigma_{fx}$ are the standard deviation of random individual effects for males and females, respectively. $x$ refers to the process concerned, either (1) the number of mating attempts or (2) the probability of successful mating. The summary comprises all chains merged.

| | $mean$ | $se\_mean$ | $sd$ | 2.5% | 25% | 50% | 75% | 97.5% | $n_{eff}$ | $Rhat$ |
|---|---|---|---|---|---|---|---|---|---|---|
| $\alpha_1$ | 3,29 | 0,01 | 0,44 | 2,32 | 3,06 | 3,32 | 3,56 | 4,03 | 4052,62 | 1,00 |
| $\alpha_2$ | 1,56 | 0,00 | 0,14 | 1,30 | 1,48 | 1,56 | 1,64 | 1,84 | 2791,11 | 1,00 |
| $\beta_1$ | 0,04 | 0,01 | 0,40 | -0,74 | -0,18 | 0,03 | 0,25 | 0,89 | 5504,37 | 1,00 |
| $\beta_{11}$ | -0,02 | 0,00 | 0,17 | -0,29 | -0,14 | -0,04 | 0,09 | 0,37 | 2094,69 | 1,00 |
| $\beta_2$ | 0,29 | 0,00 | 0,26 | -0,24 | 0,15 | 0,29 | 0,43 | 0,82 | 4589,86 | 1,00 |
| $\beta_{12}$ | 0,15 | 0,00 | 0,15 | -0,21 | 0,07 | 0,17 | 0,24 | 0,38 | 2926,51 | 1,00 |
| $\beta_3$ | -0,07 | 0,00 | 0,02 | -0,10 | -0,08 | -0,07 | -0,05 | -0,03 | 17814,56 | 1,00 |
| $\beta_{14}$ | -0,16 | 0,00 | 0,05 | -0,25 | -0,19 | -0,16 | -0,12 | -0,06 | 11662,02 | 1,00 |
| $\beta_4$ | 0,36 | 0,01 | 0,40 | -0,42 | 0,18 | 0,35 | 0,54 | 1,17 | 4775,91 | 1,00 |
| $\beta_{15}$ | -0,04 | 0,00 | 0,16 | -0,35 | -0,11 | -0,04 | 0,03 | 0,26 | 1984,36 | 1,00 |
| $\beta_5$ | 0,35 | 0,00 | 0,26 | -0,11 | 0,18 | 0,33 | 0,51 | 0,92 | 4239,83 | 1,00 |
| $\beta_{16}$ | -0,41 | 0,00 | 0,18 | -0,73 | -0,54 | -0,43 | -0,30 | -0,03 | 2263,44 | 1,00 |
| $\beta_6$ | 0,58 | 0,01 | 0,40 | -0,24 | 0,35 | 0,58 | 0,80 | 1,40 | 6255,50 | 1,00 |
| $\beta_{17}$ | -0,25 | 0,00 | 0,15 | -0,53 | -0,35 | -0,27 | -0,17 | 0,08 | 3927,81 | 1,00 |
| $\beta_7$ | 0,16 | 0,00 | 0,26 | -0,47 | 0,04 | 0,18 | 0,32 | 0,62 | 3625,58 | 1,00 |
| $\beta_{18}$ | -0,04 | 0,00 | 0,09 | -0,20 | -0,10 | -0,05 | 0,01 | 0,16 | 3703,81 | 1,00 |
| $\beta_8$ | -0,14 | 0,01 | 0,63 | -1,51 | -0,45 | -0,12 | 0,19 | 1,10 | 5054,39 | 1,00 |
| $\beta_{19}$ | 0,04 | 0,01 | 0,27 | -0,40 | -0,13 | 0,01 | 0,20 | 0,67 | 1829,72 | 1,00 |
| $\beta_9$ | -0,43 | 0,00 | 0,19 | -0,84 | -0,54 | -0,41 | -0,30 | -0,08 | 4417,67 | 1,00 |
| $\beta_{20}$ | 0,32 | 0,00 | 0,16 | -0,05 | 0,23 | 0,34 | 0,43 | 0,58 | 2065,44 | 1,00 |
| $\beta_{10}$ | -0,11 | 0,01 | 0,37 | -0,98 | -0,29 | -0,09 | 0,10 | 0,57 | 4698,07 | 1,00 |
| $\beta_{21}$ | -0,16 | 0,00 | 0,13 | -0,37 | -0,24 | -0,17 | -0,09 | 0,14 | 3397,33 | 1,00 |
| $\beta_{11}$ | 0,15 | 0,00 | 0,34 | -0,53 | -0,04 | 0,14 | 0,33 | 0,83 | 4694,93 | 1,00 |
| $\beta_{22}$ | 0,16 | 0,00 | 0,17 | -0,23 | 0,07 | 0,18 | 0,26 | 0,45 | 3459,58 | 1,00 |
| $m[1,1]$ | -0,04 | 0,01 | 0,57 | -1,01 | -0,38 | -0,11 | 0,22 | 1,34 | 4128,58 | 1,00 |
| $m[1,2]$ | -2,21 | 0,01 | 0,52 | -3,13 | -2,51 | -2,26 | -1,97 | -0,95 | 5108,04 | 1,00 |
| $m[1,3]$ | 0,50 | 0,01 | 0,79 | -0,89 | 0,02 | 0,41 | 0,91 | 2,31 | 5404,75 | 1,00 |
| $m[1,4]$ | 0,09 | 0,01 | 0,38 | -0,56 | -0,14 | 0,05 | 0,26 | 0,98 | 5051,03 | 1,00 |
| $m[1,5]$ | -0,03 | 0,01 | 0,95 | -1,90 | -0,46 | -0,06 | 0,34 | 2,03 | 4904,70 | 1,00 |
| $m[1,6]$ | 0,15 | 0,01 | 0,80 | -1,34 | -0,25 | 0,09 | 0,48 | 2,08 | 5969,21 | 1,00 |
| $m[1,7]$ | 0,29 | 0,01 | 0,59 | -0,79 | -0,05 | 0,23 | 0,58 | 1,67 | 5947,21 | 1,00 |
| $m[1,8]$ | 1,11 | 0,03 | 1,94 | -1,29 | -0,02 | 0,52 | 1,72 | 6,46 | 3758,41 | 1,00 |
| $m[1,9]$ | -0,06 | 0,01 | 0,59 | -1,17 | -0,40 | -0,09 | 0,24 | 1,29 | 4968,83 | 1,00 |
| $m[1,10]$ | -0,52 | 0,01 | 0,87 | -2,41 | -1,02 | -0,45 | -0,01 | 1,19 | 6507,46 | 1,00 |
| $m[1,11]$ | 0,26 | 0,01 | 0,75 | -1,14 | -0,11 | 0,19 | 0,58 | 1,88 | 5064,46 | 1,00 |
| $m[1,12]$ | -1,78 | 0,01 | 0,48 | -2,65 | -2,07 | -1,81 | -1,52 | -0,70 | 5395,52 | 1,00 |
| $m[1,13]$ | -1,95 | 0,01 | 0,88 | -3,51 | -2,52 | -2,03 | -1,46 | -0,04 | 4498,35 | 1,00 |
| $m[1,14]$ | 0,66 | 0,01 | 0,40 | -0,03 | 0,41 | 0,62 | 0,84 | 1,61 | 4405,74 | 1,00 |
| $m[1,15]$ | 0,20 | 0,01 | 1,02 | -1,70 | -0,28 | 0,11 | 0,58 | 2,65 | 6099,90 | 1,00 |
| $m[2,1]$ | 0,03 | 0,00 | 0,14 | -0,23 | -0,04 | 0,02 | 0,10 | 0,35 | 6920,90 | 1,00 |
| $m[2,2]$ | -0,05 | 0,00 | 0,19 | -0,51 | -0,13 | -0,02 | 0,04 | 0,30 | 10790,19 | 1,00 |
| $m[2,3]$ | 0,48 | 0,01 | 0,40 | -0,15 | 0,11 | 0,50 | 0,80 | 1,18 | 1978,76 | 1,00 |
| $m[2,4]$ | -0,10 | 0,00 | 0,13 | -0,41 | -0,17 | -0,07 | -0,01 | 0,11 | 5702,03 | 1,00 |
| $m[2,5]$ | -0,18 | 0,01 | 0,44 | -1,28 | -0,26 | -0,04 | 0,04 | 0,37 | 1938,46 | 1,00 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| $m[2,6]$ | 0,02 | 0,00 | 0,19 | -0,34 | -0,06 | 0,01 | 0,10 | 0,45 | 7255,49 | 1,00 |
| $m[2,7]$ | 0,01 | 0,00 | 0,15 | -0,31 | -0,06 | 0,01 | 0,08 | 0,32 | 8200,26 | 1,00 |
| $m[2,8]$ | -0,12 | 0,01 | 0,41 | -1,27 | -0,17 | -0,03 | 0,05 | 0,43 | 4258,78 | 1,00 |
| $m[2,9]$ | 0,04 | 0,00 | 0,17 | -0,28 | -0,05 | 0,02 | 0,11 | 0,45 | 7144,96 | 1,00 |
| $m[2,10]$ | -0,19 | 0,01 | 0,35 | -1,12 | -0,32 | -0,08 | 0,01 | 0,27 | 3575,00 | 1,00 |
| $m[2,11]$ | 0,04 | 0,01 | 0,31 | -0,43 | -0,08 | 0,00 | 0,11 | 0,80 | 1848,30 | 1,00 |
| $m[2,12]$ | 0,27 | 0,00 | 0,30 | -0,13 | 0,04 | 0,19 | 0,46 | 0,98 | 4853,88 | 1,00 |
| $m[2,13]$ | 0,17 | 0,01 | 0,47 | -0,38 | -0,04 | 0,04 | 0,20 | 1,56 | 2931,45 | 1,00 |
| $m[2,14]$ | 0,03 | 0,00 | 0,11 | -0,20 | -0,03 | 0,02 | 0,08 | 0,27 | 9701,79 | 1,00 |
| $m[2,15]$ | -0,55 | 0,01 | 0,65 | -2,08 | -0,94 | -0,29 | -0,04 | 0,17 | 1956,41 | 1,00 |
| $f[1,1]$ | -0,16 | 0,00 | 0,35 | -0,96 | -0,31 | -0,12 | 0,04 | 0,45 | 6401,45 | 1,00 |
| $f[1,2]$ | -0,04 | 0,01 | 0,40 | -0,98 | -0,21 | -0,01 | 0,17 | 0,69 | 6429,96 | 1,00 |
| $f[1,3]$ | -1,96 | 0,01 | 0,66 | -3,12 | -2,37 | -2,03 | -1,66 | -0,26 | 3430,79 | 1,00 |
| $f[1,4]$ | -0,69 | 0,01 | 0,50 | -1,79 | -1,00 | -0,66 | -0,33 | 0,18 | 4649,17 | 1,00 |
| $f[1,5]$ | 0,37 | 0,01 | 0,36 | -0,17 | 0,15 | 0,32 | 0,52 | 1,28 | 3206,85 | 1,00 |
| $f[1,6]$ | -2,58 | 0,01 | 0,51 | -3,47 | -2,90 | -2,61 | -2,31 | -1,43 | 4353,34 | 1,00 |
| $f[1,7]$ | 0,05 | 0,01 | 0,42 | -0,64 | -0,19 | 0,00 | 0,22 | 1,09 | 3441,13 | 1,00 |
| $f[1,8]$ | 0,38 | 0,00 | 0,24 | -0,09 | 0,22 | 0,38 | 0,54 | 0,84 | 4225,86 | 1,00 |
| $f[1,9]$ | -0,05 | 0,01 | 0,67 | -1,49 | -0,35 | -0,04 | 0,25 | 1,38 | 4888,97 | 1,00 |
| $f[1,10]$ | 0,15 | 0,01 | 0,54 | -0,93 | -0,13 | 0,11 | 0,42 | 1,29 | 6294,22 | 1,00 |
| $f[1,11]$ | -0,61 | 0,00 | 0,21 | -1,03 | -0,74 | -0,60 | -0,47 | -0,22 | 4432,85 | 1,00 |
| $f[1,12]$ | 0,07 | 0,01 | 0,72 | -1,21 | -0,30 | 0,00 | 0,32 | 2,01 | 3067,01 | 1,00 |
| $f[1,13]$ | 0,77 | 0,00 | 0,20 | 0,40 | 0,64 | 0,75 | 0,87 | 1,21 | 3723,38 | 1,00 |
| $f[1,14]$ | -0,30 | 0,00 | 0,29 | -0,92 | -0,47 | -0,28 | -0,11 | 0,21 | 5509,01 | 1,00 |
| $f[1,15]$ | 0,11 | 0,00 | 0,41 | -0,70 | -0,11 | 0,09 | 0,33 | 0,97 | 6935,85 | 1,00 |
| $f[1,16]$ | 0,01 | 0,00 | 0,18 | -0,34 | -0,11 | 0,01 | 0,12 | 0,36 | 4721,10 | 1,00 |
| $f[1,17]$ | -0,14 | 0,00 | 0,21 | -0,58 | -0,27 | -0,14 | -0,01 | 0,26 | 4606,89 | 1,00 |
| $f[1,18]$ | 0,51 | 0,01 | 0,42 | -0,21 | 0,21 | 0,47 | 0,75 | 1,46 | 4503,20 | 1,00 |
| $f[1,19]$ | 0,46 | 0,00 | 0,22 | 0,01 | 0,32 | 0,47 | 0,61 | 0,85 | 4206,02 | 1,00 |
| $f[1,20]$ | -0,36 | 0,01 | 0,54 | -1,64 | -0,66 | -0,26 | 0,00 | 0,53 | 4100,33 | 1,00 |
| $f[2,1]$ | 0,04 | 0,00 | 0,22 | -0,30 | -0,06 | 0,01 | 0,09 | 0,65 | 2371,11 | 1,00 |
| $f[2,2]$ | 0,20 | 0,01 | 0,33 | -0,16 | 0,00 | 0,09 | 0,29 | 1,15 | 1904,31 | 1,00 |
| $f[2,3]$ | 0,17 | 0,00 | 0,31 | -0,21 | -0,01 | 0,07 | 0,26 | 1,02 | 3960,14 | 1,00 |
| $f[2,4]$ | 0,06 | 0,00 | 0,22 | -0,29 | -0,04 | 0,02 | 0,12 | 0,64 | 3855,46 | 1,00 |
| $f[2,5]$ | -0,31 | 0,00 | 0,27 | -0,88 | -0,50 | -0,28 | -0,09 | 0,08 | 4159,73 | 1,00 |
| $f[2,6]$ | -0,31 | 0,01 | 0,53 | -1,77 | -0,46 | -0,09 | 0,01 | 0,24 | 2745,27 | 1,00 |
| $f[2,7]$ | 0,42 | 0,01 | 0,43 | -0,10 | 0,06 | 0,30 | 0,70 | 1,40 | 3032,65 | 1,00 |
| $f[2,8]$ | -0,08 | 0,00 | 0,12 | -0,36 | -0,15 | -0,06 | 0,00 | 0,11 | 3984,08 | 1,00 |
| $f[2,9]$ | 0,15 | 0,01 | 0,32 | -0,30 | -0,02 | 0,06 | 0,24 | 1,03 | 3098,01 | 1,00 |
| $f[2,10]$ | 0,07 | 0,00 | 0,22 | -0,26 | -0,03 | 0,03 | 0,14 | 0,64 | 5461,80 | 1,00 |
| $f[2,11]$ | -0,07 | 0,00 | 0,12 | -0,37 | -0,14 | -0,05 | 0,01 | 0,13 | 4905,86 | 1,00 |
| $f[2,12]$ | 0,00 | 0,00 | 0,21 | -0,46 | -0,08 | 0,00 | 0,08 | 0,46 | 7293,49 | 1,00 |
| $f[2,13]$ | -0,06 | 0,00 | 0,10 | -0,29 | -0,12 | -0,04 | 0,01 | 0,13 | 8275,62 | 1,00 |
| $f[2,14]$ | 0,16 | 0,00 | 0,19 | -0,13 | 0,02 | 0,12 | 0,27 | 0,61 | 5430,42 | 1,00 |
| $f[2,15]$ | 0,01 | 0,00 | 0,17 | -0,33 | -0,06 | 0,01 | 0,08 | 0,39 | 9013,01 | 1,00 |
| $f[2,16]$ | 0,00 | 0,00 | 0,09 | -0,20 | -0,05 | 0,00 | 0,05 | 0,20 | 12625,43 | 1,00 |
| $f[2,17]$ | 0,00 | 0,00 | 0,10 | -0,21 | -0,06 | 0,00 | 0,05 | 0,22 | 6976,98 | 1,00 |
| $f[2,18]$ | -0,11 | 0,00 | 0,17 | -0,53 | -0,18 | -0,07 | 0,00 | 0,15 | 3329,00 | 1,00 |
| $f[2,19]$ | -0,02 | 0,00 | 0,11 | -0,28 | -0,07 | -0,01 | 0,04 | 0,19 | 4131,29 | 1,00 |
| $f[2,20]$ | 0,86 | 0,01 | 0,44 | -0,01 | 0,57 | 0,92 | 1,18 | 1,63 | 2100,06 | 1,00 |
| $\sigma_{m[1]}$ | 0,67 | 0,01 | 0,34 | 0,23 | 0,43 | 0,60 | 0,83 | 1,55 | 3348,72 | 1,00 |
| $\sigma_{m[2]}$ | 0,13 | 0,00 | 0,09 | 0,03 | 0,07 | 0,11 | 0,17 | 0,36 | 2257,12 | 1,00 |
| $\sigma_{f[1]}$ | 0,41 | 0,00 | 0,16 | 0,18 | 0,30 | 0,38 | 0,49 | 0,78 | 6076,87 | 1,00 |
| $\sigma_{f[2]}$ | 0,12 | 0,00 | 0,07 | 0,02 | 0,07 | 0,10 | 0,15 | 0,28 | 1727,77 | 1,00 |
| $lp\_\_$ | -3530,08 | 0,33 | 11,47 | -3551,97 | -3537,56 | -3530,37 | -3522,89 | -3506,84 | 1198,32 | 1,00 |

## 2.2 Chapter highlights

- Defining how the strength of sexual selection varies over a breeding season poses multiple challenges;
- In the river lamprey, we found that changes in population demographics induce within-season dynamics in sexual selection;
- Depending on the social environment faced by individual, the advantage conferred by body size varies: when the size of competitors is high, larger individuals mate more;
- The spawning timing of an individual can also interact with its body size to affect its number of matings.

Chapter 3

# How changes in reproductive timing affect the strength of sexual selection

This section corresponds to an article under preparation that will be submitted for publication in ***Journal of Evolutionary Biology***.

## Contents

# Variations in reproductive timing within and between sexes affect the strength of sexual selection and drive the evolution of sexually selected traits

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**Abstract**

Phenological shifts have been reported across various taxa and are considered a common response of organisms to climate change. Research further indicates that changes in the timing of phenological events, notably reproduction, might decouple interspecific interactions due to differential plasticity in responses to similar changes in climate between interacting species, ultimately impacting population demography. However, no study has investigated how variations in the timing of reproduction, due to potential differential phenological adjustment among individuals or sex-specific constraints, influence intra-specific interactions. In this study, we combined an Agent-Based Model (ABM) with an experimental study to investigate how variations in reproductive timing, within and/or between sexes, influence the strength of sexual selection and drive the evolution of sexually selected traits (i.e. competitive and attractive traits) in observed and simulated populations of lampreys.

We found that the bias-corrected opportunity for sexual selection $Is_{bc}$ varied across breeding scenarios, being higher in the asynchronous sex when there are inter-sexual variations in reproductive synchrony. Moreover, we found that mating success was more affected by reproductive timing than phenotypic traits conferring a mating advantage. Overall, our results suggest that scramble competition may be selected in breeding scenarios where there is an unequal shift in reproductive timing between males and females. We argue that considering different responses in reproductive timing to climate change is essential to improving our understanding of how species reproduction is influenced by climate change.

**Keywords:** reproductive timing, competitive environment, synchrony/asynchrony, phenological shift.

## 3.1 Introduction

In recent decades, growing concern about predicting the impacts of climate change has led to an increased focus on the role of phenology—the study of the timing of recurring seasonal biological events—in the field of evolutionary biology (Walther et al., 2002; Parmesan, 2006; Cleland et al., 2007). As the timing of activities such as migration and reproduction mainly relies on climatic cues, many studies have investigated whether increases in temperature and associated environmental changes influence the onset of these key life-history events. This resulted in widespread reporting of phenological shifts in response to recent climate change (e.g. Dunn, 2004; Walther et al., 2002). For instance, long-term studies monitoring fish population dynamics have shown that warming water temperatures due to climate change are associated with shifts in the phenology of reproduction. In some populations that have experienced warming, earlier migrations and spawning in the spring have been observed (McQueen and Marshall, 2017; Wedekind and Küng, 2010; Legrand et al., 2021). Changes in temperature also appeared to alter the total duration of the breeding season; warming was correlated with prolonged seasons in multi-brooded species of birds and shorter seasons in single-brooders (Halupka and Halupka, 2017).

Climate-driven changes may also influence ecological interactions at different scales (individual to community to ecosystem) and trophic levels (producers to consumers) if organisms involved display differences in phenological responses to climate change. This has been widely documented in the case of interspecific interactions, where unequal phenological shifts between interacting species have been shown to affect community structure and the stability of ecosystems (e.g. Both et al., 2009; Rafferty et al., 2015). For instance, Platt et al. (2003) highlighted a "phenological mismatch" between food resource availability and consumer reproduction, which can have drastic effects on consumers' fitness, resulting in

population declines. Interestingly, there is a lack of knowledge regarding potential differences in phenological plasticity between individuals within a species, especially about the influence they may have on mating dynamics during reproduction. Indeed, climate change may also affect the coincidence of sexually available individuals, due to intra-sexual and/or inter-sexual variations in their sensitivity or responses to environmental cues. Sex-specific differences in light or temperature sensitivity could be essential in mediating responses to climate change, although the mechanisms that may underlie such sex-specific sensitivity are limited due to the lack of comparison between sexes (Williams et al., 2022). Recently, McLean et al. (2022) showed that male and female deer mice (*Peromyscus maniculatus*) use temperature as a breeding cue in different ways; females respond more negatively than males, inducing sex-specific phenological timing.

These asynchronous phenological changes, by inducing potential inter-individual variations in the onset of breeding both within and between sexes, may alter the seasonal pattern of sexual selection and the relative fitness implications for males and females. Indeed, the temporal clustering of reproduction is one of the cornerstones of sexual selection theory. The intensity of sexual selection is expected to be directly correlated to female synchrony (i.e. receptive females aggregated in time) and the number of sexually active males relative to the number of sexually active females in a population (i.e. Operational sex ratio, OSR) (Emlen and Oring, 1977; Shuster and Wade, 2003). If female sexual availability is synchronous, the potential for mate monopolisation by males is expected to be limited, and most males are likely to access and engage in mating with females. Under such circumstances, pre-copulatory sexual selection on male traits conferring high competitive ability and attractiveness is likely to be weak as they do not provide a mating advantage.

Changes in reproductive timing, both within and between sexes, are therefore likely to induce high variation in the social environment (OSR, density), resulting in major changes in mating dynamics. However, observing climate-driven shifts in reproductive timing and investigating their impact on the strength of sexual selection is difficult in nature for several reasons: (1) although phenological changes may occur rapidly over time in the wild (Burrows et al., 2011), long-term surveys, which are difficult to obtain, are still required to quantify these changes (Sims et al., 2004), (2) measurement of sexual selection may be sensitive to sampling effort, i.e the time span over which sampling occurs (Klug et al., 2010*b*; Carleial et al., 2023; Anthes et al., 2017), which may lead to biased estimations of its actual strength.

Here, we directly manipulated individual reproductive timing through both empirical and modelling approaches to investigate how intra- and/or inter-sexual variations in reproduction timing affect the potential strength of sexual selection. For instance, if females are accessible for mating asynchronously and males are all available on the first mating opportunity (in a male synchrony/female asynchrony scenario), we hypothesize that this breeding pattern may strengthen sexual selection in males by increasing the potential for monopolisation (Emlen and Oring, 1977; Kokko et al., 2012). We used lampreys as a biological model as they are excellent candidates to fill this gap. First, the role of temperature in controlling spawning activity has been highlighted multiple times (e.g. Binder and McDonald, 2008*b*). Second, lampreys are semelparous, i.e. they have just one reproductive cycle in their lifetime, allowing sexual selection to be estimated at the end of a single reproductive season. Thirdly, previous studies showed that the duration of individual activity is short compared with the length of the breeding season (Hardisty and Potter, 1971; Docker, 2019; Daupagne et al., accepted for publication). Therefore, this pattern may induce high variations in the social environment, which may be even more pronounced in asynchronous breeding scenarios. We first estimated the

opportunity for sexual selection in two experimental groups of the European brook lamprey (*Lampetra planeri*) with two distinct breeding scenarios in which we manipulated female synchrony. However, as an empirical approach may encompass only a minor part of all possible breeding synchrony scenarios, modelling approaches can be used as a tool for extrapolation across a wider range of synchrony contexts and gradients. Among them, Agent-Based Models (hereafter, ABMs) are an intuitive and flexible class of computational models for simulating ecological scenarios (DeAngelis and Grimm, 2014; Lamarins et al., 2022) and therefore assessing the short- and long-term effects of variations in reproductive timing. By explicitly modelling interactions between individuals, this approach allows us to identify how sexually selected traits interact with demographic effects in response to environmental pressures (Dunlop et al., 2009). The reliability of the model predictions was tested by comparing the predicted strength of sexual selection between simulated populations based on the reproductive ecology of lampreys with estimates derived from actually observed reproductive acts. Combining experimental and modelling approaches therefore enabled us to provide formal predictions on how intra-sexual and/or inter-sexual variations in reproduction timing affect the potential strength of sexual selection.

## 3.2 Methods

### 3.2.1 Empirical study

#### 3.2.1.1 Field collection and maintenance

Individuals were sampled on 21 March 2022, as the European Brook lamprey spawns between April and June (Hardisty and Potter, 1971). Fourty-two individuals (21 females, 21 males) were electrofished during their upstream migration on the Nivelle river (Southwest France). Lampreys were transferred to the INRAE experimental facilities in Saint-Pée-sur-Nivelle, France

(ECP, INRAE, 2018). On the $22^{nd}$ of March (i.e. one day before the start of the experiment), each individual was tagged with a unique combination of one or two spots of UV-fluorescent visible implant elastomer (VIE, yellow, orange, red or blue) injected in the posterior dorsal fin to allow individual recognition under both white light and UV light (Silver et al., 2009). We measured two morphological traits: total body length ($\pm$0.5 mm) and total mass ($\pm$0.5 g) as the two traits may be targeted by sexual selection (Malmqvist, 1983) and their combination is an indicator of fish condition (i.e. their quality and fecundity). Biometry and tagging were performed after the fish were placed in an anaesthetic bath containing benzocaine solution (0.3ml/L) for 5 minutes.

#### 3.2.1.2 Experimental setup

The experiment took place in a 25 meters long annular tank, supplied with water from the Nivelle river, in a semi-open circuit, with a water replacement of 6 litres per minute. We separated the tank into two linear sections of 1.5 m3 (2 m long, 1 m wide, 0.7 m water depth) corresponding to respectively the "synchronous" spawning group and the "asynchronous" group. Ten males and ten females were placed in the synchronous group on the $23^{rd}$ of March. Eleven males and two females were placed in the asynchronous on the same day; then nine females were progressively added, one every other day (so the last one was added on the $10^{th}$ of April). To mimic natural spawning conditions, current speed was set to 0.2 m/s, spawning substrate and shelters (tiles, woody debris) were provided, and water temperature (known to affect spawning activity, Hardisty and Potter, 1971) was monitored daily and followed that of the river. To facilitate observation, the spawning substrate was limited to one 0.48 m2 (0.6 x 0.8 m) box filled (0.1 m depth) with a mixture of gravels and pebbles corresponding to the spawning habitat usually selected by lampreys (Jang and Lucas, 2005; Daupagne et al., 2022). The aquarium was lighted with white neon bulbs following the natural photoperiod (12:12 with 30 minutes of dawn and dusk), but since brook lamprey is active 24 h per day

during the spawning period (Sjoberg, 1977), we positioned UV light above substrate boxes to identify individuals by night. One video camera (Basler acA1920-40gc) continuously recorded lamprey's activity in each spawning group throughout the experiment. The experiment ended on the $20^{th}$ of April, at the death of the last individual.

#### 3.2.1.3 Mating behaviour characterisation and definition of mating success

All video footage was analysed with BORIS software (Friard and Gamba, 2016) to note the exact timing of each mating behaviour and the identity of the individuals involved. For each day of the experiment, we analysed 12 daily video sequences of 5 minutes by hour, thus amounting to 1 hour per day. Numerous attempts to copulate were interrupted before the male could squeeze the female's abdomen. We therefore distinguished successful matings acts (i.e. those ending with squeezing and quivering) from unsuccessful mating acts. Each mating act usually involved one male and one female but sometimes, two or more males copulated simultaneously with the same female, as highlighted by previous studies (Case, 1970; Docker, 2015; Huggins and Thompson, 1970; Malmqvist, 1983, Daupagne et al., accepted for publication). In such a case, the identity of each male involved was noted, so the female was considered to have mated with each of them. To estimate sexual selection related to both mate choice and mating competition, we calculated several measures of sexual selection based on the mating success of both males and females. To fit the genetic definition of mating success (Jones and Ratterman, 2009), we calculated the $MS_P$ defined as the number of partners with which mating occurred (i.e. the number of mates). However, since we have the necessary data, we also calculated the $MS_M$ as the number of mating acts to fit the behavioural definition of mating success.

#### 3.2.1.4 Statistical analysis

We estimated the potential strength of sexual selection by calculating the opportunity for sexual selection ($Is$) as follows:

$$I_s = \frac{\sum_{i=1}^{N}(w_i - \overline{w_i})}{N} * \frac{1}{\overline{w}^2} \tag{3.1}$$

where $N$ is the total number of males/females in the population, $w_i$ the mating success of each male/female, and $\overline{w_i}$ the mean male/female mating success of all males/females (Wade, 1979; Wade and Arnold, 1980).

Recent works by Klug et al. (2010*a*), Krakauer et al. (2011) and Jennions et al. (2012) demonstrated that $Is$ is connected to OSR, even in the absence of sexual selection, due to a decrease in the mean mating success of the dominant sex as the OSR becomes more biased. To account for this bias, we characterised the expected $Is$ under random mating given the observed OSR and mean mating success. For this purpose, we randomly distributed the total number of mating acts among all individuals in each sex. We iterated this distribution 10000 times and we subtracted the median $Is$ of these simulations from the observed $Is$. The obtained number was defined as the bias-corrected $Is$ ($Is_{bc}$). When simulating $MS_P$, we made sure that no individual was assigned a higher mating success than the actual total number of individuals of the opposite sex. Sex-specific differences in variances were assessed using Levene's F test.

We also characterised pre-copulatory sexual selection acting on male or female body size by fitting a quadratic regression between individual relative mating success and individual body size in each sex and in both AF-SM and SF-SM scenarios. As body size and body mass were highly correlated (Spearman's rank correlation test, $p$ = 0.84 in males and $p$ = 0.75 in females), the selection gradients were only performed with body size. All statistical analyses were performed using R software version 4.0.4 (R Core Team, 2022).

### 3.2.2 Agent-Based Model

We designed an agent-based model (ABM) to simulate populations in which both males and females interact according to individual characteristics (time of arrival in the mating pool, competitivity) and have a preference for a certain sexually attractive trait (e.g. morphological traits such as size or courtship display) that reflects individual quality in term of fecundity. As recently reviewed by Lamarins et al. (2022), traditional analytical approaches (i.e. differential-equation and difference equation models) do not allow to simulate complex ecological and evolutionary scenarios as they consider those processes to be homogeneous within groups of individuals (the population or life stages). Yet, group composition is constantly changing in terms of phenotypes and genotypes, impacting individual choices, related to local and proximate conditions, and their group-level outcomes (i.e. emerging fitness effects). The general approach of our model will be defined following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006; Grimm and Railsback, 2005). We used the modelling platform NetLogo version 6.2.1 (Wilensky, 1999) to design our ABM.

#### 3.2.2.1 Purpose

We used an ABM to explore how the level of reproductive timing between individuals of the same population (within and between sexes) affects the opportunity for sexual selection through a breeding season.

#### 3.2.2.2 Entities, state variables, and scales

The model has two kinds of entities: lampreys (individual level) and the global environment (population level). Each individual is characterised by its identity number, sex, and other state variables described in Table 3.1. Those descriptors are values that vary among individuals within each population and scenario. We parameterised these variables based on an

experiment made on *L. fluviatilis* in which we had complete knowledge of the mating acts that occurred. We first consider the attractive trait ($z_m$ and $z_f$) as an honest indicator of an individual's fecundity. Therefore, we modelled both males' and females' fecundity ($g_m$ and $g_f$) as:

$$\begin{aligned} g_m &= z_m * 114.4 \\ g_f &= z_f * 3444.6 \end{aligned} \tag{3.2}$$

These calculations (see Table 3.2 for $z_m$ and $z_f$ mean values) give a mean of 580 possible mating acts in males (mean number of mating attempts observed in *L. fluviatilis* males, Daupagne et al., accepted for publication) and of 17223 eggs in females (estimated number of eggs for *L. fluviatilis* females with a observed mean size of 284.2 mm, Daupagne et al., accepted for publication). This estimation is based on the relationship between fecundity (the total number of eggs, y) and the total length (x) as y = 0.0014x 2.8896 (Docker, 2019). Gametes stock is complete from the beginning of the spawning period and there is no stock renewal through it.

We then calculated the number of mating opportunities in males and females ($o_m$ and $o_f$) according to the values of the attractive and competitive traits. Indeed, we assumed a trade-off between reproductive investment (i.e. energy allocated to the reproductive activity) and somatic investment (e.g. energy allocated to tissue maintenance). Individuals that allocate more energy to their competitive ability (highly competitive individuals) and gamete production (highly attractive individuals) during reproduction had a reduced number of mating opportunities (i.e. lower longevity). This implies a cost associated with a "missed mating event". We therefore modelled $o_m$ and $o_f$ as:

$$o_m = 2550 - [(z_m + c_m) * 127.5]$$
$$o_f = 1862 - [(z_f + c_f) * 93.1] \quad (3.3)$$

These calculations (see Table 3.2 for $z_m$, $z_f$, $c_m$ and $c_f$ mean values) give a mean of 1275 mating opportunities in males (mean number of time steps between the start of the experiment and the death of one male, Daupagne et al., accepted for publication) and of 931 mating opportunities in females (mean number of time steps between the start of the experiment and the death of one female, Daupagne et al., accepted for publication). See below how we modelled the "temporal resolution" of the model.

The global environment was first characterised by the type of *breeding scenario*. The type of breeding scenario reflected whether or not reproductive timing varied between individuals of the same sex as well as between males and females. There are four types of scenarios: (1) male asynchrony/female asynchrony (hereafter, AM-AF), (2) male asynchrony/female synchrony (AM-SF), (3) male synchrony/female asynchrony (SM-AF) and (4) male synchrony/female synchrony SM-SF) (see section 3.2.2.4 for more details). We also investigated how the *level of asynchrony* (weak asynchrony/strong asynchrony) may impact sexual selection. Therefore, both the type of breeding scenario and the level of asynchrony defined the parameter value of $t_m$ and $t_f$ (see Table 3.1, and section 3.2.2.4 for more details). We also compared these four breeding scenarios at two distinct levels of *population density*: (1) at low density, in populations constituted of 22 individuals, corresponding to the density of individuals used in the experimental study (see section 3.2.1) (2) at high density, in population constituted of 200 individuals. The initial sex ratio remained fixed (1:1) in each population simulation. Overall, the global environment was characterised by: the type of breeding scenario, the level of asynchrony and the population density.

**Table 3.1.** Individual parameters are values that vary among individuals within each population/simulation and determine mating probabilities. m subscript is for male traits, and f subscript is for female traits. $t_m$ and $t_f$ may be fixed depending on the breeding scenario (see section 3.2.2.4)

| Symbol | Description | Distribution/values |
|---|---|---|
| $z_m$ or $z_f$ | Attractive male or female trait value under sexual selection | Truncated Gaussian distribution with mean $\overline{z_m}$ or $\overline{z_f}$, standard deviation $\sigma z_m$ or $\sigma z_f$, and minimum zero |
| $c_m$ or $c_f$ | Competitive male or female trait value under sexual selection | Truncated Gaussian distribution with mean $\overline{c_m}$ or $\overline{c_f}$, standard deviation $\sigma c_m$ or $\sigma c_f$, and minimum zero |
| $t_m$ or $t_f$ | Time of arrival of males or females in the mating pool | If synchronous: $t_m$ or $t_f$ = 1, if asynchronous $t_m$ or $t_f$ = [1:900] or [1:3000], see details 3.2.2.4 |
| $g_m$ or $g_f$ | Number of possible mating acts in males or absolute fecundity of females | Given by Equation 3.2 |
| $o_m$ or $o_f$ | Total number of mating opportunities | Given by Equation 3.3 |
| $P$ | Number of progeny produced | Truncated Gaussian distribution with mean $\overline{P}$, standard deviation $\sigma P$, and minimum zero |

**Table 3.2.** Input variables are model parameters that are fixed within each population/simulation. m subscript is for male traits, and f subscript is for female traits.

| Symbol | Description | Values |
|---|---|---|
| $N$ | Population density | 22 or 200 |
| - | Sex-ratio | 1:1 |
| $p_m$ or $p_f$ | Individual male or female preference | 5 |
| $s_m$ or $s_f$ | Male or Female preference strength | 2 |
| $\overline{z_m}$ or $\overline{z_f}$ | Mean value of male or female attractive trait $z$ | 5 |
| $\sigma z_m$ or $\sigma z_f$ | Standard deviation of male or female attractive trait $z$ | 1 |
| $\overline{c_m}$ or $\overline{c_f}$ | Mean value of male or female competitive trait $c$ | 5 |
| $\sigma c_m$ or $\sigma c_f$ | Standard deviation of male or female competitive trait $c$ | 1 |
| $\overline{P}$ | Mean number of progeny produced $P$ | 60 |
| $\sigma P$ | Standard deviation of number of progeny produced $P$ | 15 |

The "temporal extent" scale of the model is one generation, i.e. the time for all individuals to become sexually available, mate, produce offspring and die. The passage of time (i.e. the "temporal resolution") is simulated in our model using discrete time steps. In a previous experiment on *L. fluviatilis* (Daupagne et al, accepted for publication), we highlighted that the average duration of individual mating activity is 234,52 hours and that individual attempts to mate on average 490.4 times. Thus, an individual attempts to mate every 0.48 hours on average. We therefore decided to represent one time step as one mating opportunity and we fixed $\Delta t$ = 28.8 minutes as the increment at which time is advanced.

This model is not spatially explicit; we did not subdivide the global environment to create multiple mating subgroups. We consider that all the individuals that are simultaneously active in a population may meet and that there are no spatially formed subgroups.

#### 3.2.2.3 Process overview and scheduling

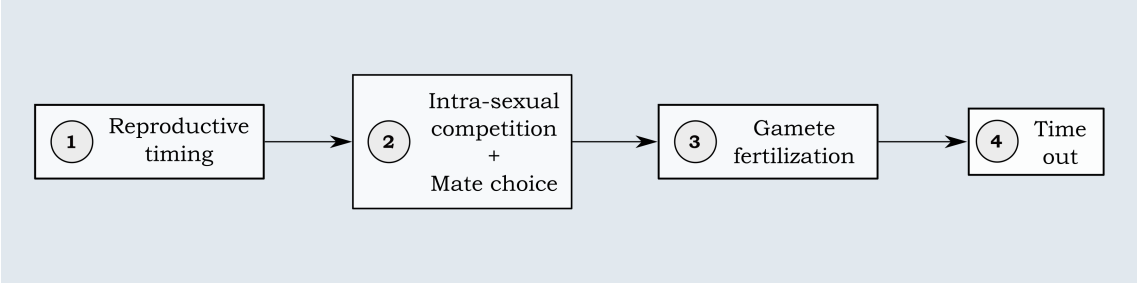


**Figure 3.1.** Process overview and scheduling

#### 3.2.2.4 Submodels

**1 - Reproductive timing**

The first process executed by the model is the time of arrival of individuals in the mating pool. This variable determines the sexual availability of individuals and therefore their reproductive timing. If one sex is considered as "synchronous", there is no inter-individual variation in reproductive timing and all individuals of this sex are sexually available at the beginning

of the experiment i.e. at the first time step. If one sex is considered "asynchronous", individuals join the mating group progressively. We designed the timing of arrival to mimic the asynchrony level induced in our experiment (see 3.2.1). As each female was added every 48 hours and that one time-step represent 0.48 hours, we simulated the arrival of asynchronous individuals every 100 time steps. We then modelled the temporal extent of arrival in two different ways. In *weak asynchrony* conditions (see section 3.2.2.2), we simulated the timing of arrival of asynchronous individuals until day 18 (= 432 hours = 900 time steps) as we experimentally did. In *strong asynchrony* conditions, we extended the timing arrival until day 60 (= 1440 hours = 3000 time steps, i.e. average duration of a breeding season) to reproduce the level of asynchrony we may find in natural conditions (Johnson et al., 2015).To do that, we generated for each sex a sequence of numeric values ranging from 1 to 900 or 3000, with an increment of 100. We then randomly attributed a value to each individual that would define its own timing of arrival in the mating pool ($p_{m/f}$). If the number of individuals was greater than the number of values in the sequence (e.g. in weak asynchrony and high-density conditions), a new sequence was immediately generated once the previous sequence had become empty. Under such conditions, this means that some individuals had the same $t_{m/f}$ values.

**2 - Intra-sexual competition and mate choice**

The mate choice procedure is the following: all sexually available individuals of the population can encounter each other but the probability of meeting is related to the competitiveness trait values of both males and females. Two individuals with high competitiveness values meet first, followed by individuals with intermediate values and finally individuals with low competitiveness values. Each individual decides then to mate or not with its potential partner based on a threshold decision rule (Janetos, 1980). In our simulations, individual mate choice is probabilistic and is described by an open-ended preference function, i.e. a sigmoid describing a preference for potential mates with higher $z$ values.

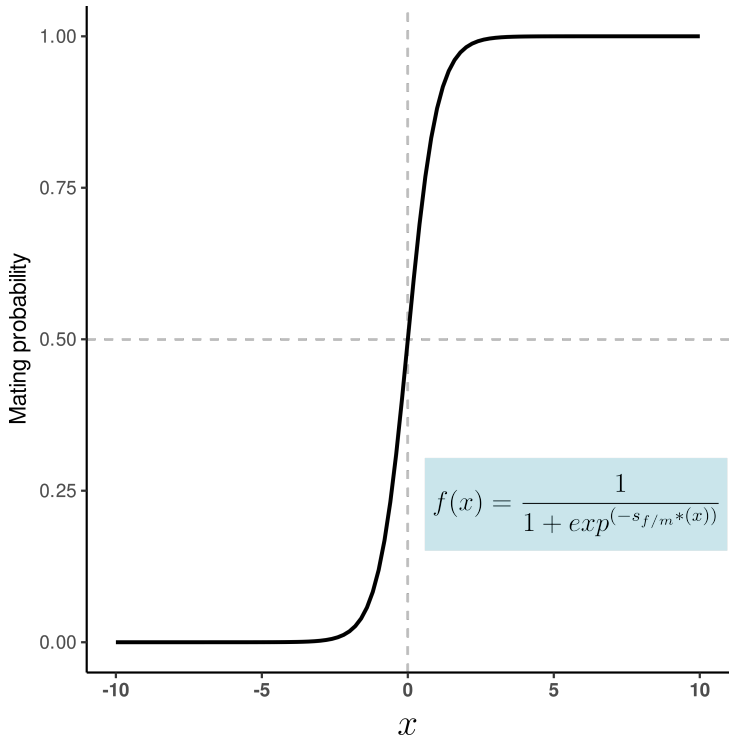


**Figure 3.2.** Open-ended preference function describing the probabilities of an individual mating with a partner showing a sexually selected trait value $z$. The $x$ axis refers to the difference between the trait value of the partner $z_{m/f}$ and the focal individual preference $p_{m/f}$ (see 3.4)

Sigmoid functions are described by two parameters: an intercept and a slope. In females for instance, the intercept is the $p_f$ value above which a male has a 50% probability of being accepted, i.e. when a male $z$ value is equal to the female preference value ($z_m = p_f = 5$). The slope $s_f$ determines the steepness of the sigmoid and is here fixed to two. Fixing this parameter to two means, for instance, that males with a $z_m$ trait value at 5% of the normal distribution of the male trait in the population have a 5% probability of being accepted.

$$\begin{aligned} P_f &= \frac{1}{1 + exp^{(-s_f * (z_m - p_f))}} \\ P_m &= \frac{1}{1 + exp^{(-s_m * (z_f - p_m))}} \end{aligned} \tag{3.4}$$

If both a male and female mutually accept to mate, they form a pair and are no longer

available to mate again for the current time step. If at least one individual rejects the mating, neither of them returns to the mating group and both are single for the current time step. When the population's size is an odd number, or if one sex is no more available, the least competitive individuals or the least attractive individuals of the mating group remain unmated. As implicitly suggested above, we consider there is no within-population variation in male and female mating preference (i.e. individuals from the same sex and population have similar preferences for mate traits) and no variation in preference strength (i.e. in their choosiness).

We estimated the opportunity for sexual selection for each sex at the end of the simulation (i.e. generation) $I_s$ (see section 3.1). As recommended by Janicke and Morrow (2018), we also calculated the expected $Is$ values under random mating for each simulation condition. Under random mating conditions, the modelling process of the intra-sexual competition was not determined by competitive traits values and occurred randomly while the mate choice procedure was not implemented.

In addition to $Is$, we characterised sexual selection acting on male $c_m$, $z_m$ and $t_m$ traits as well as female $c_f$, $z_f$ and $t_f$ traits by fitting a quadratic regression between individual relative mating success and the trait of interest of a given sex for every replicate. This enabled us to investigate whether sexual selection in each simulation was either directional, stabilizing or disruptive. We also fitted Bateman gradients ($\beta_{SS}$) by fitting a linear regression between relative reproductive success and relative mating success of a given sex (Bateman, 1948). Each individual's relative mating/reproductive success was calculated by dividing the mating/reproductive success of that individual by the mean mating/reproductive success for all individuals of its sex. This enables to compare and interpret selection gradients between

scenarios with varying mean fitness.

#### 3 - Gamete fertilisation

The gamete fertilisation period following each mating occurs as follows: the female produces on average 60 eggs at each mating (Malmqvist, 1983; see 3.1) and we consider that each male that succeeds to mate with a female fertilises all the eggs released. For simplicity, we do not integrate alternative mating behaviours (e.g. sneaky matings by satellite males) which would potentially affect fertilisation success. Similarly, every fertilised egg hatches; we do not integrate external mortality factors affecting hatching success (e.g. predation or egg contamination).

#### 4 - Permanent time out

Individuals permanently leave the mating pool when they reached either their total number of possible mating events/do not have any eggs left ($g_m$ and $g_f$) or their total number of mating opportunities ($o_m$ and $o_f$).

#### 3.2.2.5 Design concepts

The *basic principle* in this model is the concept of reproductive synchrony – temporal variability in the individual starting time of the reproduction between and among sexes - which is incorporated in the model design through the $t_m$ and $t_f$ variable (see 3.2.2.4). The model also implements hypotheses in its design related to the theory of energy allocation. We consider there is a trade-off between energy allocated to somatic investment and reproductive investment: since the energy used for reproduction (gamete production, competition) is not allocated to somatic investment (e.g. tissue repair, immune function), it has a cost on survival. Here, the number of possible mating acts in males ($g_m$) and the absolute fecundity of females ($g_f$) is directly related to gametic investment while the total number of mating opportunities

($o_m$ and $o_f$) is related to somatic investment. Both attractive and competitive traits can indirectly improve individual fitness: high values of competitiveness and attractiveness improve the mating success of individuals through respectively priority access to mating partners and higher probability of being chosen but implies survival cost (i.e. reduced mating opportunities in males and females).

*Sensing* is important in this model: lampreys are assumed to have a criterion (attractive trait) to discriminate individuals' genotypes. This model assumption is quite common as numerous studies highlighted a "good genes" mechanism that is defined as a mate preference for traits that are honest indicators of a partner's ability to pass on genes that will increase the offspring's reproductive success (gamete quantity) (Yasui, 1998). *Interactions* play a significant part of the model. Individuals of one sex indirectly interact with each other through same-sex competition to access and mate with partners of the opposite sex. Second, males and females directly interact with each other via reciprocal choice, mating and gamete release.

*Stochasticity* appears at different scales. First, individuals are sampled randomly to constitute the mating pool. Mate choice itself is a highly stochastic process as it results from mutual acceptance of both partners, through their respective mating preferences.

## 3.3 Results

### 3.3.1 Empirical study

Body size did not differ between sexes (Kruskal-Wallis test: $H_1$ = 1.6, P > 0.1), males measured on average (±SD, minimum:maximum) 130 mm (±6.9, 119:145) while females measured on average 133 mm (±8.1, 120:153). The body size of females and males did not differ between the two groups (Kruskal-Wallis test: $H_1$ = 0.2, P > 0.5).

The length of the mating season, calculated as the time between the first and last day on which matings were observed, lasted 18 days in the AF-SM group and 6 days in the SF-SM group. In the AF-SM individual group, females individually took part in spawning during a much shorter period than males in terms of number of hours between the first and last mating attempt, on average 32.8 hours in females and 145.1 hours in males (Kruskal-Wallis test: $H_1$ = 0.02, P < 0.05). In the SF-SM group, no differences were observed between sexes (Kruskal-Wallis test: $H_1$ = 0.37, P > 0.1), and the duration of the individual mating season was 99.6 hours in females and 95.2 in males.

In the AF-SM group, a total of 62 mating attempts were observed, among which 44 were successful matings while in the SF-SM group, 120 mating attempts were observed, among which 100 were successful. A chi-square test of independence was performed to examine the relationship between the breeding scenario and the proportion of successful matings. The relation between these variables was not significant, $\chi^2$ (1, N = 182) = 2, p = 0.16). The number of successful matings was correlated to the number of mates for males (Spearman rank correlation: rs = 0.86, N = 21, P < 0.001) and for females (rs = 0.98, N = 21, P < 0.001).

In the SF-SM group, $Is_{bc}$ with $MS_P$ was slightly higher for males than for females while $Is_{bc}$ with $MS_M$ was slightly lower for males (Table 3.3). A large part of observed $Is$ was explained by random variation in both sexes when $Is$ was calculated with $MS_P$. When females

arrived asynchronously (AF-SM group scenario), $Is_{bc}$ was much higher for females than for males, both when mating success was calculated as $MS_P$ and $MS_M$. The observed variation was not induced by random variation in females but was in males when mating was calculated as $MS_P$. $Is_{bc}$ values observed are similar to those obtained in the ABM simulations where the asynchrony was strong and the density low (Fig. 3.5, c). Variances in relative mating success were not significantly different as a function of sex, neither for $MS_P$ or $MS_M$ (F = 2.08, P = 0.16 and F = 0.76, P = 0.39 respectively, 3.3).

**Table 3.3.** Estimates of mating success and the potential strength of sexual selection in *Lampetra planeri* males and females. Number of individuals (N), mean mating success, standard deviation (SD), observed opportunity for sexual selection ($ObsIs$), and bias-corrected Is ($Is_{bc}$) are presented with mating success calculated either as the number of partners ($MS_P$) or the number of successful mating acts ($MS_M$). Differences in variances for mating success were estimated via Levene's test.

| | **Males** | | | | | **Females** | | | | | **Levene's test** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $N$ | $Mean$ | $SD$ | Obs$Is$ | $Is_{bc}$ | $N$ | $Mean$ | $SD$ | Obs$Is$ | $Is_{bc}$ | F | Df | P |
| $MS_P$ | | | | | | | | | | | | | |
| **AF/SM** | 11 | 2.09 | 1.37 | 0.43 | **0** | 11 | 2.09 | 2.84 | 1.85 | **1.37** | 0.6 | 20 | 0.4 |
| **SF/SM** | 10 | 5.1 | 2.64 | 0.27 | **0.09** | 10 | 5.1 | 2.23 | 0.19 | **0.02** | 0 | 18 | 1 |
| $MS_M$ | | | | | | | | | | | | | |
| **AF/SM** | 11 | 4 | 3.32 | 0.69 | **0.56** | 11 | 4 | 7.03 | 3.09 | **2.96** | 0.3 | 20 | 0.6 |
| **SF/SM** | 10 | 10 | 5.29 | 0.28 | **0.22** | 10 | 10 | 5.42 | 0.29 | **0.24** | 0.4 | 18 | 0.5 |

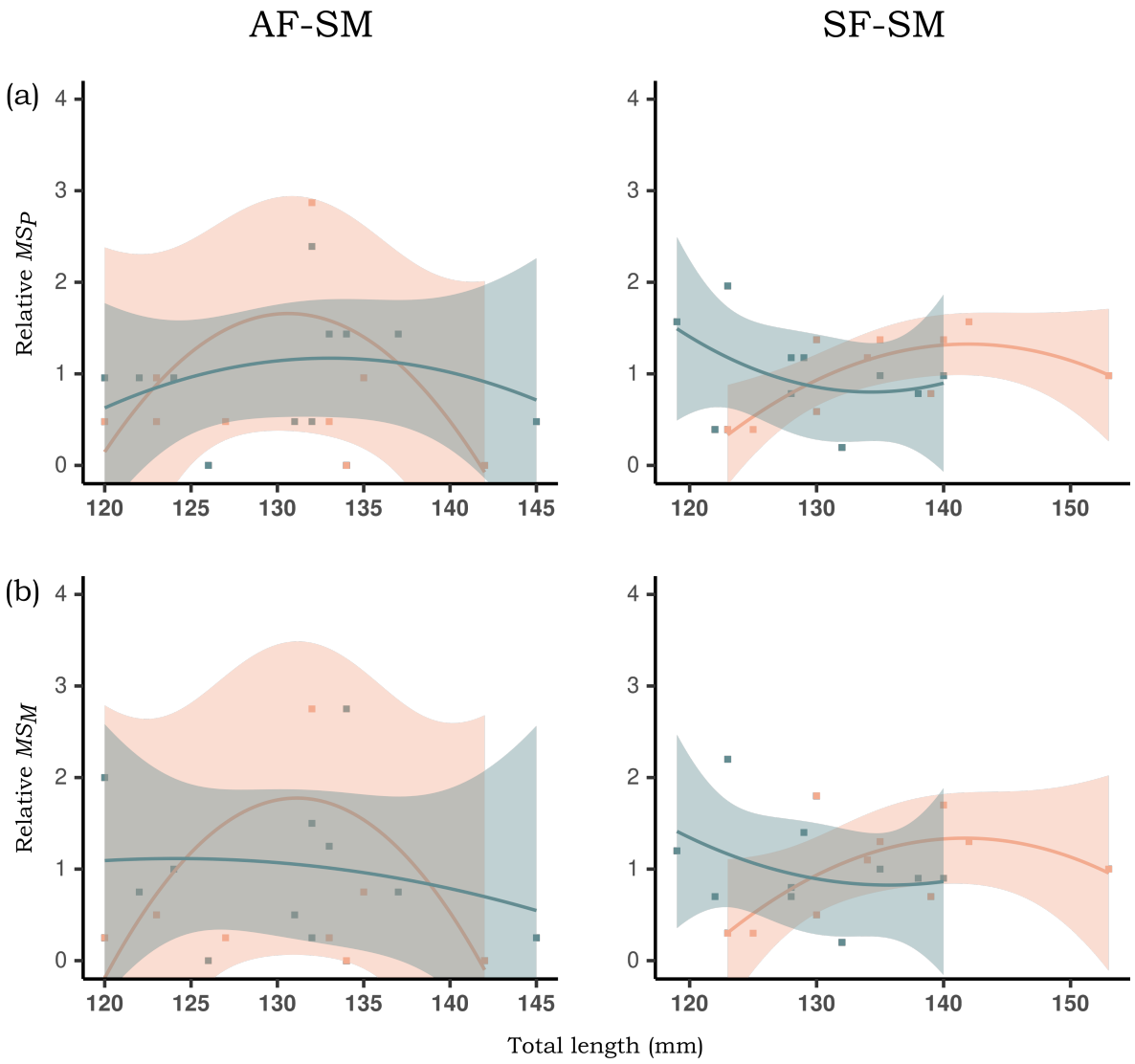


**Figure 3.3.** Selection gradient on total length obtained from the experimental study (AF-SM: asynchronous females/synchronous males, SF-SM: synchronous females/synchronous males) in a population with low density (11M/11F) and weak asynchrony (females arrival within 18 days). Mating success is calculated either as **(a)** the number of partners or **(b)** the number of matings. Colours represent the 95% confidence interval for each sex (blue: males, orange: females).

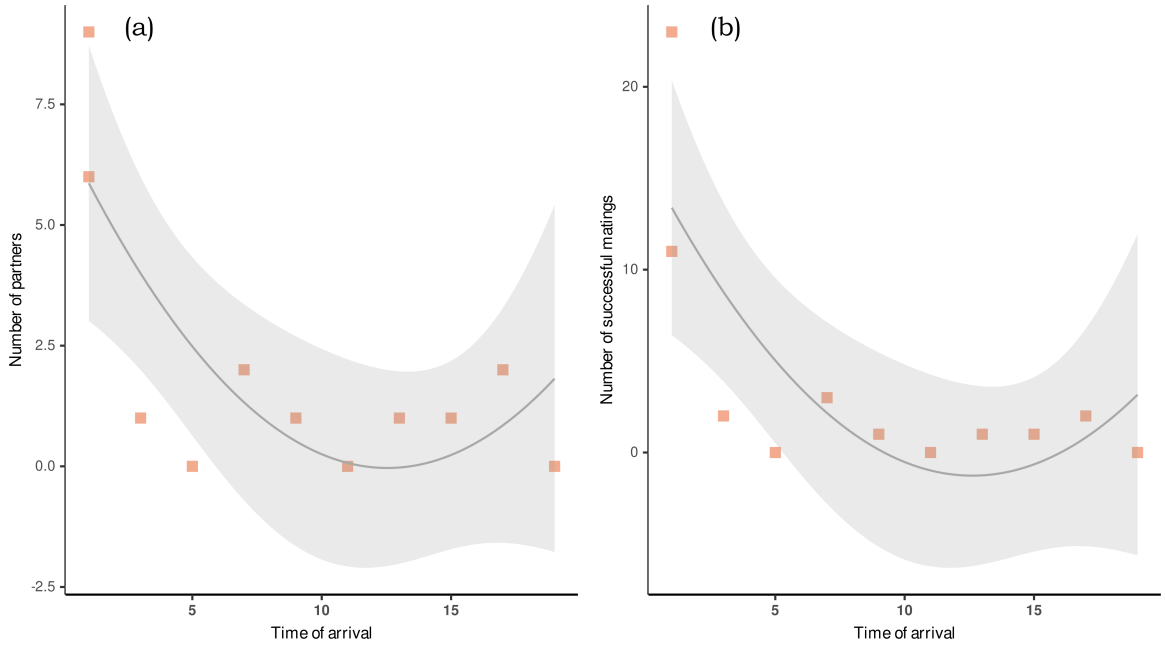


**Figure 3.4.** Selection gradient on the timing of arrival obtained from the experimental study in a population with low density (11M/11F) and weak asynchrony (females arrival within 18 days). Mating success is calculated either as **(a)** the number of partners or **(b)** the number of matings. The grey area represents the 95% confidence interval

## 3.3.2 Agent-Based Model

### 3.3.2.1 Opportunity for sexual selection

In weak asynchrony conditions (Fig. 3.5 a, b), $Is$ values slightly differed between the four breeding scenarios (AF-AM, AF-SM, SF-AM and SF-SM) and between the sexes but remained low, although higher than what would be expected under random mating. In simulations at low density (Fig. 3.5, a), females $Is$ values were higher than males' in the AF-SM (mean $Is_{females}$ = 0.18, $Is_{males}$ = 0.11) and SF-SM ($Is_{females}$ = 0.41, $Is_{males}$ = 0.21) scenarios while they were lower in the SF-AM scenario ($Is_{females}$ = 0.12, $Is_{males}$ = 0.22). In simulations at high density (Fig. 3.5 b), the $Is$ values pattern was similar to that of the simulations at low density although values were slightly higher overall.

In strong asynchrony and low-density conditions (Fig. 3.5 c), the pattern of $I_s$ values remained similar: $Is_{females}$ values were on average higher than males' values in the AF-SM ($Is_{females}$ = 1.36, $Is_{males}$ = 0.45) and SF-SM ($Is_{females}$ = 0.42, $Is_{males}$ = 0.20) scenarios while they were lower in the SF-AM scenario ($Is_{females}$ = 0.48, $Is_{males}$ = 2.20). In simulations with high density (Fig. 3.5 d), $Is_{females}$ values were even higher in the AF-SM scenario ($Is_{females}$ = 1.92, $Is_{males}$ = 0.36) as well as $Is_{males}$ values in the SF-AM scenario ($Is_{females}$ = 0.35, $Is_{males}$ = 2.93). As $Is_{bc}$ obtained in the experiment were closer to the $Is$ obtained in simulated populations with low density and strong asynchrony (Fig. 3.5 c), the results presented in the next section (3.3.2.2) result from these simulations.

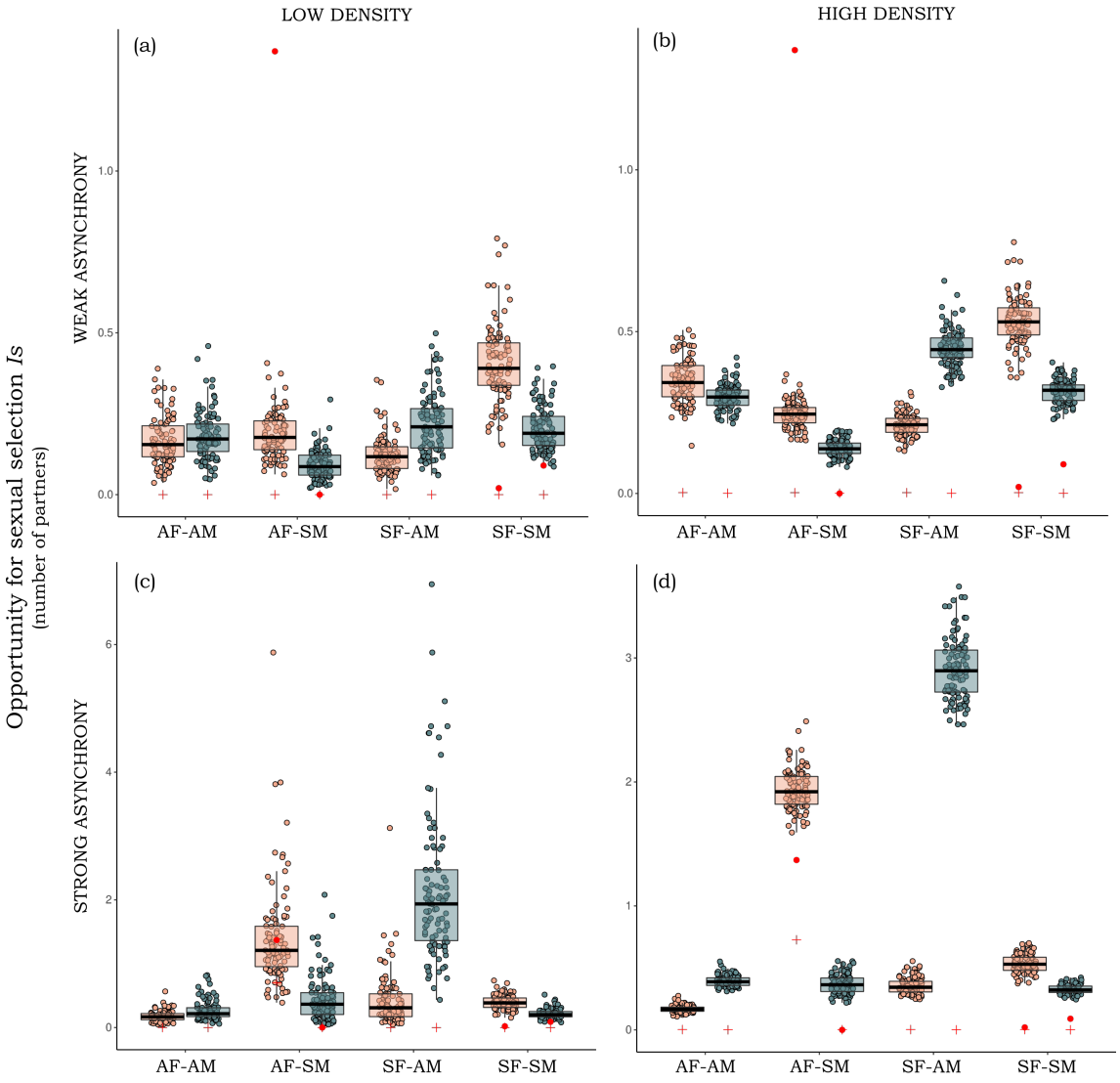


**Figure 3.5.** Influence of four scenarios of breeding synchrony (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males, SF-SM: synchronous females/synchronous males) on the opportunity for sexual selection $Is$ calculated as the number of partners. We simulated populations with: **(a)** low density (11M/11F) and weak asynchrony (males/females arrival within 18 days) **(b)** high density (100M/100F) and weak asynchrony (males/females arrival within 18 days) **(c)** low density (11M/11F) and strong asynchrony (males/females arrival within 60 days) **(d)** high density (100M/100F) and strong asynchrony (males/females arrival within 60 days). Boxplots' colours represent the sex (blue: males, orange: females). The horizontal lines indicate the median (50th percentile) and quartiles (25th and 75th percentiles), the vertical whiskers are drawn to 1.5 times the interquartile range and the open circles represent the jittered data points. The red crosses represent the average expected $Is$ values under random mating for each scenario and condition while the full red circles represent the $Is$ values obtained in the experiment.

#### 3.3.2.2 Selection gradients: strong asynchrony / low-density conditions

With relative mating success calculated as $MS_P$, the selection gradient was always stabilizing for male $z_m$ and female $z_f$ attractive traits across breeding scenarios. The selection gradient was also stabilizing for male $c_m$ competitive trait in AF-AM, SF-AM, and SF-SM breeding scenarios (Fig. 3.A.2, a). However, the stabilizing selection gradient was flatter in the SF-AM scenario even though males with low $c_m$ values had a slightly higher mating success. The same pattern was observed for the female $c_f$ competitive trait in the AF-SM scenario. In males, $c_m$ trait was under disruptive selection in the AF-SM scenario while the female $c_f$ trait was in the SF-AM scenario. Sexual selection was directional on female $c_f$ trait in the SF-SM scenario and favoured females with lower $c_f$ values. The selection gradient was always stabilizing on male $t_m$ and female $t_f$ timing of arrival in the AF-AM scenario (Fig. 3.A.6, a). In the AF-SM scenario, selection was directional on $t_f$ and favoured early-arriving females. Similarly, the selection gradient revealed a pattern of strong directional selection favouring earlier timing of arrival in males (i.e. males with low $t_f$ values).

With relative mating success calculated as $MS_M$, sexual selection always favoured males and females with higher $z_m$ and $z_f$ values in AF-AM and SF-AM scenarios (Fig. 3.A.2, b). In females, $z_f$ trait was also under direction selection in the AF-SM scenario while the male $z_m$ trait was in the SF-AM scenario, favouring individuals with higher attractive values. However, $z_m$ trait was rather under stabilizing selection in the AF-SM scenario while the female $z_f$ trait was in the SF-AM scenario. The selection gradient was stabilizing for both $c_m$ and $c_f$ traits in AF-AM and SF-SM scenarios although $MS_M$ was weakly correlated to $c_m$ and $c_f$ traits. This flat stabilizing pattern also occurred for $c_f$ trait in AF-SM and $c_m$ trait in SF-AM. In contrast, sexual selection was directional for $c_m$ in the AF-SM scenario and for $c_f$ in SF-AM and strongly favoured individuals with high competitive values. Selection gradient on $t_m$ and $t_f$ has a similar pattern to these with mating success calculated as $MS_P$.

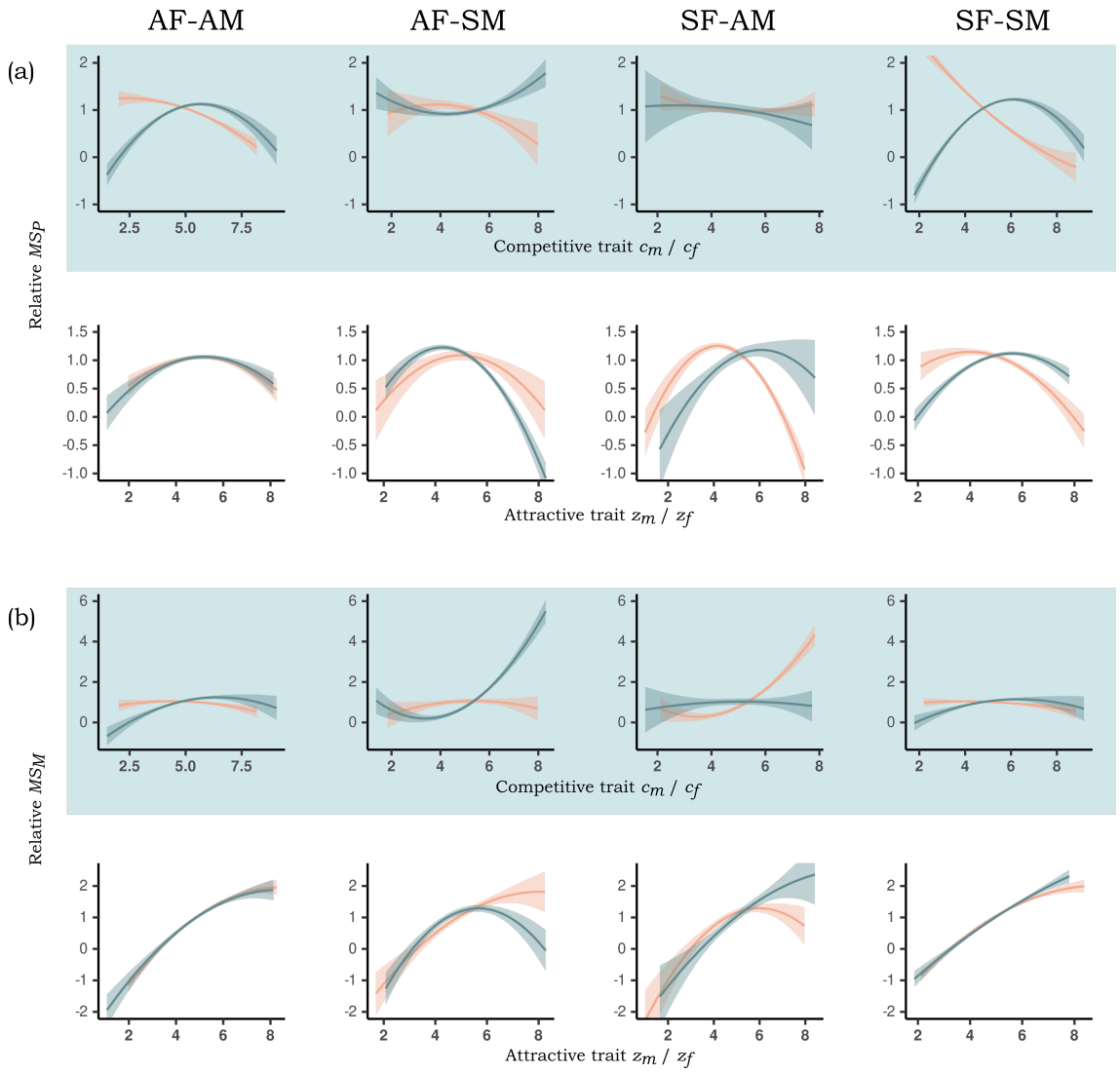


**Figure 3.6.** Selection gradients on competitive ($c_m$ and $c_f$) and attractive ($z_m$ and $z_f$) traits obtained for four scenarios of breeding synchrony (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males, SF-SM: synchronous females/synchronous males) and in a population with **low density** (11M/11F) and **strong asynchrony** (males/females arrival within 60 days). Each panel shows the selection gradient estimated from 100 simulated populations. Relative mating success is calculated either as (a) the number of partners $MS_P$ or (b) the number of matings $MS_M$. Colours represent each sex (blue: males, orange: females).

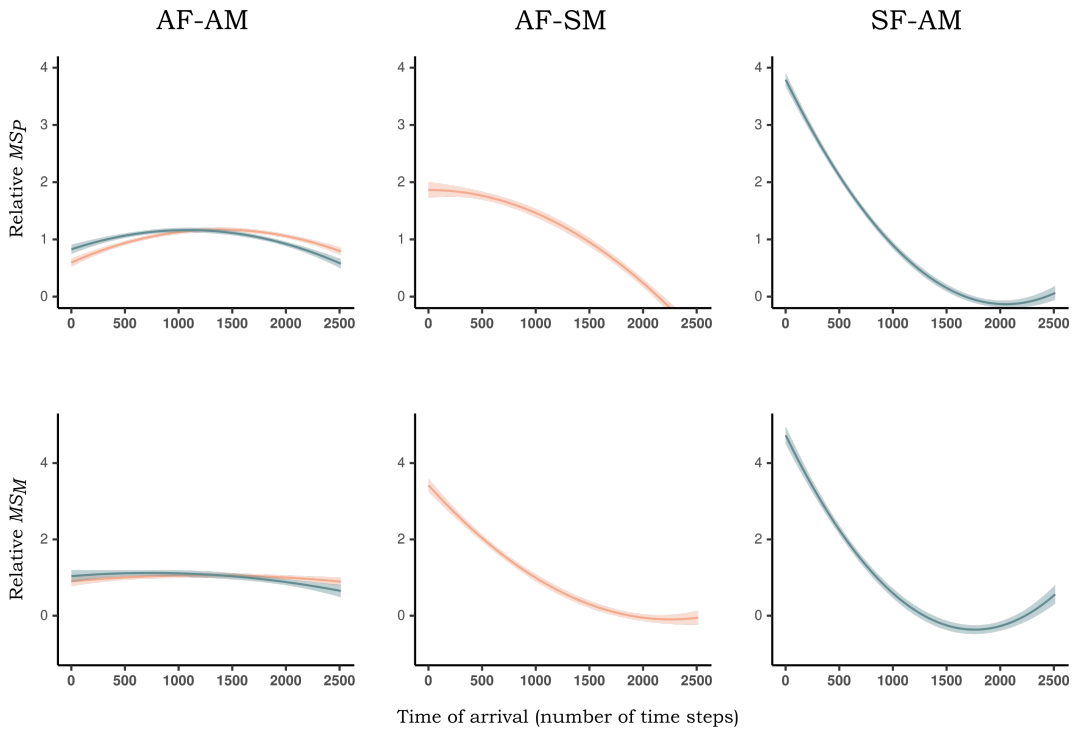


**Figure 3.7.** Selection gradient on the timing of arrival ($t_m$ and $t_f$) (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males) in a population with **low density** (11M/11F) and **strong asynchrony** (females arrival within 60 days). Relative mating success is calculated either as the number of partners $MS_P$ or the number of matings $MS_M$. Colours represent each sex (blue: males, orange: females).

#### 3.3.2.3 Selection gradients: overall comparisons between the level of densities and asynchrony

Selection gradients had a similar pattern between low and high-density conditions for both levels of asynchrony. However, when the asynchrony was stronger, the shape of the selection gradient with $MS_M$ in AF-SM and SF-AM breeding scenarios was steeper on respectively $c_m$ and $c_f$ traits at both low and high-density populations (Fig. 3.6 and 3.A.4). Additionally, the selection gradient with $MS_M$ on either male (in AF-SM scenario) or female (in SF-AM scenario) competitive trait ($c_m$ and $c_f$) was even steeper in high-density conditions (Fig. 3.A.4), highlighting a density effect when the asynchrony is stronger.

## 3.4 Discussion

We demonstrated, by combining an experiment and an agent-based model, that the bias-corrected opportunity for sexual selection $Is_{bc}$ was related to both males' and females' reproductive timing but that, contrary to the generally accepted theory (Emlen and Oring, 1977), $Is_{bc}$ was higher in the asynchronous sex in scenarios with inter-sexual variations in reproductive synchrony (i.e. in females in AF-SM scenario and in males in SF-AM scenario) (Tab. 3.3 and Fig. 3.5, 3.A.1). In the ABM, this pattern was even more pronounced in conditions with high density and strong asynchrony (Fig. 3.5 and 3.A.1, d).

In the AF-SM scenario, for instance, we initially expected that males would experience strong pre-copulatory sexual selection as the capacity of certain males to control and dominate access to potential partners is expected to be higher at a male-biased sex ratio. Although male $Is_{bc}$ was similar in AF-SM and SF-SM breeding scenarios when mating success was calculated as the number of partners (Fig. 3.5), refuting our initial prediction, it is interesting to notice that when mating success is calculated as the number of matings, male $Is_{bc}$ is higher in the AF-SM scenario. This pattern was observed in both the experimental study and in simulated populations (Fig. 3.A.1 and 3.3). In addition, a stabilizing gradient on male competitive trait was consistently observed except in the simulated AF-SM scenario, in which there was a directional selection gradient towards males with highly competitive values (Fig. 3.6, b). The same pattern is observed in females in the SF-AM scenario. This only occurs when mating success is calculated as the number of matings, suggesting that competitive individuals are unable to control total access to mating partners, but still reproduce at a higher rate than less competitive individuals when the opposite sex is asynchronous. Still considering the simulated AF-SM scenario, we can also observe that the selection gradient on the male attractive trait stabilises around mean values, whereas it is always directional

toward large values in all the other breeding scenarios. This may be explained by the trade-off we modelled between reproductive investment and somatic investment: individuals that allocated more energy to their competitive ability and gamete production during reproduction had lower longevity. In initially non-biased (AF/AM, SM/SF) and female-biased (AF/SM) scenarios, being very competitive does not bring a strong mating advantage in males as all of them may form a mating pair. In such a case, being highly attractive is more advantageous as it confers higher reproductive success. In the AF/SM scenario, on the other hand, being both competitive and attractive is too costly in terms of potential mating opportunities. We studied the selection gradient on total length obtained from the experimental study to test whether the potential advantage of large size in acquiring mates or matings differed between the two breeding scenarios, but no clear pattern emerged from this analysis (Fig. 3.3).

Interestingly, variations in $Is_{bc}$ translated into strong selection on male $t_m$ and female $t_f$ reproductive timing in SF-AM and AF-SM scenarios, respectively; both when $Is_{bc}$ is calculated as the number of partners and the number of matings (Fig. 3.7). Individual mating success and reproductive success were, therefore, both negatively correlated with $t_m$ and $t_f$, generating directional sexual selection for early arrival. This correlation was also observed in the experimental study, where the two females arriving first in the mating pool mated with a higher number of males and at a higher frequency (Fig. 3.4). Surprisingly, early-arriving individuals did not have a mating advantage in the AF-AM scenario. We initially expected that early-arriving individuals would maximise mating opportunities with multiple partners and achieve greater reproductive success. This may be explained by the fact that the time between two successive arrivals is relatively long (even in weak asynchrony conditions, Fig. 3.A.6, 3.A.7) and that individuals that start mating early deplete their stock of gametes or energy (mating opportunities) before the arrival of new potential partners.

In our ABM, we implemented males' and females' timing of arrival ($t_m$ and $t_f$) based solely on the breeding scenario and the level of asynchrony. It would be interesting to investigate how sex-specific phenological shifts, initially determined by environmental changes, may ultimately alter the mating system by favouring scramble competition. Scramble competition characterises a mating system under which sexual selection favours enhanced mate-searching effort (Wiklund and Fagerström, 1977; Parker and Courtney, 1983; Bulmer, 1983). In such a mating system, mating success indeed correlates with variation in traits that enable them to efficiently locate and follow sexually available mates, rather than traits promoting dominance over competitors or attractiveness towards potential mates. Scramble competition may select individuals capable of being less fine-tuned to environmental parameters, relying instead on the social context to adjust the timing of their sexual activity. By triggering phenological changes between males and females, climate change may favour this pattern through increased sexual selection on traits favouring, for example, spatial ability to locate other sexually available mates (Gaulin and Fitzgerald, 1989).

One limitation of our modelling approach is the way we approached mating preference. Although theoretical models on sexual selection generally assume that individuals of a given sex (mainly females) are consistent in their preferences for particular phenotypic traits within the same population, several studies highlighted that variation in mating preference may be quite common due to the context dependency of mating interactions (Chevalier et al., 2020; Kokko and Mappes, 2005). Indeed, variation in mating preference may be determined by the interaction between genes and environmental conditions such as the availability of mating partners (both in quantity and quality). These fluctuations in the availability and quality of partners may generate variation in the preference strength, i.i. *choosiness*, how strongly an individual rejects a potential partner with trait values different from her preference. For instance, Kokko and Mappes (2005); De Jong and Sabelis (1991) suggested that an individual's

acceptance threshold should reduce when its risk of remaining unmated is high i.e. when there are opportunity costs of being choosy. Calabrese and Fagan (2004) specifically highlighted that such cost may arise in situations of reproductive asynchrony. I, therefore, encourage future studies to further investigate the link between within-season variation in mate availability and choosiness. In this study, we investigated the effects of both (1) differential seasonal timing between members of the same sex and (2) sex differences in seasonal timing on sexual selection. An interesting next step would be to define whether a relationship exists between environmental variation and phenological variation for alternative life history forms of the same species occupying the same habitats. Recent research in salmonid species showed that there was intra-specific variation in phenological trends, where alternative life histories of the same population show contrasting temporal trends in reproductive timing (Kovach et al., 2013). Morita et al. (2014) investigated the effect of temperature-driven modifications on reproductive timing in migratory and partially migratory masu salmon *Oncorhynchus masou* populations. Individuals pursuing alternative life histories responded differently to environmental variation: partially migratory individuals were little affected by temperature increases, while migratory individuals displayed earlier migrations. Intra-population heterogeneity in response to climate change could potentially be an important aspect to take into consideration in lampreys.

Overall, our study reveals that the direction and intensity of sexual selection depend more on sex-biased arrival timing rather than on intra-sexual variations. Our experiments also provide some support for the hypothesis that scramble competition selects for individuals with better cognitive ability when sex differences in seasonal timing occur.

# 3.A Appendix

**Table 3.A.1.** Estimates of mating success and the potential strength of sexual selection $Is$ in males and females in a **low density** population with **weak asynchrony**. Number of individuals (N), mean mating success, standard deviation (SD), opportunity for sexual selection ($Is$) are presented with mating success calculated either as the number of partners ($MS_P$) or the number of successful mating acts ($MS_M$).

| | **Males** | | | | | **Females** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $N$ | $Mean$ | $SD$ | $Is$ | $SD$ | $N$ | $Mean$ | $SD$ | $Is$ | $SD$ |
| $MS_P$ | | | | | | | | | | |
| **AF/AM** | 100 | 4.1 | 1.9 | **0.18** | 0.07 | 100 | 4.1 | 1.8 | **0.17** | 0.07 |
| **AF/SM** | 100 | 4.9 | 1.7 | **0.09** | 0.04 | 100 | 4.9 | 2.2 | **0.19** | 0.07 |
| **SF/AM** | 100 | 5.7 | 2.7 | **0.22** | 0.09 | 100 | 5.7 | 2.1 | **0.12** | 0.06 |
| **SF/SM** | 100 | 3.5 | 1.7 | **0.2** | 0.07 | 100 | 3.5 | 2.3 | **0.41** | 0.12 |
| $MS_M$ | | | | | | | | | | |
| **AF/AM** | 100 | 188 | 156 | **0.64** | 0.27 | 100 | 188 | 119 | **0.39** | 0.2 |
| **AF/SM** | 100 | 166 | 137 | **0.59** | 0.26 | 100 | 166 | 118 | **0.51** | 0.27 |
| **SF/AM** | 100 | 122 | 121 | **0.87** | 0.32 | 100 | 122 | 89 | **0.47** | 0.21 |
| **SF/SM** | 100 | 190 | 154 | **0.64** | 0.27 | 100 | 190 | 121 | **0.40** | 0.20 |

**Table 3.A.2.** Estimates of mating success and the potential strength of sexual selection $Is$ in males and females in a **low density** population with **strong asynchrony**. Number of individuals (N), mean mating success, standard deviation (SD), opportunity for sexual selection ($Is$) are presented with mating success calculated either as the number of partners ($MS_P$) or the number of successful mating acts ($MS_M$).

| | **Males** | | | | | **Females** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $N$ | $Mean$ | $SD$ | $Is$ | $SD$ | $N$ | $Mean$ | $SD$ | $Is$ | $SD$ |
| $MS_P$ | | | | | | | | | | |
| **AF/AM** | 11 | 3.2 | 1.7 | **0.27** | 0.15 | 11 | 3.2 | 1.4 | **0.18** | 0.08 |
| **AF/SM** | 11 | 2.2 | 1.5 | **0.44** | 0.36 | 11 | 2.2 | 2.6 | **1.4** | 0.79 |
| **SF/AM** | 11 | 2.1 | 3.0 | **2.15** | 1.17 | 11 | 2.1 | 1.4 | **0.42** | 0.41 |
| **SF/SM** | 11 | 3.4 | 1.7 | **0.21** | 0.07 | 11 | 3.4 | 2.2 | **0.39** | 0.11 |
| $MS_M$ | | | | | | | | | | |
| **AF/AM** | 11 | 163 | 155 | **0.82** | 0.34 | 11 | 163 | 116 | **0.5** | 0.27 |
| **AF/SM** | 11 | 64 | 101 | **2.19** | 1.58 | 11 | 64 | 103 | **2.54** | 1.46 |
| **SF/AM** | 11 | 47 | 98 | **3.71** | 1.82 | 11 | 47 | 71 | **1.9** | 1.33 |
| **SF/SM** | 11 | 191 | 156 | **0.66** | 0.27 | 11 | 191 | 121 | **0.41** | 0.22 |

**Table 3.A.3.** Estimates of mating success and the potential strength of sexual selection $Is$ in males and females in a **high density** population with **weak asynchrony**. Number of individuals (N), mean mating success, standard deviation (SD), opportunity for sexual selection ($Is$) are presented with mating success calculated either as the number of partners ($MS_P$) or the number of successful mating acts ($MS_M$).

| | **Males** | | | | | **Females** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $N$ | $Mean$ | $SD$ | $Is$ | $SD$ | $N$ | $Mean$ | $SD$ | $Is$ | $SD$ |
| $MS_P$ | | | | | | | | | | |
| **AF/AM** | 100 | 14.2 | 8.0 | **0.3** | 0.04 | 100 | 14.2 | 8.5 | **0.35** | 0.07 |
| **AF/SM** | 100 | 19.4 | 7.4 | **0.14** | 0.02 | 100 | 19.4 | 9.7 | **0.24** | 0.04 |
| **SF/AM** | 100 | 19.2 | 13.0 | **0.45** | 0.06 | 100 | 19.2 | 8.9 | **0.21** | 0.03 |
| **SF/SM** | 100 | 16.4 | 9.4 | **0.32** | 0.04 | 100 | 16.4 | 12.1 | **0.53** | 0.07 |
| $MS_M$ | | | | | | | | | | |
| **AF/AM** | 100 | 197 | 156 | **0.63** | 0.09 | 100 | 197 | 117 | **0.35** | 0.07 |
| **AF/SM** | 100 | 163 | 118 | **0.52** | 0.08 | 100 | 163 | 113 | **0.48** | 0.07 |
| **SF/AM** | 100 | 105 | 113 | **1.13** | 0.16 | 100 | 105 | 81 | **0.58** | 0.08 |
| **SF/SM** | 100 | 193 | 151 | **0.61** | 0.08 | 100 | 193 | 117 | **0.36** | 0.06 |

**Table 3.A.4.** Estimates of mating success and the potential strength of sexual selection $Is$ in males and females in a **high density** population with **strong asynchrony**. Number of individuals (N), mean mating success, standard deviation (SD), opportunity for sexual selection ($Is$) are presented with mating success calculated either as the number of partners ($MS_P$) or the number of successful mating acts ($MS_M$).

| | **Males** | | | | | **Females** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $N$ | $Mean$ | $SD$ | $Is$ | $SD$ | $N$ | $Mean$ | $SD$ | $Is$ | $SD$ |
| $MS_P$ | | | | | | | | | | |
| **AF/AM** | 100 | 8.3 | 5.2 | **0.4** | 0.04 | 100 | 8.3 | 3.5 | **0.17** | 0.03 |
| **AF/SM** | 100 | 8.4 | 5.1 | **0.4** | 0.08 | 100 | 8.4 | 11.7 | **1.94** | 0.16 |
| **SF/AM** | 100 | 7.5 | 12.9 | **2.9** | 0.25 | 100 | 7.5 | 4.5 | **0.36** | 0.07 |
| **SF/SM** | 100 | 16.7 | 9.7 | **0.33** | 0.04 | 100 | 16.7 | 12.3 | **0.53** | 0.07 |
| $MS_M$ | | | | | | | | | | |
| **AF/AM** | 100 | 194 | 174 | **0.79** | 0.11 | 100 | 194 | 116 | **0.35** | 0.06 |
| **AF/SM** | 100 | 61 | 92 | **2.21** | 0.43 | 100 | 61 | 101 | **2.72** | 0.3 |
| **SF/AM** | 100 | 39 | 86 | **4.79** | 0.58 | 100 | 39 | 59 | **2.22** | 0.44 |
| **SF/SM** | 100 | 194 | 152 | **0.61** | 0.08 | 100 | 194 | 116 | **0.36** | 0.07 |

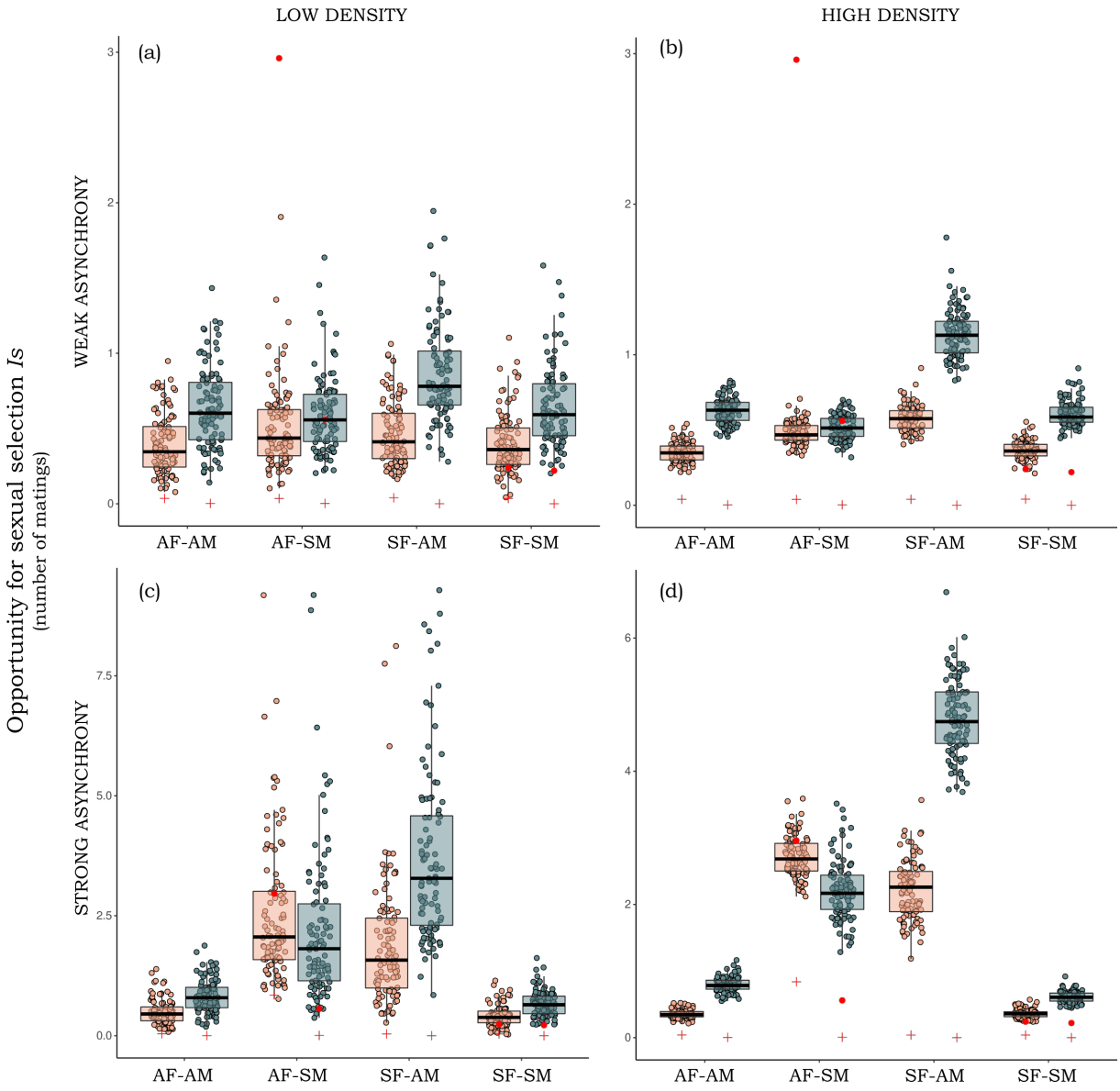


**Figure 3.A.1.** Influence of four scenarios of breeding synchrony (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males, SF-SM: synchronous females/synchronous males) on the opportunity for sexual selection $Is$ calculated as the number of matings. We simulated populations with: **(a)** low density (11M/11F) and weak asynchrony (females arrival within 18 days) **(b)** high density (100M/100F) and weak asynchrony (females arrival within 18 days) **(c)** low density (11M/11F) and strong asynchrony (females arrival within 60 days) **(d)** high density (100M/100F) and strong asynchrony (females arrival within 60 days). Boxplots' colours represent the sex (blue: males, orange: females). In the box plots, the horizontal lines indicate the median (50th percentile) and quartiles (25th and 75th percentiles), the vertical whiskers are drawn to 1.5 times the interquartile range and the open circles the jittered data points. The red crosses represent the expected $Is$ values under random mating for each scenario and condition while the full red circles represent the $Is$ values obtained in the experiment.

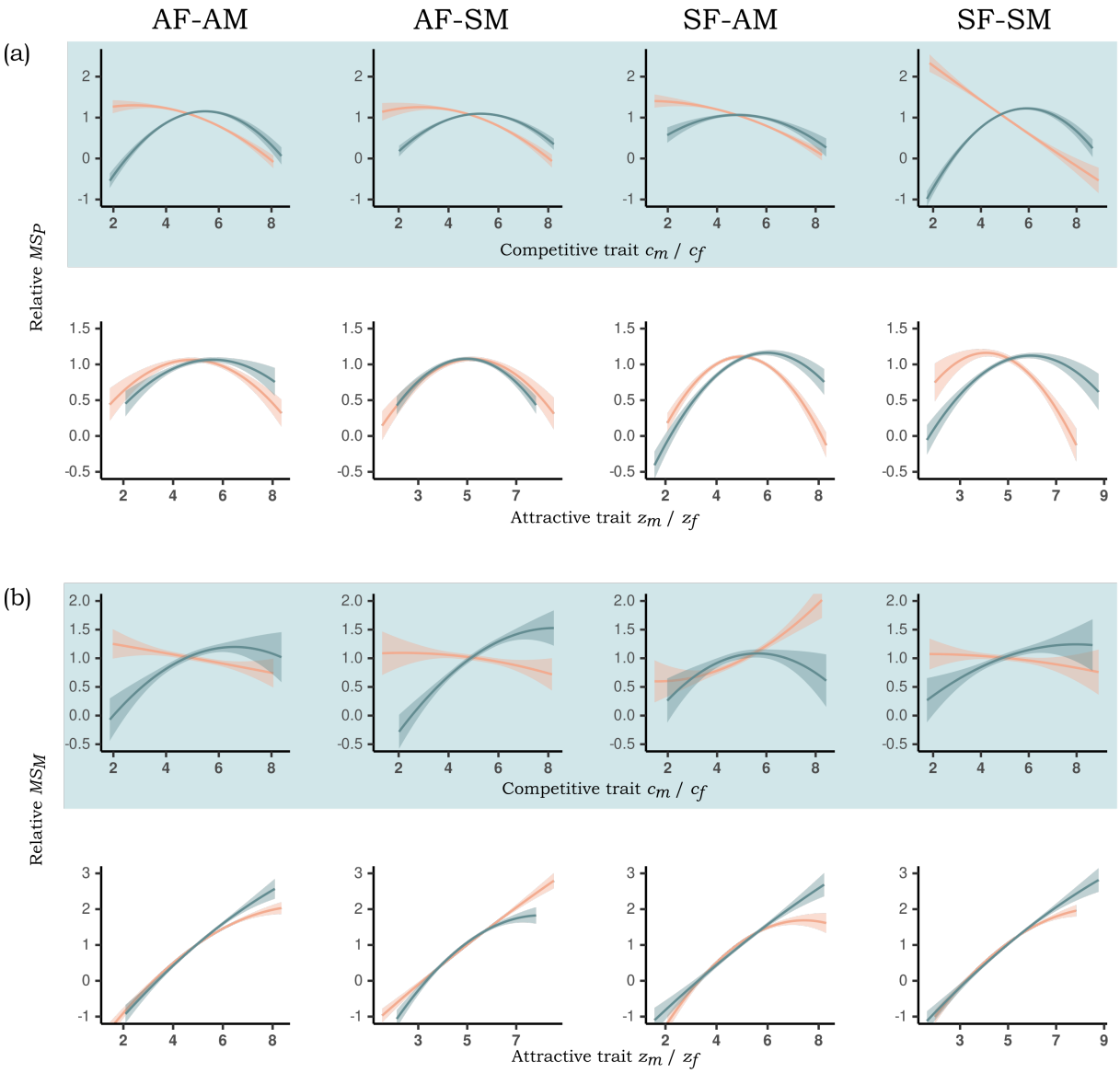


**Figure 3.A.2.** Selection gradient on competitive $c_m/c_f$ and attractive $z_m/z_f$ traits obtained for the four scenarios of breeding synchrony (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males, SF-SM: synchronous females/synchronous males) and in a population with **low density** (11M/11F) and **weak asynchrony** (females arrival within 18 days). Each panel shows the selection gradient estimated from 100 simulated populations. Mating success is calculated either as the number of partners **(a)** or the number of matings. Colours represent each sex (blue: males, orange: females).

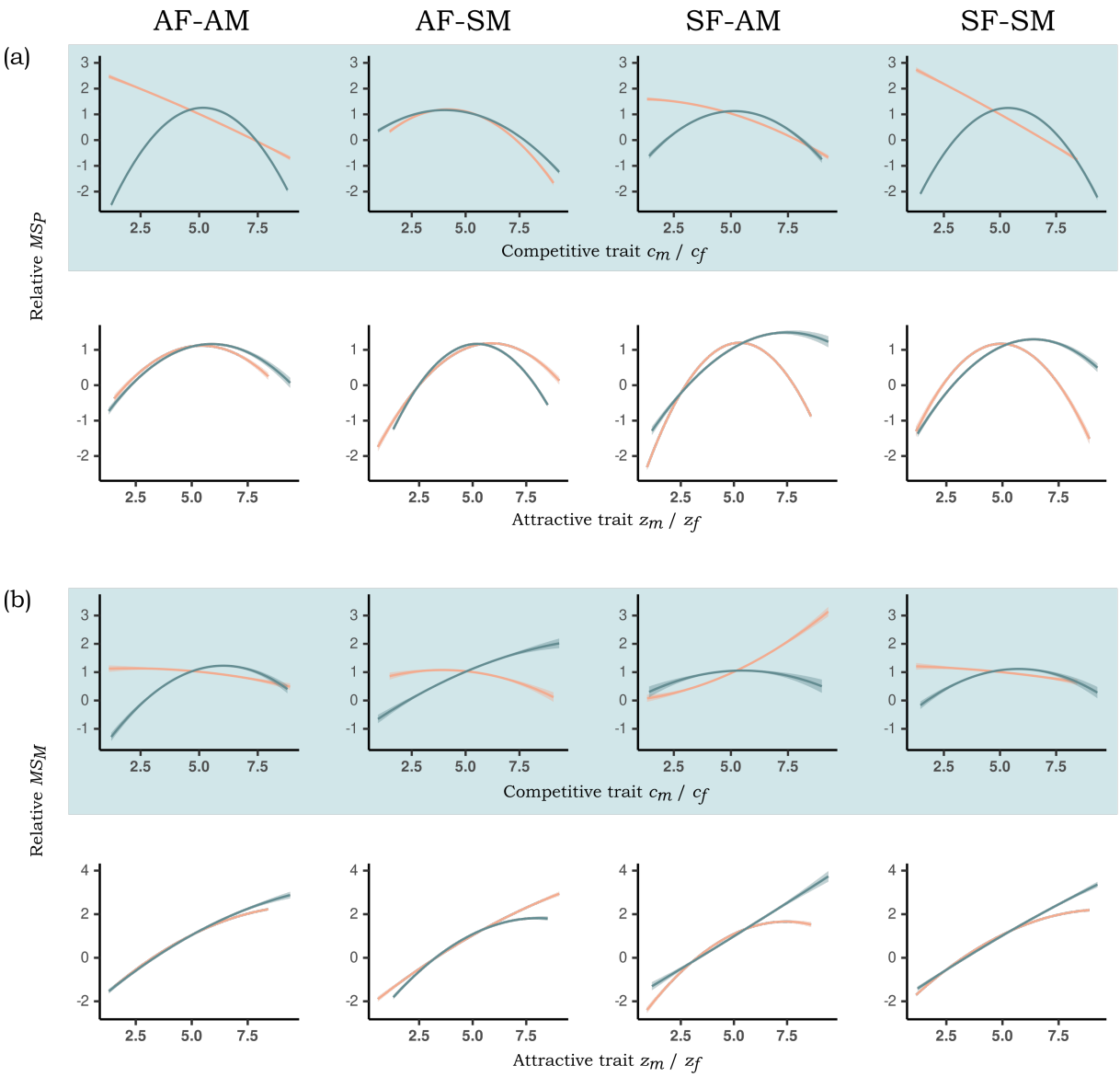


**Figure 3.A.3.** Selection gradient on competitive $c_m/c_f$ and attractive $z_m/z_f$ traits obtained for the four scenarios of breeding synchrony (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males, SF-SM: synchronous females/synchronous males) and in a population with **high density** (100M/100F) and **weak asynchrony** (females arrival within 18 days). Each panel shows the selection gradient estimated from 100 simulated populations. Mating success is calculated either as **(a)** the number of partners or **(b)** the number of matings. Colours represent each sex (blue: males, orange: females).

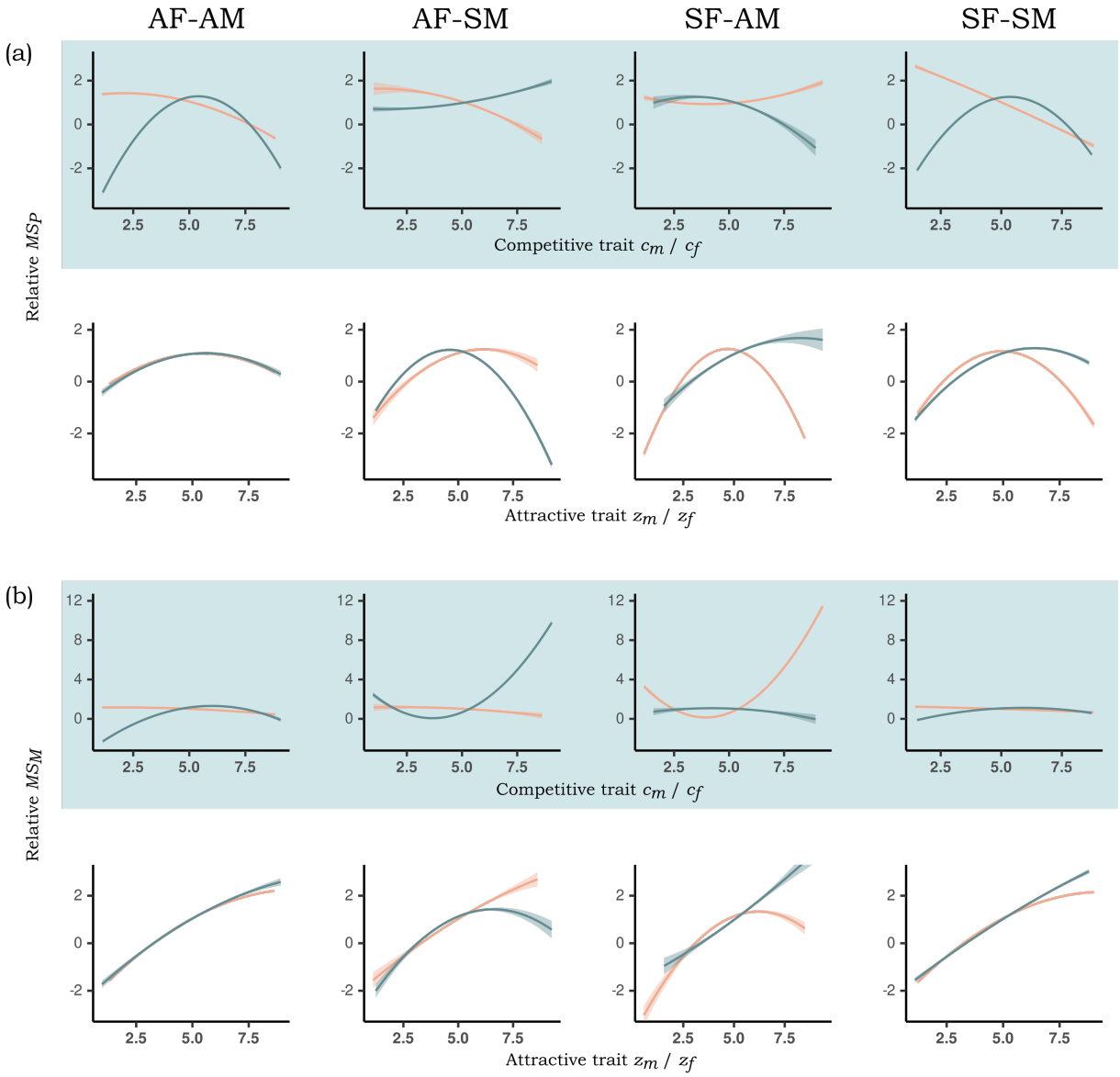


**Figure 3.A.4.** Selection gradient on competitive $c_m/c_f$ and attractive $z_m/z_f$ traits obtained for the four scenarios of breeding synchrony (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males, SF-SM: synchronous females/synchronous males) and in a population with **high density** (100M/100F) and **strong asynchrony** (females arrival within 60 days). Each panel shows the selection gradient estimated from 100 simulated populations. Mating success is calculated either as **(a)** the number of partners or **b** the number of matings. Colours represent each sex (blue: males, orange: females).

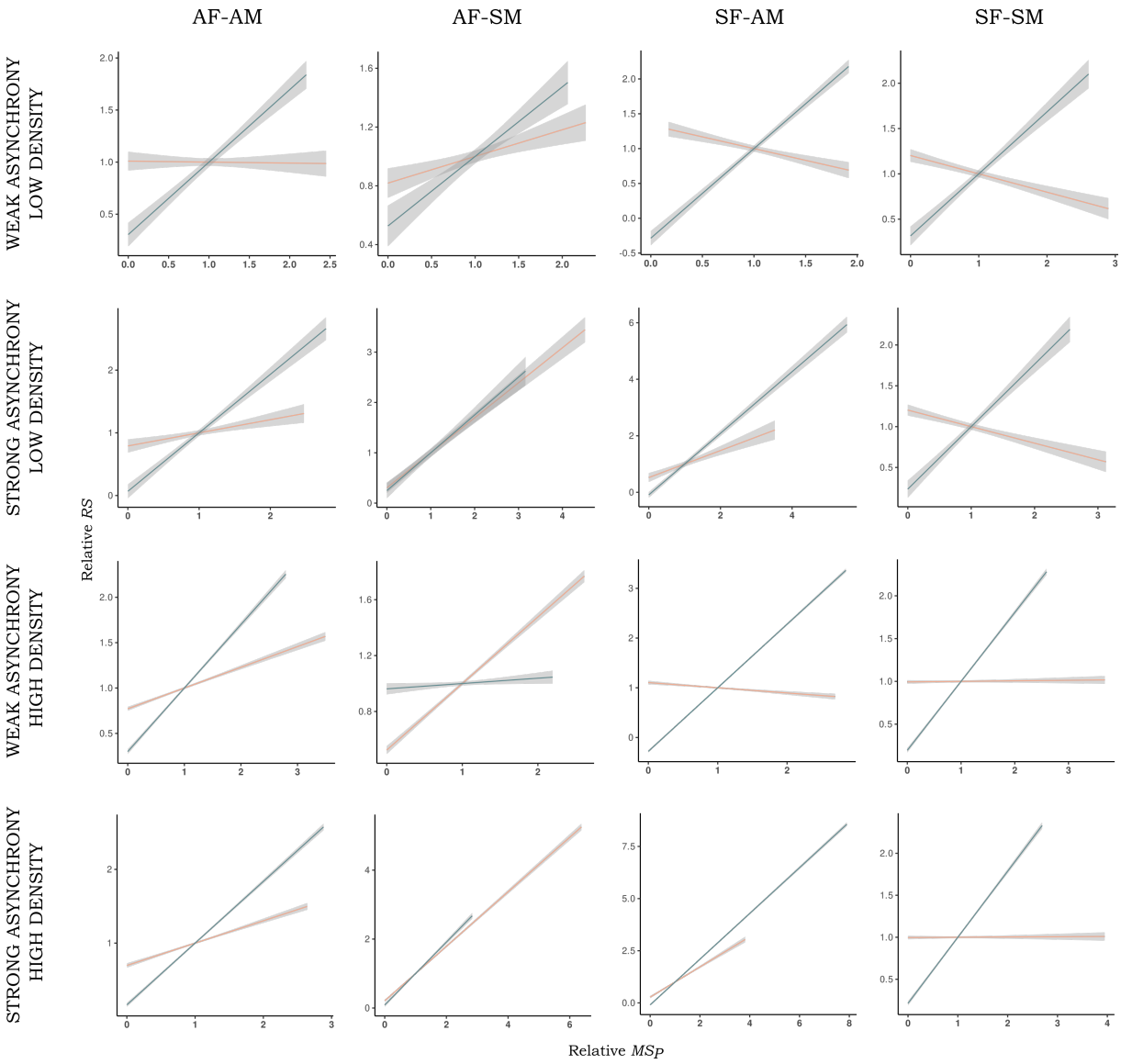


**Figure 3.A.5.** Bateman gradients obtained for the four scenarios of breeding synchrony (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males, SF-SM: synchronous females/synchronous males). Each panel shows the selection gradient estimated from 100 simulated populations. Relative $RS$ corresponds to the relative reproductive success while relative $MS_P$ corresponds to the relative mating success calculated as the number of mating partners. Colours represent each sex (blue: males, orange: females).

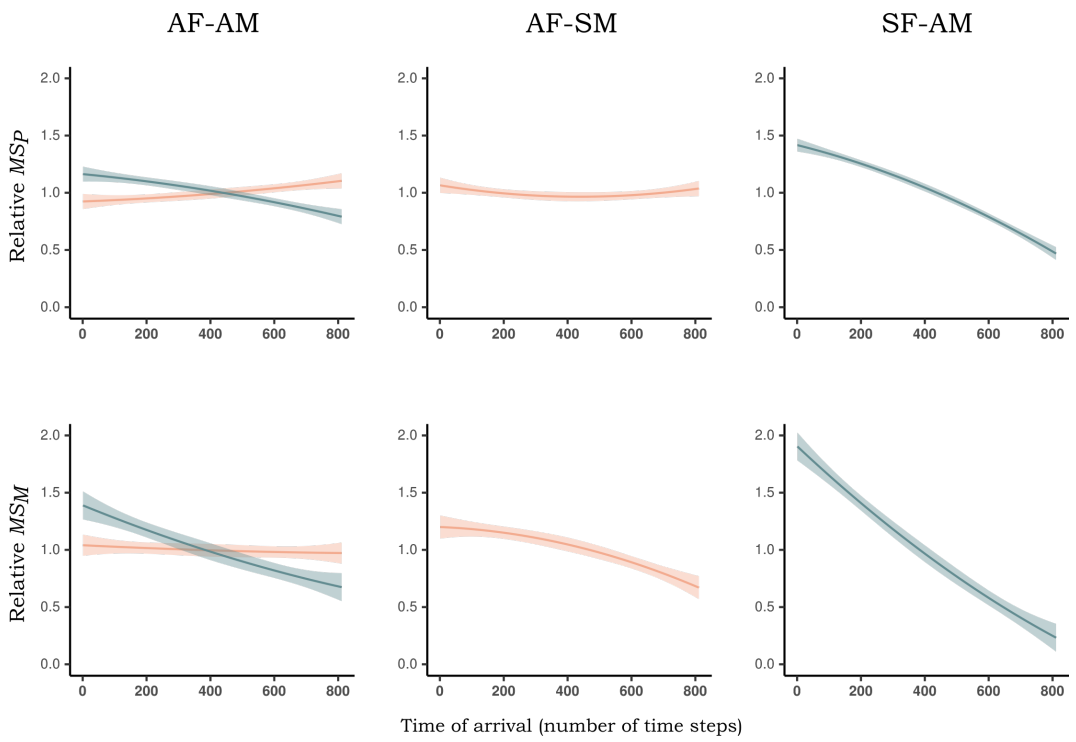


**Figure 3.A.6.** Selection gradient on the timing of arrival ($t_m$ and $t_f$) (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males) in a population with **low density** (11M/11F) and **weak asynchrony** (females arrival within 18 days). Relative mating success is calculated either as the number of partners $MS_P$ or the number of matings $MS_M$. Colours represent each sex (blue: males, orange: females).

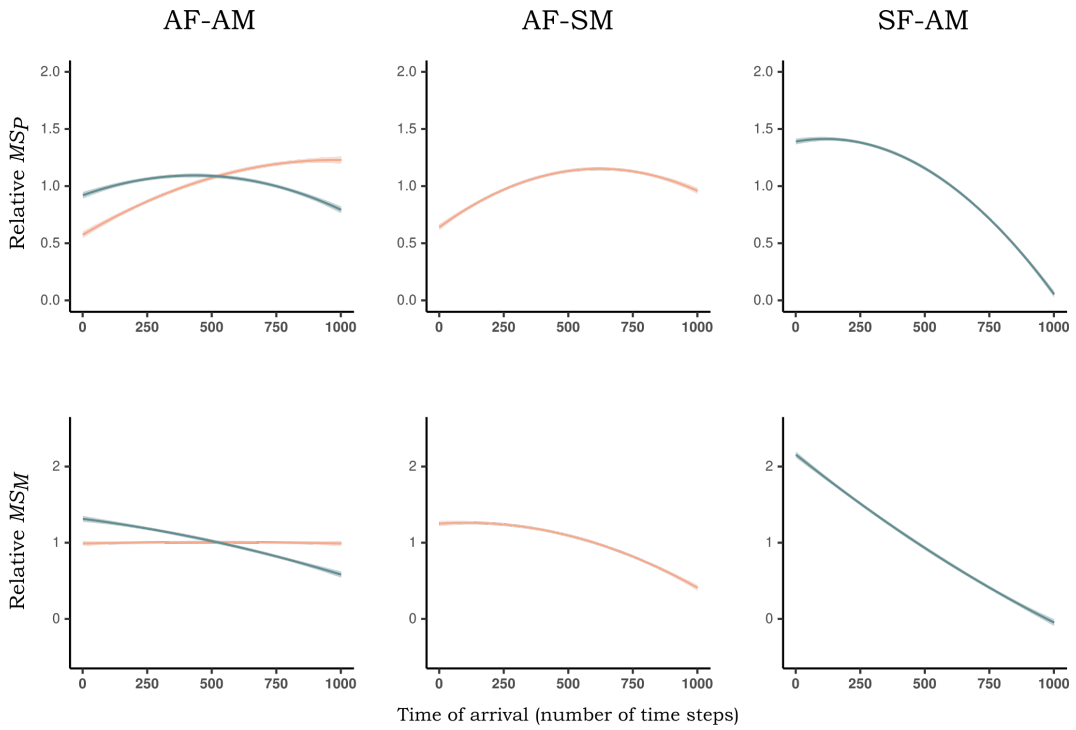


**Figure 3.A.7.** Selection gradient on the timing of arrival ($t_m$ and $t_f$) (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males) in a population with **high density** (100M/100F) and **weak asynchrony** (females arrival within 18 days). Relative mating success is calculated either as the number of partners $MS_P$ or the number of matings $MS_M$. Colours represent each sex (blue: males, orange: females).

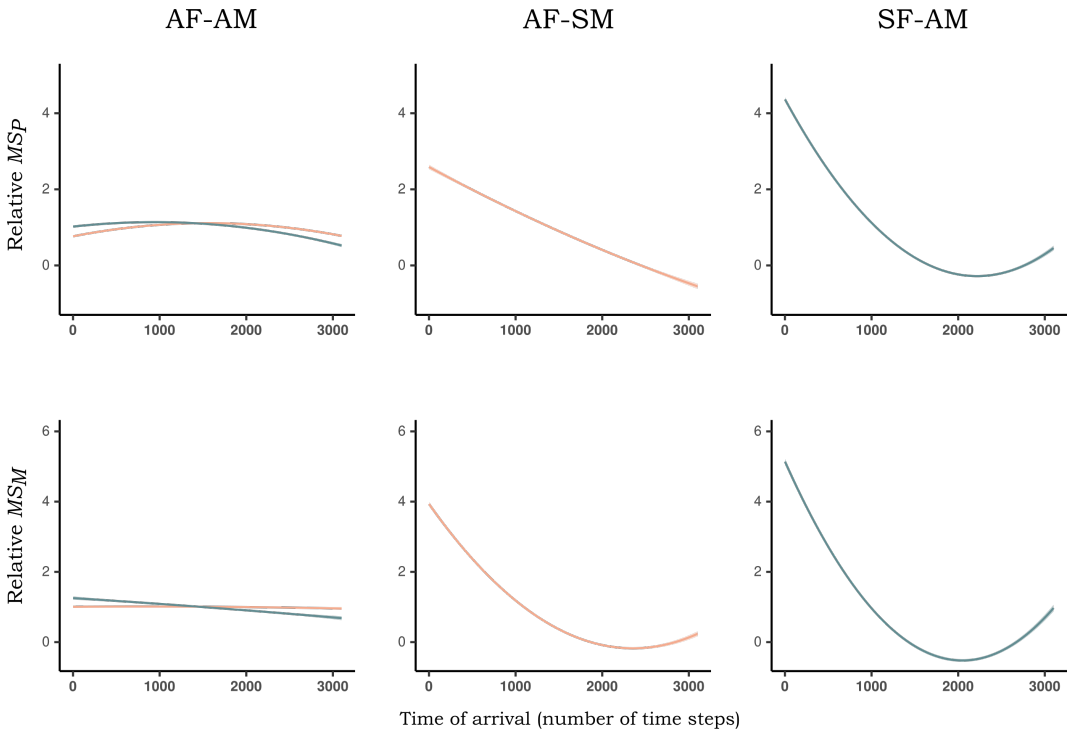


**Figure 3.A.8.** Selection gradient on the timing of arrival ($t_m$ and $t_f$) (AF-AM: asynchronous females/asynchronous males, AF-SM: asynchronous females/synchronous males, SF-AM: synchronous females/asynchronous males) in a population with **high density** (100M/100F) and **strong asynchrony** (females arrival within 60 days). Relative mating success is calculated either as the number of partners $MS_P$ or the number of matings $MS_M$. Colours represent each sex (blue: males, orange: females).

## 3.2 Chapter highlights

- By combining an Agent-Based Model (ABM) with an experimental study, we found that the opportunity for sexual selection $Is$ varied across breeding scenarios, being higher in the asynchronous sex when there are inter-sexual variations in reproductive synchrony;
- We show that mating success is more affected by reproductive timing than phenotypic traits conferring a mating advantage;
- Our results suggest that scramble competition may be selected in breeding scenarios where there is an unequal shift in reproductive timing between males and females as early arriving individuals have higher fitness.

Chapter 4

# The occurrence of form-assortative mating in lampreys

This section corresponds to an article submitted for publication in ***Behavioral Ecology*** and under review. This work was carried out as part of a 5-month project I did at the University of Hokkaido, Japan in 2022.

## Contents

**Size-assortative mating and sneaking behaviours between alternative morphs of the Arctic lamprey (*Lethenteron camtschaticum*): implications in a sympatric speciation context**

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**Abstract**

Evolutionary theory predicts that assortative mating is crucial for sympatric speciation by generating reproductive isolation between diverging populations. Here, we investigate the potential of size-assortative mating, an assumed mating pattern in lampreys, for sympatric speciation. By continuously recording mating activity between anadromous and resident forms of *L. camtschaticum* that greatly differ in body size, we show that lampreys tend to mate with individuals of similar size in experimental conditions. However, we highlight that this pattern does not result from a choice of same-form partner but is the result of the simultaneous action of a preference of males – whatever their size – for anadromous females, a higher competitive ability of aggressive males and physical constraints on mismatched pairs. Moreover, we do not advocate that sympatric speciation, as the sole consequence of size-assortative mating through sexual selection, is a plausible mechanism for the diversification of lampreys as a significant number of sneaking behaviours were observed in resident males toward large anadromous females. Broader attention should be given to other mechanisms than sexual selection potentially leading to size-assortative mating, such as variations in spatial or temporal distribution during the reproductive season.

**Keywords:** size-assortative mating, mate preference, sneaking behaviour, intra-sexual competition

## 4.1 Introduction

Since Darwin's pioneering work (Darwin, 1859) the traditional view has been that most speciation processes occur as a consequence of geographic barriers to gene flow. However, more recent work suggests that sympatric speciation - speciation with no physical isolation and high levels of gene flow - is possible and may be more common than previously expected (Bush, 1994; Higashi et al., 1999; Via, 2001). Theoretical research supposes that sympatric speciation is an ecological process resulting from the simultaneous action of two processes: (1) disruptive natural selection, which favours two extreme phenotypes within a single population and (2) assortative mating, the occurrence of matings of like with like, which reduces gene flow between diverging groups and thus amplify the initial force driving differentiation among them. One of the biological mechanisms that can generate assortative mating is mate choice. Indeed, if disruptive natural selection occurs on traits also involved in mate choice, implying a connection between sexual and ecological traits, divergent sexual selection may emerge, ultimately generating premating isolation in sympatry (Lande, 1981; Lande and Kirkpatrick, 1988; Schluter and Price, 1993).

Of the phenotypic traits whose divergence is linked to the exploitation of different resource environments, body size is probably the most distinctive. Indeed, large differences in body size between phenotypes correspond closely to distinct shifts in habitat use and divergence in trophic preferences. Mainly documented in fishes (Skulason and Smith, 1995), examples include stream and lake forms (Keast, 1978; in brown trout, Hendry, 2001; in artic charr, Sandlund et al., 1992; Hendry et al., 2002) or fluvial-resident or anadromous forms (in lampreys, Malmquist et al., 1992; Docker, 2019). Size at reproduction often involves an alternative solution to a trade-off between growth and survival (Houston et al., 1993; Mangel and Stamps, 2002; Werner and Anholt, 1993). For instance, there is a trade-off among life

history forms in lampreys: either becoming a juvenile parasite with high growth potential, fecundity but also mortality due to a more risky life, or remaining a detritivore larvae with lower growth, fecundity and mortality (Docker, 2019; Evans and Limburg, 2019; Hardisty, 2006); the optimal life history depending on the environmental conditions encountered during either the ammocoete or juvenile stages (Evans and Limburg, 2019). In addition to being subject to natural selection, body size is also a key trait behind assortative mating. Indeed, one of the most common examples of ecological factors influencing sexual isolation is size-assortative mating: a mating pattern that is defined by a positive correlation between the body sizes of mating partners. Size-assortative mating has been highlighted as a powerful evolutionary force that may induce speciation and morphological evolution in many taxa, including sticklebacks (McKinnon et al., 2004; Nagel and Schluter, 1998) and seahorses (Jones et al., 2003).

In this paper, we investigated the potential of size-assortative mating as a key mechanism ensuring reproductive isolation in lampreys. This class of vertebrates comprises at least ten complexes of parasitic stem species, which mostly have an anadromous life history, and non-parasitic satellite species, which are fluvial resident (Hardisty and Potter, 1971). Within each stem-satellite species complex, the non-parasitic species are thought to be derived from a single parasitic species (Hardisty and Potter, 1971; Salewski, 2003; Vladykov and Kott, 1979), from which it is more or less genetically differentiated (Docker, 2019). More precisely, a fluvial non-parasitic form is considered to be derived directly from an anadromous parasitic species (Hardisty and Potter, 1971; Yamazaki and Goto, 2000; Zanandrea, 1959) or via a fluvial parasitic form (Beamish, 1985, 1987). Interestingly, it has been observed that distinct life-history forms can coexist within the same species (Beamish, 1987; Holcik, 1986; Kucheryavyi et al., 2007; Yamazaki et al., 1998), which provides the opportunity to study

size-assortative mating as a factor of reproductive isolation in an early stage of speciation. Focusing on a potential premating barrier during early population divergence is valuable because it can evaluate the influence of this early barrier on the evolution of subsequent ones within closely related species (Butlin et al., 2008; Rundle and Nosil, 2005). The early divergence between life history forms may indeed be considered as the process constituting the first step in lamprey's speciation continuum. In the genus *Lethenteron*, Yamazaki et al. (1998) first reported the coexistence of anadromous parasitic and fluvial non-parasitic *L. camtschaticum* adults from the Ohno River, in Hokkaido Island, Japan. Life-history forms can be easily differentiated at the adult stage based on significant differences in body size at the onset of sexual maturity due to the ecological divergence between parasitic and non-parasitic life history forms. Hardisty and Potter, 1971 therefore predicted that size-assortative mating was occurring in lampreys and may promote reproductive isolation between forms in sympatry. This hypothesis is often considered valid in the literature, even though the only experimental test confirming it, made on the *Lampetra ayresi* - *L. richardsoni* pair species, was inconclusive due to a lack of proper statistical analysis (Beamish and Neville, 1992). Moreover, the evolutionary consequences of size-assortative mating may be counteracted by alternative mating behaviours employed by males (Taborsky, 1998). "Satellite" spawning behaviours have been observed in two lamprey genera (*Lethenteron* and *Lampetra*) where males, also referred as sneakers, rapidly circle the urogenital area of a mating pair at the time of gamete release, attempting to gain fertilisation of the female's eggs (Cochran et al., 2008; Hume et al., 2013*b*). Recently, Rougemont et al. (2015) demonstrated that the European brook lamprey (*Lampetra planeri*) males could reproduce with European river lamprey *L. fluviatilis* females under semi-natural conditions by calculating reproductive success through genetic parentage analysis. However, as they did not calculate male mating success through behavioural observations, they were not able to distinguish the fertilisation of females' eggs

gained directly by regular mating or indirectly by sneaking behaviour. Moreover, in the absence of *L. planeri* females in their experiment trials, resident males may have had no choice but to reproduce with interspecific females. This experimental setting may have led to a potentially underestimate of the strength of size-assortative mating as a pre-zygotic barrier to hybridisation in natural populations.

The objective of this study was therefore to experimentally evaluate the potential of size-assortative mating as a central role in reproductive isolation by tracking mating behaviours between anadromous parasitic and fluvial non-parasitic *L. camtschaticum* adults in a realistic multiple-choice experimental design. Based on the very unique winding spawning behaviour of lampreys (Malmqvist, 1983), which physically constrains mating between individuals, we hypothesize that we should observe a positive correlation between male and female size pair (size-assortative mating), resulting in pairs only constituted of individuals with the same life history (form-assortative mating). A pattern of size-assortative mating could emerge through two size-dependent courting strategies in mates if male-male competition operates in combination with mate choice. The first mate choice strategy, referred to here as the "high quality" strategy may result from mate choice for large size by one or both sexes. Mating with larger females is advantageous as they are more fecund (Andersson, 1994). Larger males, on the other hand, may contribute "good genes" for offspring or are less likely to be sperm limited (e.g. Kokko et al., 2002). However, as larger males are generally better at competing for large fecund females, smaller, physically inferior males may be less discriminating and court smaller females. Alternatively, size assortative mating may also emerge through a "prudent" mating strategy when individuals favour mates with trait values similar to their own in which case low-quality males ignore too high-quality females and prefer similar small low-quality females. If intra-sexual competition in males is sufficiently costly, the benefits conferred by

mating with large females are outweighed, which may ultimately lead to a "prudent" courting strategy in males (Härdling and Kokko, 2005). Under the "high quality" mating strategy, one should observe (1) a preference of all males for large anadromous females through a higher number of mating attempts or sneaking behaviours towards them, (2) a superior competitive ability of anadromous males via a higher number of aggressive behaviours and (3) a higher rate of success among mating attempts for larger males, irrespective of female size. Alternatively, under the "prudent" mating strategy, one should observe (1) preference of males for females of the same life history form through a higher number of mating attempts towards them (2) a higher rate of success among mating attempts for homotypic pairs than for heterotypic pairs. Considering the apparent strong male-male competition (i.e. intermale aggressivity, Docker, 2019), we hypothesize that size-assortative mating in lampreys should result from a choice for a same-size partner via a "prudent" courting strategy.

## 4.2 Methods

### 4.2.1 Species description

The Arctic lamprey *Lethenteron camtschaticum* is distributed in parts of the northern hemisphere, occurring mainly in Hokkaido and the northern part of Honshu Island, Japan but also in certain areas of North America and Europe. *Lethenteron camtschaticum* generally has an anadromous parasitic life history; after spawning, larvae hatch and live in rivers for five years, metamorphose into juvenile lamprey and migrate to the sea where they undertake a parasitic feeding phase for approximately two years until they migrate back to rivers in spring to reproduce and die (Hardisty and Potter, 1971). Despite their extensive geographic range around Japan, the current subpopulations of anadromous parasitic *L. camtschaticum* seem to be panmictic with little to no genetic structure (Yamazaki et al., 2011). A few studies also

reported the presence of dwarf freshwater forms in Hokkaido and northern Honshu Island, Japan (Iwata and Hamada, 1986; Yamazaki et al., 1998). The total length of the dwarf individuals (138.0-161.2 mm TL) was similar to those of individuals at metamorphosis (153.1-215.0 mm TL) and clearly shorter than that of mature anadromous individuals (352.3-533 mm TL) (Iwata and Hamada, 1986; Yamazaki et al., 1998). Despite the large size difference due to their divergence in life history, the two types are morphologically identical, sharing in particular the same distinctive characteristic: a second dorsal fin with a dark blotch near the apex. The mating system of *L. camtschaticum* has been described as polygynandrous; adults form spawning aggregations of tens of individuals (Iwata, 1989; Yamazaki et al., 1998).

### 4.2.2 Sample collection

In May 2022, mature *L. camtschaticum* adults were collected at the Horikappu River and the Onoppunai River, Hokkaido Island, Japan by hand-netting and electrofishing. The peak breeding seasons of anadromous and freshwater forms in the Northern part of Japan mainly overlap in late May (Iwata, 1989; Yamazaki et al., 1998). 20 freshwater (14 males and 6 females) and 12 anadromous individuals (8 males and 4 females) were collected in the Horikappu river on May, $22nd$ while 12 anadromous individuals (8 males and 4 females) were collected in the Onoppunai river on May, $24^th$. Individuals were transported to the Tomakomai Experimental Forest (TOEF; 42°40'34.8"N 141°35'59.3"E), Hokkaido Island, Japan. All individuals were sexually mature as we were able to distinguish genital characteristics for all individuals. Ripe females develop a post-cloacal finfold (Hagelin and Steffner, 1958) and eggs are sometimes visible through a patch of translucent skin near the cloaca. Sexually mature male lampreys can be identified by an obvious genital papilla that extends several millimetres from the cloaca. Adult anadromous and freshwater-resident *L. camtschaticum* can be separated using body length as seen in the previous section (Iwata, 1989; Renaud, 2011). Individuals were separated accord-

ing to their sampling site, life history forms and sex, and were acclimated between 3 to 5 days according to the fishing date in boxes supplied with Horonai river water in TOEF. One day before the start of the experiment, all 44 individuals were tagged with a unique combination of one or two spots of UV-fluorescent visible implant elastomer (VIE, yellow, pink, green, red or blue) injected in the posterior dorsal fin to allow individual recognition under natural light (Silver et al., 2009). We measured two morphological traits: total body length ($\pm$0.5 mm) and total mass ($\pm$0.5 g). The first two traits may be targeted by sexual selection (Malmqvist, 1983) while dorsal fins develop just before the onset of spawning and may therefore be considered as a secondary sexual character in males (Hagelin and Steffner, 1958). Biometry and tagging were performed after fish were placed in a water tank containing eugenol anaesthetic (FA-100, DS Pharma Animal Health, Osaka, Japan) at a concentration of 0.3ml/L for 5 minutes.

### 4.2.3 Experimental design

The experiment took place in a 5 meters long annular tank, supplied with water from the Horonai river, in a semi-open circuit, with water replacement of 1 litre per minute. We separated the tank into two linear sections of 1 $m^3$ (2 m long, 1 m wide, 0.5 m water depth) corresponding to respectively the "G1" group and the "G2" group. To mimic natural spawning conditions, current speed was set to 0.05 m/s, spawning substrate was provided, and water temperature (known to affect spawning activity, Hardisty and Potter, 1971) was monitored daily and followed that of the river. To facilitate observation, spawning substrate was limited to one 0.48 $m^2$ (0.6 x 0.8 m) box filled with a mixture of gravels and pebbles (0.1 m depth) corresponding to the spawning habitat usually selected by lampreys (Daupagne et al., 2022; Jang and Lucas, 2005). The aquarium was lit by natural light. Two video cameras (JVC Everio GZ-L330-s) continuously recorded lampreys' dial activity in each spawning group throughout the experiment. Individuals were placed in the experimental tank on the $27^{th}$ of May and

the experiment ended on the $6^{th}$ of June, at the death of the last individual. Both groups had the same density and sex ratio of both life history forms: 8 anadromous males, 4 anadromous females, 7 resident males and 3 resident females. Within each group and sex, we mixed the anadromous individuals caught from the two localities in equal proportions.

### 4.2.4 Definition of mating success and mating behaviour characterisation

All video footage was analysed with BORIS software (Friard and Gamba, 2016) to note the exact timing of each mating behaviour and the identity of the individuals involved. Lamprey's mating act consists of a fixed sequence of behaviours: female positioning, male mounting (i.e. attaching with his mouth to the female's head), tail wrapping and squeezing (Docker, 2019), followed by simultaneous release of gametes, when the pair quivers for approximately two seconds. Such distinctive behaviours allow us to visually discriminate the focal individuals during copulations. Numerous attempts to copulate were interrupted before the male could squeeze the female's abdomen. We therefore distinguished successful matings (i.e. those ending with squeezing and quivering) from failed matings. Each mating act usually involves one male and one female but sometimes, two or more males can copulate simultaneously with the same female, as highlighted by previous studies (Case, 1970; Docker, 2015; Huggins and Thompson, 1970; Malmqvist, 1983). If such a case occurred, the identity of each male involved was noted, so the female was considered to have mated with each of them. Sneaking behaviours were also recorded. Sneaky mating tactics are characterised by the following observation: sneaker male approaches the urogenital area of the typically spawning pair, tightly circling around their bodies at the point of squeezing. The sneaker male then unwinds and travels rapidly away from the mating pair. Finally, we analysed aggressive behaviours in males as this could reflect the competitive ability of individuals to defend the breeding arena and

monopolise potential female partners. For each of the 10 days of experiment, we analysed 28 video sequences of 10 minutes separated by 20 minutes, thus amounting to 4.6 hours per day, and 44 hours overall. As mating activity appears to be higher during the day (Binder and McDonald, 2008*b*,*a*) and is challenging to observe at night, we only observed diurnal behaviours.

### 4.2.5 Statistical analysis

#### 4.2.5.1 Pattern of assortative mating

The body size of all potential mating partners was first compared and a Spearman's rank correlation test was performed between the body size of successfully mated partners regardless of the group to test for size assortative mating. Additionally, we explored the occurrence of form-assortative mating by assessing the expected number of successful matings in each pair's types (AM-AF = anadromous male/anadromous female, AM-RF = anadromous male/resident female, RM-AF = resident male/anadromous female, RM-RF = resident male/resident female) under random mating. Specifically, we computed the total number of matings and we distributed the obtained number randomly among all the possible mating pairs. These simulations were iterated 10 000 times and the results were compared to the ones observed in each type. Additionally, we used a Scheirere-Raye-Hare test followed by Dunn's post hoc multiple comparisons to compare the number of successful matings between pairs' types and between groups (G1/G2). We also performed Fisher's exact tests followed by pairwise comparisons to evaluate whether the number of successfully mated pairs was related to the type of pairing in each group.

#### 4.2.5.2 Mate choice

Two additional Scheirere-Raye-Hare tests followed by Dunn's post hoc multiple comparisons were then used to compare (1) the number of failed matings and (2) the number of sneaky

matings between pairs' types and between groups in order to define mate preference in males. Under the "prudent" mating strategy one should observe a higher number of successful, failed and sneaky matings in homotypic pairs. Under the "high quality" mating strategy, successful matings should only concern homotypic pairs and one should observe a higher number of failed matings and sneaking behaviours in RM-AF than in RM-RF.

#### 4.2.5.3 Male-male competition

A positive correlation between male and female size in pairs could emerge only if male-male competition operates in combination with mate choice, so we used a Spearman's rank correlation test to investigate whether individuals that were the most competitive (i.e. aggressive) were the ones that attempted to mate more. We employed a Scheirere-Raye-Hare test followed by a Dunn's post hoc multiple comparison to evaluate whether the aggressive ability of males was related to their form type and the group (G1/G2). To investigate whether the number of intermale aggressions was related to each male's form (AP-AT = anadromous perpetrator/anadromous target, AP-RT = anadromous perpetrator/resident target, RP-AT = resident perpetrator/anadromous target, RP-RT = resident perpetrator/resident target), we assessed the expected number of aggressions in each type under a random pattern, in the same way as above. We also performed Fisher's exact tests followed by pairwise comparisons to evaluate whether the number of male-male aggressive pairs is related to the type of pairing in each group.

All Scheirer-Raye-Hare tests were performed on all possible combinations of pairs to account for the fact that the number of individuals in each combination differed. Statistics were performed with R software (R Core Team, 2022).

### 4.2.6 Ethical statement

Permission for the collection of animals was given by the Hokkaido prefectural government. Experimental design and handling of animals were approved and carried out in accordance with the guidelines established by the Institutional Animal Care and Use Committee of the National University Corporation Hokkaido University.

## 4.3 Results

### 4.3.1 Pattern of size-assortative mating

Anadromous lampreys measured on average (±SD) 36.13 cm (±2.12) with males measuring on average 36.58 cm (±1.84) and females 35.22 (±2.48). Residents measured on average (±SD) 15.11 cm (±1.12) with males measuring on average 15.4 cm (±1.02) and females 14.45 (±1.15). Body size of anadromous and residents did not differ between groups (Kruskal-Wallis test: $H_{11}$ = 9.16, $P$ < 0.001). The behavioural observations of successful matings combined with the body-size measurements did not clearly verify the occurrence of size-assortative mating in this lamprey population (Fig. 4.1). Spearman's rank correlation was used to assess the relationship between the size of successfully mated partners. There was no significant correlation between the two (r = 0.42, $P$ = 0.09).

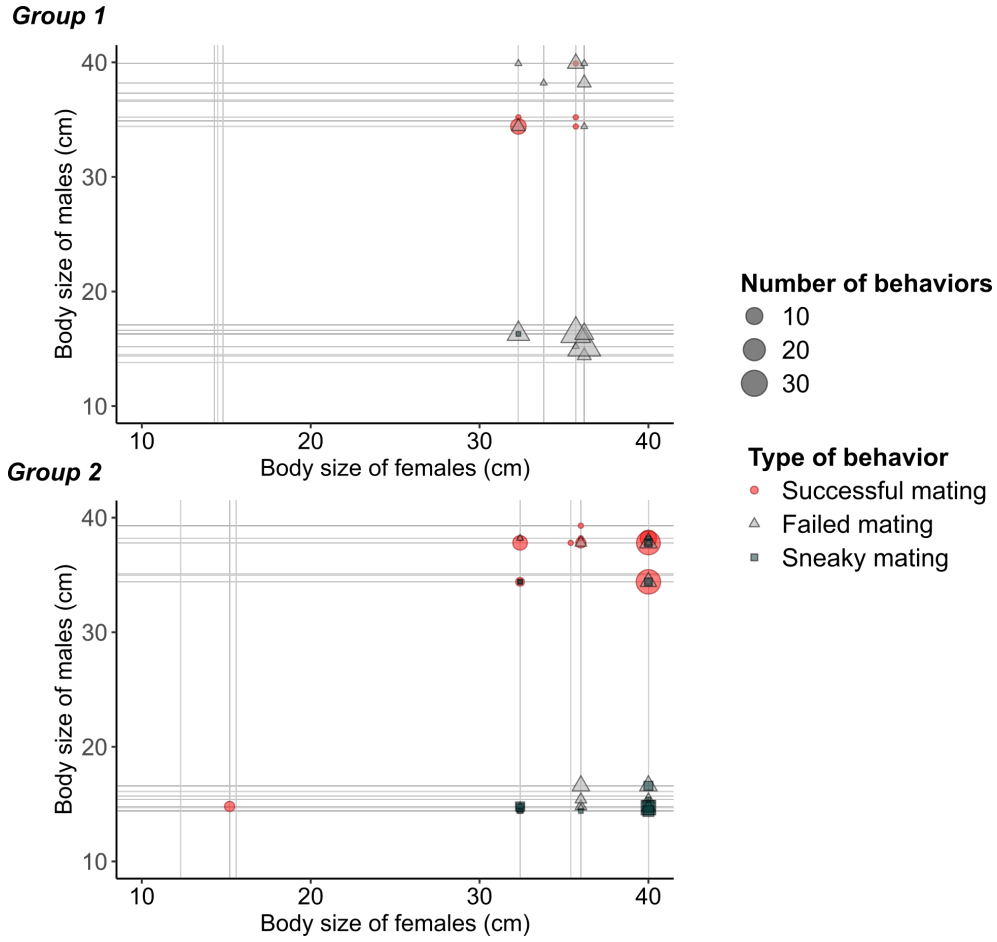


**Figure 4.1.** Body size (in cm) of males and females that mated successfully (red circles), unsuccessfully (grey triangles) and were involved in sneaky matings (blue squares). The regression between the size of successfully mated partners is not significant (r = 0.42, $P$ = 0.09, Spearman test).

### 4.3.2 Pattern of form-assortative mating

Our results verified the occurrence of form-assortative mating lamprey population as successful matings only concerned homotypic (AM-AF and RM-RF) pairs (Fig. 4.2, Appendix Tab. 4.A.1). However, the number of successful matings in RM-RF pairs was low and under what would be expected from random matings. The analysis (Fig. 4.2) combines the two experimental groups as no differences were observed between them (Appendix. Fig. 4.A.1). A Scheirer-Ray-Hare test revealed that there was no statistically significant interaction between

the effects of group and paring type on the number of successful matings ($H(3)$ = 3.48,$P$ = 0.32). Simple main effects analysis showed that the group did not have a statistically significant effect on the number of successful matings ($H(1)$ = 2.95, $P$ = 0.08). However, the pairing type did have a statistically significant effect on the number of successful matings ($H(3)$ = 33.56, $P$ < 0.001). Pairwise comparisons indicated that the number of successful matings was statistically higher in AM-AF pairs than in other pairing types. No other differences were statistically significant.

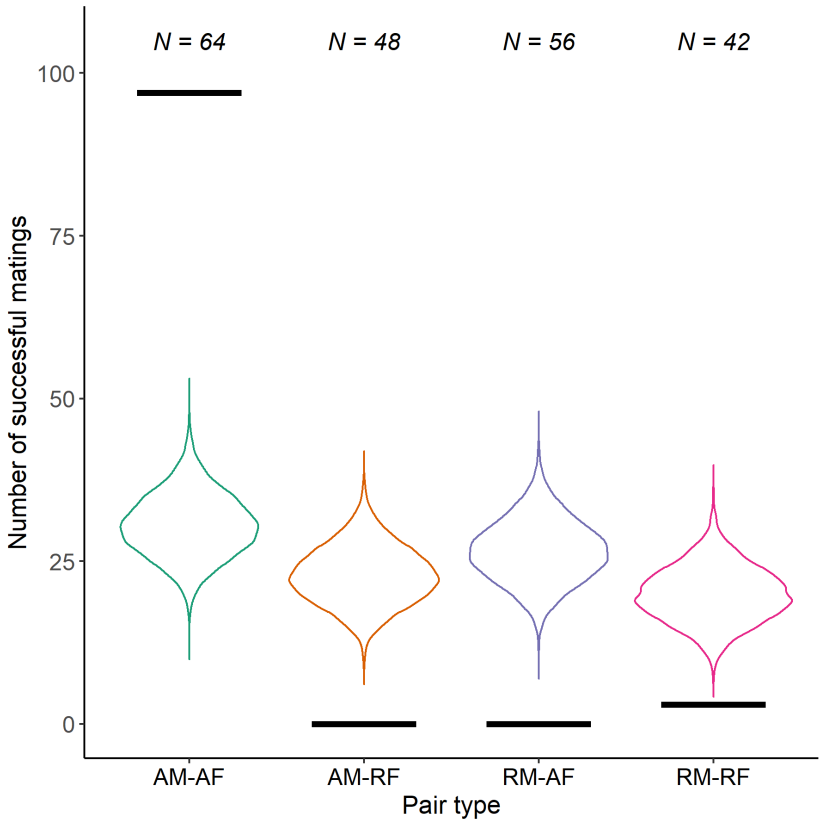


**Figure 4.2.** Number of successful matings observed (horizontal bars) and expected under random matings (density plots) in each mating pair type (AM-AF = anadromous male/anadromous female, AM-RF = anadromous male/resident female, RM-AF = resident male/anadromous female, RM-RF = resident male/resident female). The number above each section refers to the total number of possible combinations within each pairing type. Simulations were iterated 10000 times in R (R Core Team, 2022).

### 4.3.3 Mate choice

Two additional Scheirer-Ray-Hare tests were performed to analyse the effect of group and pairing type on respectively the number of failed matings and the number of sneaky matings (Fig. 4.3). The first test revealed that there was not a statistically significant interaction between the effects of group and paring type on the number of failed matings ($H(3)$ = 1.04, $P$ = 0.79). Simple main effects analysis showed that the group did not have a statistically significant effect on the number of failed matings ($H(1)$ = 0.49, $P$ = 0.48); but the pairing type did have a statistically significant effect ($H(3)$ = 22.20, $P$ < 0.001). Pairwise comparisons showed that the number of failed matings was statistically higher in AM-AF pairs and RM-AF pairs than in the two remaining pairing types: RM-AF and RM-RF. Finally, the second test revealed that there was not a statistically significant interaction between the effects of both explanatory variables on the number of sneaky matings ($H(3)$ = 7.22, $P$ = 0.06). Simple main effects analysis showed that the group did have a statistically significant effect on the number of sneaky matings ($H(1)$ = 9.43, $P$ < 0.001). Similarly, the pairing type did have a statistically significant effect on the number of sneaky matings ($H(3)$ = 13.07, $P$ = 0.004). Post hoc test revealed that the number of sneaky matings is higher in RM-AF pairs than in AM-RF and in RM-RF pairs.

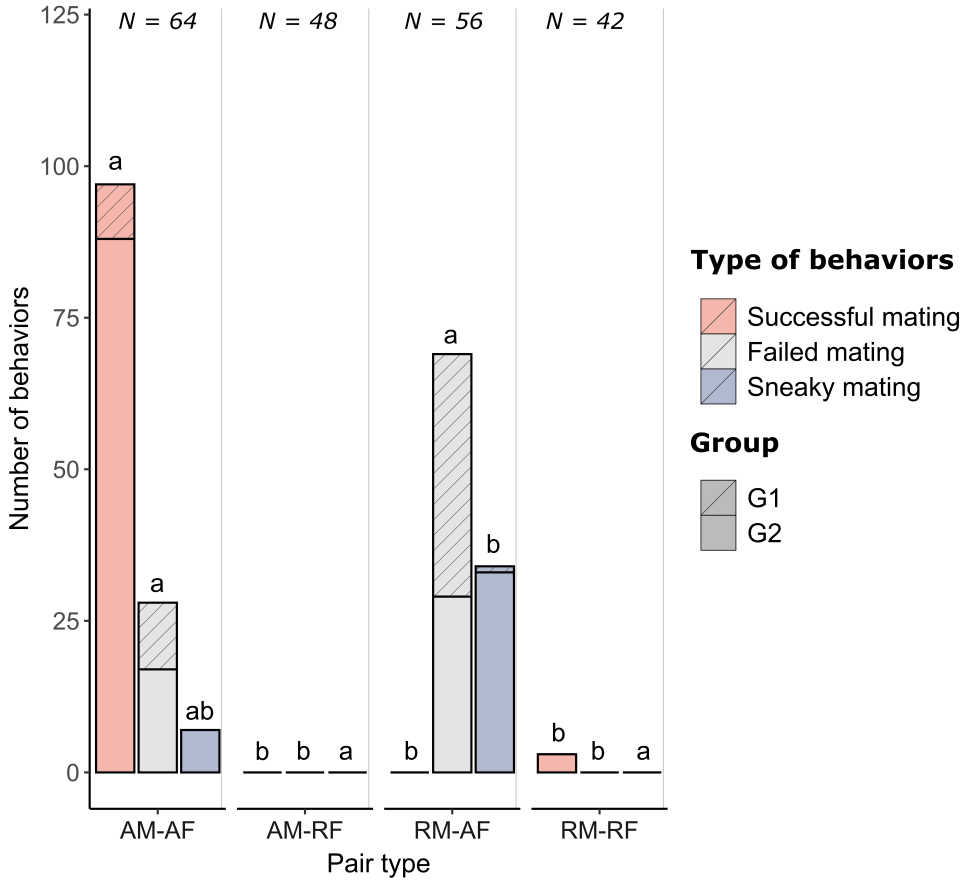


**Figure 4.3.** Total number of successful matings (red), failed matings (grey) and sneaky matings (blue) observed for each pairing type. Bars for mating groups G1 (hatched) and G2 (plain) are stacked. The number above each section refers to the total number of possible combinations within each pairing type. Significant post hoc differences between pairs are indicated with different letters (pairwise Wilcoxon test: $P < 0.05$) for each behaviour.

### 4.3.4 Male-male competition

The combined behavioural observations of matings and intermale aggressions verified the influence of competitive ability on male access to females (Fig. 4.4). Spearman's rank correlation was computed to assess the relationship between the number of intermale aggressions and the number of mating attempts. There was a strong positive correlation between the two

variables, r = 0.88, $P < 0.001$). However, the aggressive ability of males was not related to their form type and the group. Indeed, the Scheirer-Ray-Hare test revealed that there was no statistically significant interaction between the effects of group and form type on the number of intermale aggressions ($H(1) = 0.24$, $p = 0.63$). Simple main effects analysis showed that neither the group nor the individual form type had a statistically significant effect on the number of intermale aggressions (respectively $H(1) = 1.71$, $P = 0.19$ and $H(1) = 0.21$, $P = 0.65$). A total number of 241 intermale aggressions occurred during the breeding season among which 56 (23%) took place in G1 and 185 (77%) in G2. Overall, 150 (62%) intermale aggressions were perpetrated by six anadromous males while 91 (38%) were done by seven resident males. Moreover, 215 (89%) of aggressions targeted anadromous males while 26 (11%) targeted resident males. Simulations of the expected number of male-male aggressions under random associations showed that the observed pattern differs between the two experimental groups (Appendix. Fig. 4.A.2). In group 1, only the number of male-male aggressions in RP-AT was slightly higher than what would be expected from random associations. In group 2, the number of male-male aggressions in AP-AT was very high and above the expected number of aggressions while, on the opposite, it was lower in AP-RT and RP-RT pairs. Pairwise comparisons using Fisher's exact test also showed that in group 1, the number of male-male aggressive pairs was similar within each pair (Appendix Tab. 4.A.2). In group 2, the number of AP-AT aggressive pairs was statistically higher than the number of AP-RT and RP-RT pairs. Moreover, the number of RP-AT aggressive pairs was statistically higher than the number of RP-RT pairs.

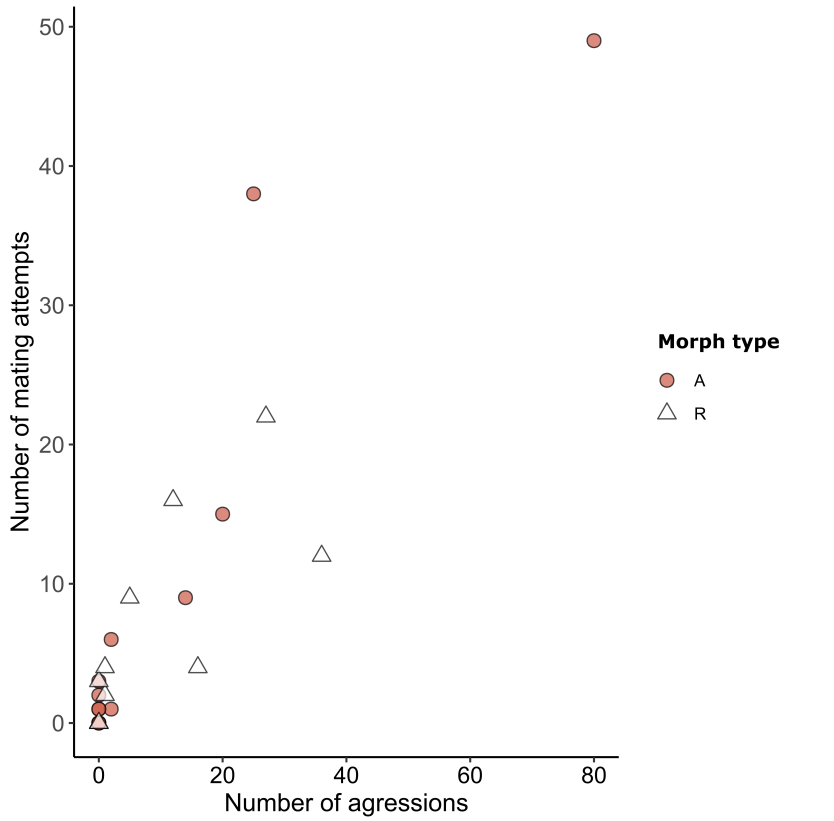


**Figure 4.4.** Relation between the number of mating attempts (i.e. both successful and failed matings) and aggressive behaviours in anadromous (orange circles) and resident (white triangles) males. The Spearman's rank correlation test is significant (r = 0.88, $P < 0.001$).

## 4.4 Discussion

With our experiment, we highlight that form-assortative mating occurs in the arctic lamprey *Lethenteron camtschaticum* since, contrary to what would be expected from random mating patterns, successfully mated pairs were composed only of individuals with the same life history strategy (Fig. 4.2). However, we were not able to demonstrate size-assortative mating as no positive correlation was found between the size of mating partners across forms (Fig. 4.1), and too few pairs were observed to test size-assortative mating within

forms. Interestingly, our results indicate that form-assortative mating in lampreys does not result from a "prudent choice strategy", as we had initially assumed. Indeed, this mating pattern is not the result of a choice for a same-size partner, as males, independently of their life history strategy, preferentially courted large anadromous females (Fig. 4.1, 4.3). However, the physical constraint on pairings involving males and females with high size differences led to a majority of unsuccessful mating attempts among resident males targeting large anadromous females (Fig.4.3). Indeed, unsuccessful matings in resident males were all characterised by the attachment of males' mouths to the females' heads and the consequent inability to reach anadromous females' cloacal contact. Thus, the mechanical constraint due to the large difference in body size between life history forms rendered regular mating between mismatched partners inefficient.

Surprisingly, the assumed superiority in intra-sexual competition of anadromous males due to their larger size was not demonstrated in this experiment as the number of aggressive behaviours was not higher (Fig. 4.4). However, it is important to point out the dominance in intra-sexual competition of one single anadromous male that perpetrated 43% of all aggressions in G2. Moreover, most of the intermale aggressions (89%) targeted anadromous males, which could be explained by their constant presence in the spawning area throughout the experiment. It is also possible that resident males were not considered as potential rivals due to the mating constraint they encounter to fertilise high-quality females and the fact that the aggressive ones were mostly not successful in undoing the establishment of an anadromous male from spawning substrate.

Overall, the physical constraint imposed by large size differences explains the majority of unsuccessful matings observed among pairs constituted of one anadromous female and

one resident male (Fig. 4.1, 4.3). Our results therefore refute our initial hypothesis that size-assortative mating would arise as the consequence of a prudent mate choice and rather reflects the occurrence of form-assortative mating resulting from the simultaneous action of (1) male preference for larger females, independently of the life history of males and (2) physical constraint on mismatched pairings. The observed high-quality mating strategy in males is in accordance with the traditional theory that larger females are preferred in reason to their higher fecundity. This is particularly true in lampreys, as actual fecundity (i.e. the number of eggs at maturity) varies by at least two orders of magnitude between anadromous and brook lamprey species (reviewed by Docker, 2015). In *L. camtschaticum*, previous studies have estimated that fecundity averaged 1,478 eggs in resident females (Kucheryavyi et al., 2007) and up to 119 180 eggs in anadromous females (Yamazaki et al., 2001). Additionally, Bird et al. (1993) discovered significant variations in the fatty acid composition of the ovary of European brook and river lampreys, which correspond to variations in the lipids ingested and stored during the preceding microphagous and parasitic feeding phases, respectively. It is however still unknown whether such differences related to parasitic and non-parasitic life histories affect egg viability and embryo survival. The cost related to the uncertainty of successful fertilisation for males involved in mismatched pairs is therefore potentially outweighed by the benefit of mating at least once with highly fecund anadromous females. This would ultimately disfavour the evolution of mate preference towards females of similar phenotype in resident males.

Moreover, the unsuccessful matings associated with strong size differences in heteroform pairs as well as male-male competition may explain the emergence of an alternative mating behaviour we have observed extensively in our study: sneaking behaviour in males. Satellite male mating behaviours were reported previously within European and American brook

lampreys (Cochran et al., 2008; Malmqvist, 1983). Interestingly, sneaking behaviours mainly concerned resident males towards large anadromous females. The low success of small males in regular matings with large females may select for alternative mating behaviours to gain fertilisation of high-quality females' eggs rather than a prudent mate choice through phenotype matching. This type of alternative mating tactics is common to many teleost species, including salmonids (Gross, 1984; Taborsky, 1994), in which there are often important intrasexual size differences due to the divergence in the anadromous and resident life history form. As males cannot engage in fair competition for the fertilisation of eggs, divergence in optimal reproductive tactics would emerge, with large individuals monopolising mate access and small ones employing alternative tactics (reviewed by Taborsky, 2008). Sneaking male mating behaviour has been once reported in lamprey's species exhibiting alternative life-history strategies (Hume et al., 2013*a*); but as only one female was present in their experiment design, males may have been forced to attempt to reproduce with interspecific females, leading to an incomplete evaluation of the importance of such alternative behaviour in the wild. Our multi-choice experiment, including males and females of both life history forms, confirms their initial observation that sneaking tactics do occur between individuals of different life history forms in complex settings. Although our experiment does not allow us to define the proportion of eggs from an anadromous female's clutch that is fertilised by a resident sneaker male, we believe that such alternative mating tactics contribute to limiting the evolution of sexual isolation. In a previous study on *L.planeri* and *L. fluviatilis*, Rougemont et al. (2015) highlighted that male brook lampreys reproduced with river lamprey females under semi-natural conditions despite the high size difference between those species, which is similar to that observed between life history forms of *L. camtschaticum*. Although the social context in which mating occurred differed between our two studies, the absence of "regular" mating between life history forms in our experiment suggests that the observed

pattern of fertilisation in their study may result from successful sneaking behaviours and not regular matings. Some studies reported mixed-species spawning aggregations in the wild (Cochran et al., 2008; Huggins and Thompson, 1970; Kucheryavyi et al., 2007; Lasne et al., 2010), so the observed pattern in our study is probably not restricted to artificial conditions and may also occur in the wild under natural conditions. It is however important to point out that sneaking behaviours were also employed by anadromous males, highlighting that the choice of tactics (regular mating vs sneaky mating) is not only dependent on relative body size. Additionally, every male that exhibited a sneaking strategy also attempted to mate in a regular way, demonstrating how male lampreys may be able to switch repeatedly between tactics. Changes in reproductive tactics may therefore result from opportunistic responses to specific factors other than body size such as sex ratio and density. The simultaneous use of alternative mating tactics has been shown in many fish species with external fertilisation such as wrasses and cichlids (reviewed by Taborsky, 2008).

Although our study focuses on the life history forms of a single species, our findings can be extrapolated to already diverged lamprey species. Under the same circumstances (populations living in sympatry and displaying similar size differences), male preferences for large fecund females in the small resident species may favour interbreeding in paired species, which could oppose sexual isolation. Our results indeed suggest the potential antagonism between size-based preference towards interspecifics and species-based assortative mating necessary to maintain reproductive isolation. The high frequency of sneaking behaviours observed in lampreys calls into question the assumption that size-assortative mating is a sufficient pre-mating barrier to gene flow in sympatric populations. In addition, recent genetic studies have also shown that no post-zygotic barriers to gene flow appear to exist between different pairs of lampreys species. For instance, recent results from artificial inseminations between reciprocal

crosses of *L. fluviatilis* and *L. planeri* (Hume et al., 2013*b*) demonstrated that a high proportion of hybrid embryos are able to reach the burrowing pro-larval stage. Similarly, Rougemont et al. (2015) showed that the hatching survival of hybrid larvae was nearly 100%, suggesting no post-zygotic isolation between the species. However, the viability of hybrids could not be comprehensively assessed, as the individuals studied were only raised for a few weeks due to the difficulty of maintaining larvae under experimental conditions (Docker, 2019).

### Conclusion

To conclude, the present study indicates that pre-mating barrier to gene flow between alternative forms, in the form of form-assortative through sexual selection, seems to occur in the Arctic lamprey but may not be as strong as previously thought due to the high occurrence of alternative sneaking behaviours between small resident males and large anadromous females. The apparent weakness of this mating pattern as a pre-mating barrier, in addition to the apparent absence of post-zygotic barriers, may explain all together the variable levels of gene flow found between sympatric populations of paired species in both *Lampetra* and *Lethenteron* genera. Such a gradient of genetic divergence reflects that some population pairs may be relatively sexually isolated in some rivers while others may instead correspond to alternative ecotypes of the same species. Others patterns of form or size-assortative mating may however exist in absence of mate choice in lampreys as a consequence of covariation between body size and ecological processes that affects the timing, duration or location of spawning sites (Bracken et al., 2015). Temporal and spatial isolation between alternative forms during breeding season may prevent gene flow between them (review by Docker, 2019) and therefore explain the genetic differentiation observed in some sympatric populations.

# 4.A Appendix

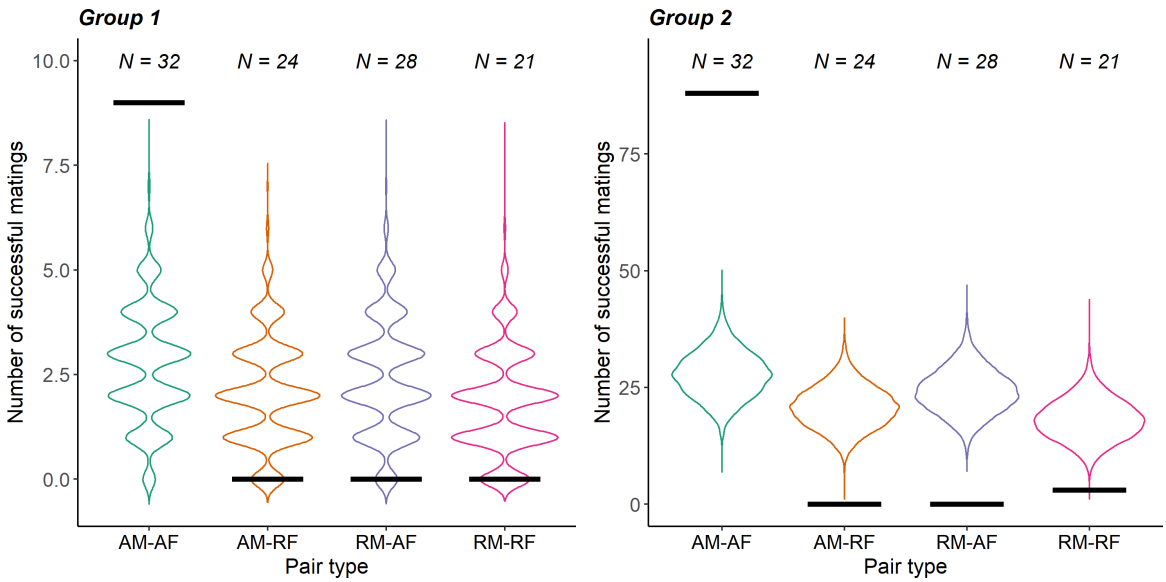


**Figure 4.A.1.** Number of successful matings observed (horizontal bars) and expected under random matings (density plots) in each pair type (AM-AF = anadromous male/anadromous female, AM-RF = anadromous male/resident female, RM-AF = resident male/anadromous female, RM-RF = resident male/resident female) and in each group. Simulations were iterated 10000 times in R (R Core Team, 2022).

**Table 4.A.1.** Number of successfully mated pairs in each pairing type (AM-AF = anadromous male/anadromous female, AM-RF = anadromous male/resident female, RM-AF = resident male/anadromous female, RM-RF = resident male/resident female) and in each group. Parentheses indicate the number of males:females involved. Significant post hoc differences between pairs are indicated with different letters (pairwise comparisons using Fisher's exact test: $P < 0.05$).

| Group | Pair type | Active | Non-active | *Total* | Significance |
|---|---|---|---|---|---|
| *Group 1* | | | | | |
| | **AM-AF** | 5 (3:2) | 27 | 32 | **a** |
| | **AM-RF** | 0 (0:0) | 27 | 32 | **b** |
| | **RM-AF** | 0 (0:0) | 27 | 32 | **b** |
| | **RM-RF** | 0 (0:0) | 27 | 32 | **b** |
| | *Total* | 5 | 100 | 105 | |
| *Group 2* | | | | | |
| | **AM-AF** | 10 (4:4) | 22 | 32 | **a** |
| | **AM-RF** | 0 (0:0) | 24 | 24 | **b** |
| | **RM-AF** | 0 (0:0) | 28 | 28 | **b** |
| | **RM-RF** | 1 (1:1) | 20 | 21 | **b** |
| | *Total* | 11 | 94 | 105 | |

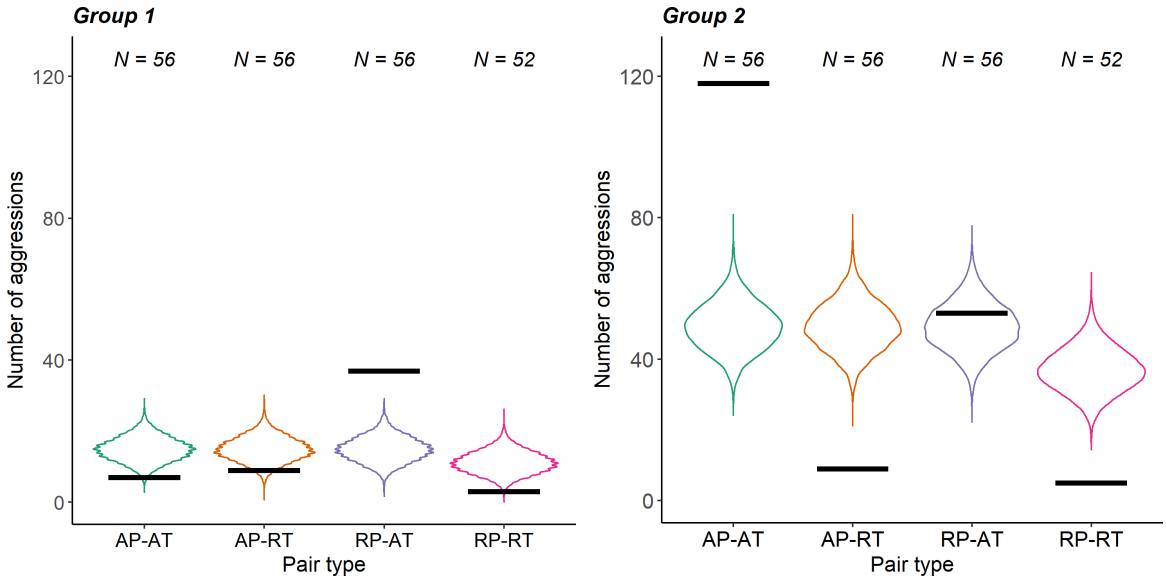


**Figure 4.A.2.** Number of intermale aggressions observed (horizontal bars) and expected under random matings (density plots) in each pair type (AP-AT = anadromous perpetrator/anadromous target, AP-RT = anadromous perpetrator/resident target, RP-AT = resident perpetrator/anadromous target, RP-RT = resident perpetrator/resident target) and in each group. Simulations were iterated 10000 times in R (R Core Team, 2022).

**Table 4.A.2.** Number of male-male aggressive pairs in each pairing type (AP-AT = anadromous perpetrator/anadromous target, AP-RT = anadromous perpetrator/resident target, RP-AT = resident perpetrator/anadromous target, RP-RT = resident perpetrator/resident target) and in each group. Parentheses indicate the number of perpetrator:target individuals involved. Significant post hoc differences between pairs are indicated with different letters pairwise comparisons using Fisher's exact test: P < 0.05)

| Group | Pair type | Active | Non-active | *Total* | Significance |
|---|---|---|---|---|---|
| *Group 1* | | | | | |
| | **AP-AT** | 3 (2:3) | 53 | 56 | **a** |
| | **AP-RT** | 3 (1:3) | 53 | 56 | **a** |
| | **RP-AT** | 5 (3:3) | 51 | 56 | **a** |
| | **RP-RT** | 3 (2:2) | 49 | 52 | **a** |
| | *Total* | 14 | 206 | 220 | |
| *Group 2* | | | | | |
| | **AP-AT** | 16 (4:8) | 40 | 56 | **a** |
| | **AP-RT** | 5 (3:3) | 51 | 56 | **bc** |
| | **RP-AT** | 12 (4:6) | 44 | 56 | **ab** |
| | **RP-RT** | 1 (1:1) | 51 | 52 | **c** |
| | *Total* | 34 | 186 | 220 | |

## 4.2 Chapter highlights

- Evolutionary theory predicts that assortative mating is crucial for sympatric speciation by generating reproductive isolation between diverging populations;
- In anadromous and resident forms of *Lethenteron camtschaticum* that greatly differ in body size, we found that form-assortative mating occurs but does not result from a preference of same-form partner as males – whatever their size – preferred anadromous females;
- The occurrence of sneaking behaviours in males towards anadromous females questions the strength of size-assortative mating as a pre-mating barrier to hybridisation in already diverged species.

Chapter 5

# General discussion

The aim of this general discussion is first to provide a clear and brief summary of the main results of my thesis, then to place this work in a broader perspective, and finally to discuss the implications of my work in the field of sexual selection. I will also present two additional analyses I realised to tackle some limitations I faced or questions I had. These latter approaches will be presented as boxes placed in the appropriate section of the discussion.

## Contents

## 5.1 Results summary

The main objective of my thesis work was to investigate the effects of within-season variations in the social environment on the strength and direction of pre-copulatory sexual selection in lampreys and more precisely to better understand how social factors can shape the evolution of traits and behavioural responses. In **Chapter 2**, I firstly demonstrated in an experiment on *Lampetra fluviatilis* that populations demographics fluctuated during the breeding season and induced within-season dynamics in the opportunity for pre-copulatory sexual selection ($Is_{bc}$). I also showed that the mating advantage conferred by body size is contingent upon the social environment (OSR, size of competitors) with which individuals are faced. Additionally, the spawning timing of an individual can interact with its body size to affect its number of matings: for instance, small females are selected to start early. In line with the recent work of Carleial et al. (2023), this chapter demonstrated that daily calculations of $Is_{bc}$ are constantly higher than the overall $Is_{bc}$, leading to an overall overestimation of the actual strength of pre-copulatory sexual selection. Overall, this chapter revealed the importance of scales at which sexual selection metrics are calculated and emphasized the necessity to collect longitudinal behavioural data. By combining an experiment on *Lampetra planeri* and a modelling approach based on the reproduction of lampreys, **Chapter 3** then explored how intra- and/or inter-sexual variations in reproductive timing may affect the strength of sexual selection and the evolution of sexually selected traits. I showed that opportunity for sexual selection $Is$ was related to both males' and female's reproductive timing but $Is$ was higher in the asynchronous sex in scenarios with inter-sexual variations in reproductive synchrony, which contradicts traditional theory. Specifically, I pointed out that early reproduction can be selected in breeding scenarios where there is an unequal shift in reproductive timing between males and females. Finally, **Chapter 4** complexified the social environment in which individuals interact by including the effect of conspecifics with alternative life history. In anadromous

and resident forms of *Lethenteron camtschaticum* that greatly differ in body size, I showed that form-assortative mating occurs through mechanical isolation and not mate choice. Moreover, the high frequency of sneaking behaviours in small resident males towards large anadromous females questions the strength of size-assortative mating as a pre-mating barrier to hybridisation in already diverged species.

## 5.2 A look at the methodology used

### 5.2.1 Reconsidering mating success

As presented in the introduction of my thesis, a major bias in sexual selection studies is the way mating success is calculated. Due to the widespread use of genetic methods and the difficulty of observing mating sequences, mating success is generally inferred from offspring sampling via parentage analysis, which distorts the definition of a "mate" as a partner with which a focal individual produced offspring. One of the originality of my thesis work was therefore to approach the concept of mating success from a behavioural rather than genetic perspective. This approach is biologically more relevant as it enables us to define more accurately the covariance between a trait of interest and the number of mates acquired by an individual by excluding pre-zygotic (failed fertilisation) as well as post-zygotic (embryo death) events. Adopting this behavioural approach also allowed me to decompose mating success into two successive processes (**Chapter** 2): the mating attempt and the probability of mating success. Considering the reproductive behaviour of lampreys, the first process allowed to investigate females traits that may be under male preference as well as male traits that provide better access to females while the second one rather sheds light on female preference for certain male traits as well as a morphological mismatch between mating partners. In the latter case, directly calculating mating success from mating interactions

enabled me to consider the process as not resulting solely from the phenotype of the focal individual (traditional selection gradients are generally calculated separately for each sex) but rather as the consequence of both partners' phenotypes.

By using this approach, I thus demonstrated that partners with large size differences were less likely to attempt to mate than partners with small size differences (**Chapter** 2). This result was in accordance with the traditional theory that size-assortative mating occurs in lampreys and results from a choice of same-size partner. Surprisingly, I then showed in **Chapter** 4 that all males preferred to mate with large anadromous females, indicating that the size difference between mating partners had no effect on the first process leading to mating success (i.e. the number of mating attempts). The discrepancy between these two results would suggest that at the intra-form scale (at least in *L. fluviatilis*) males preferentially select partners of similar size. Alternatively, we can hypothesize that male-male competition was higher in the **Chapter** 2 experiment in contrast to the **Chapter** 4 experiment, where small resident males were often able to escape aggression attempts perpetrated by anadromous males due to their large size differences (personal observation). Consequently, resident *L. camtschaticum* males might have been able to express their preference for larger and more fecund females more freely than the small males from the **Chapter** 2 experiment.

### 5.2.2 Assessing female preference

One of the difficulties I faced during my PhD was to clearly determine whether there was an active female choice. In lampreys, spawning behaviour is mainly turned towards males gaining access to females through their success in intra-sexual competition. As explained in the previous section (5.2.1), it can be challenging to distinguish the relative role of males' capacity to grab females (physical constraint) from females' mate acceptance (inter-sexual

choice) in the probability that a mating attempt is successful (**Chapter** 2).

During spawning, pre-copulatory active female choice appears to be limited. Although avoidance behaviours may have occurred (e.g. females detaching from the substrate), I have not observed any direct intersexual aggressions from females. Females mating preferences and their mate choice ability may be tested in more artificial situations using *simultaneous choice* and *no-choice* tests (Dougherty and Shuker, 2015; Wagner, 1998). By presenting simultaneously multiple males to females, choice tests would allow for comparisons between available options, and therefore facilitate the assessment of directional preferences between stimuli. Moreover, by spatially separating males from each other and from the female, this measure of preference would preclude forced copulations by males and mechanisms of intrasexual competition. In no-choice tests, on the other hand, each female would be presented with a single male with no physical barrier separating them. Such experimental design would subsequently indicate the occurrence of active female choice by comparing the number of female aggressions or avoidance behaviours. Overall, this would nicely reflect both female mate preference and their ability to express it, thereby providing a means to confirm or reject the theoretical hypothesis I developed in **Chapter** 2 regarding female preference for male body size and how it fluctuates according to the operational sex ratio.

### 5.2.3 Collecting complete behavioural data: is it worth the effort?

The analysis presented in **Chapter** 2 required full knowledge of the copulations occurring in a freely mating group constituted of 20 females and 15 males. Due to the reproductive biology of lampreys (highly polygynandrous, absence of refractory period, high re-mating rate, both diurnal and nocturnal mating activity), observing all mating individuals among individuals was highly time-consuming. Although a complete observation has the advantage of providing a full description of the temporal distribution of individual reproductive activity, I came to wonder whether such exhaustive knowledge of mating sequences was a prerequisite to accurately define variance in copulatory activity. To that end, I realised an additional analysis to compare sexual selection metrics (OSR, $Is_{bc}$) based on the whole copulatory sequences (**Chapter** 2 results) and based on partial data (5 min/h, 12 times a day, in accordance with the approach used in **Chapter** 3). Overall, this additional analysis emphasized that complete knowledge of mating behaviours is not necessary in lampreys to correctly estimate the overall opportunity for sexual selection when longitudinal data collection is available. This further implies that the sub-sampling used in **Chapter** 3 was sufficiently adequate for the results obtained to be accurately interpreted. The results of this additional analysis are presented and discussed in more detail in the Box 5.1.

**Box 5.1.** Comparison of sexual selection metrics estimated from partial or complete data

Taborsky and Brockmann (2010) advocated that *"optimization, not maximization should be the aim"* when choosing an adequate sample size in behavioural studies. While too small sample sizes may give unreliable results, there may be no benefit in large sample sizes if practical constraints make them unfeasible to implement. As described in the previous paragraph, I encountered such difficulties when I started to analyse the behavioural data of **Chapter 2**. This led me to question how to choose the appropriate range and time frame over which to calculate mating success in order to minimize the sample sizes while preserving enough statistical power to accurately estimate the strength and direction of sexual selection.

Thus, the objective of this additional analysis was to investigate whether (1) daily sexual selection metrics (OSR, $Is_{bc}$) calculated from more partial data reflected the temporal variation in selection observed from complete data and (2) the overall opportunity for sexual selection calculated ($Is_{bc}$) was similar between both analyses. In **Chapter 2**, I examined potential within-season fluctuations in sexual selection by calculating sexual selection metrics at a fine-grained scale that segments mating events at daily time steps. I then compared these measures to the overall sexual selection estimated by pooling all mating events that occurred during the breeding season.

Here, I therefore first compared the operational sex-ratio (OSR, i.e. the ratio of sexually receptive males to females; Emlen and Oring, 1977) calculated from partial data to the OSR calculated from the full sequence of mating copulations (Fig. 5.1). Although the temporal pattern was similar in both analyses, we can observe that on 16 days out of 22 days, the daily OSR calculated from partial data was higher than the one from complete data, especially at the end of the breeding season. Such a result suggests that female activity tends to be undervalued when sampling is more limited. This is in accordance with the results presented in Fig. 2.1 that showed that the total duration of female activity was shorter than that of males and that their activity was more asynchronous. By limiting sampling effort, the starting point of female activity has a higher probability to be delayed, resulting in a higher daily sex ratio. This is particularly true at the end of the season where under-evaluation of female activity led to a particularly high OSR due to a decrease in the mean number of active individuals.

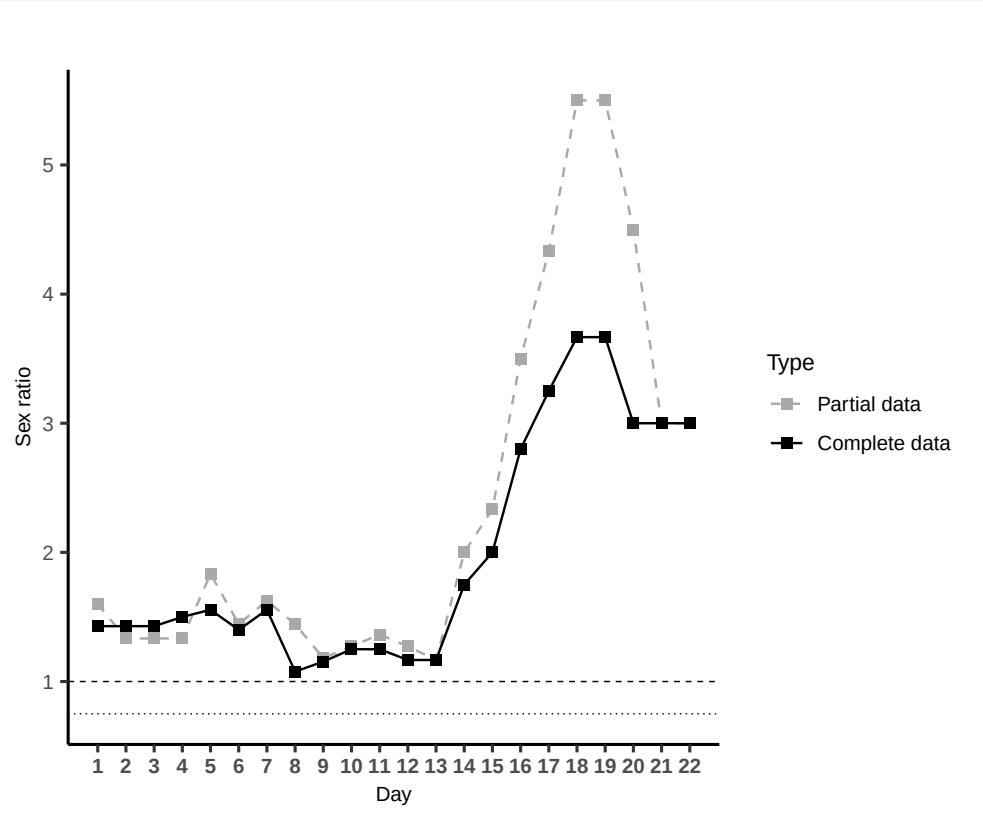


**Figure 5.1.** The operational sex ratio (OSR) each day of the breeding season. The OSR corresponds to the ratio of males to females who are ready to mate on a given day. The grey dashed line corresponds to the OSR calculated from partial data (5 minutes/hour, 12 times a day) while the black solid line corresponds to the OSR calculated with complete data. The horizontal dashed line corresponds to an unbiased sex ratio (1) while the horizontal dotted line represents the adult sex ratio in the breeding group (0.75).

I then compared the bias-corrected opportunity for sexual selection $Is_{bc}$ (Crow, 1989; Wade, 1979; Janicke and Morrow, 2018) calculated from partial and complete data (see 2.2.6 for details on $Is_{bc}$ calculation). In **Chapter 2**, I showed that daily estimates of $Is_{bc}$ changed throughout the breeding season and consistently overestimated the actual opportunity for sexual selection. Here, I demonstrate that this is particularly true if daily $Is_{bc}$ are calculated from partial data, as daily $Is_{bc}$ were even higher on 15 days (Fig. 5.2, a) and 9 days (Fig. 5.2, b) in females and males respectively when $Is_{bc}$ was calculated as the number of partners. Similarly, daily $Is_{bc}$ were higher on 13 days (Fig. 5.2, c) and 16 days (Fig. 5.2, d) in females and males respectively when $Is_{bc}$ was calculated as the number of matings. Interestingly, the overall $Is_{bc}$ is quite similar between the type of data used.

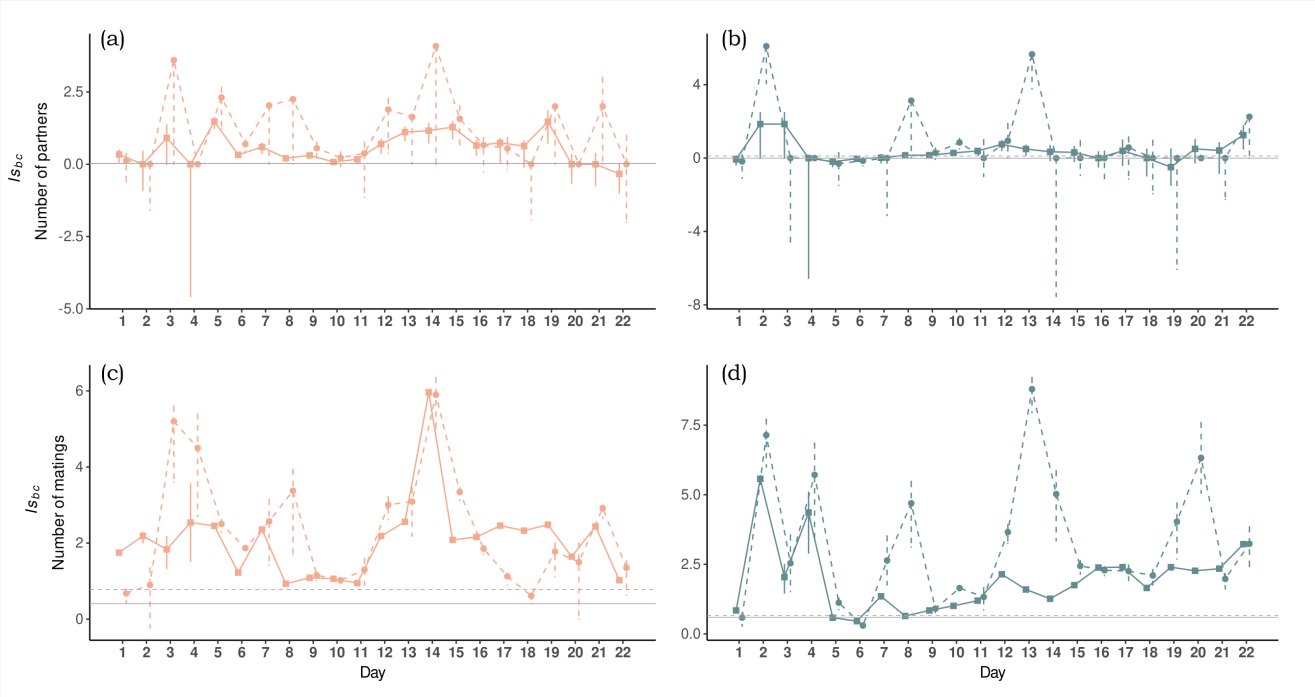


**Figure 5.2.** Bias-corrected opportunity for sexual selection ($Is_{bc}$) with mating success calculated either as the number of partners ($MS_P$, a, c) or as the number of matings ($MS_M$, b, d) in males (blue) and females (orange) on each day of the breeding season. The dashed and solid lines correspond to the overall $Is_{bc}$ calculated from partial data or from complete data, respectively.

This additional analysis first demonstrates that a complete knowledge of the mating sequences is not required to accurately estimate the maximum potential strength of sexual selection at the end of a breeding event as the overall $Is_{bc}$ was similar between both methods. On the other hand, it reveals that daily estimates of $Is_{bc}$ further overestimate the actual opportunity for sexual selection when metrics are estimated from partial data. This suggests that daily measures may be even more biased when assessed from very short snapshots of time. However, such a pattern might only concern highly polygynandrous mating systems where intra-sexual variation in mating success may erode over time. I therefore recommend future studies to perform longitudinal measures of selection metrics across species with variable mating systems (e.g. monogamous species or species with strong social dominance) to perform cross-species comparisons of temporal patterns of pre-copulatory sexual selection. This would give valuable information on the duration and frequency of sampling needed depending on the biological model under study.

### 5.2.4 The use of ABM and future opportunities

During the development of the ABM used in **Chapter 3**, I was forced to make some modelling choices regarding mating behaviours, the reproductive traits considered, and the representation of reproductive timing. In the next paragraph, I discuss in more detail the reasons why I made these decisions, their limits, and the opportunities this ABM offers to further investigate how variations in the social environment influence sexual selection.

**Considering spatial distribution:** the model I have developed is not spatially explicit. I considered that all the individuals which were simultaneously active in the population could meet and that there were no spatially formed subgroups. I made this modelling choice for the following reasons. First, there is currently no empirical research that has determined the relationship between population size and nesting activity on spawning grounds in polygynandrous species of lampreys. Only a recent study on the sea lamprey (*Petromyzon marinus*) highlighted that 202 nests were occupied by around 115 mature individuals; males and females visited around 2 and 1.5 nests and encountered around 2.3 mates for males and 2.2 mates for females (Dhamelincourt et al., 2021). However, sea lamprey is known to be mostly monogamous with generally fewer than five individuals per nest (Applegate, 1950; Manion and Hanson, 1980) while communal spawning of multiple males and females occurs in species such as *L. fluviatilis* and *L. planeri*. Secondly, I wanted to avoid the potential consequences that subsetting the environment into multiple subgroups would have had in the synchronous scenario. Indeed, although individuals would still have been sexually receptive at the same time, including multiple spatial subgroups would have acted as a random variable, with subgroups being more or less made up of mature breeding individuals. Thus, even with an unbiased population sex ratio at the beginning of the breeding season, there would still be variability in the sex ratio within sub-groups. However, depending on

the research question, it might be appropriate to subdivide the global environment into multiple mating subgroups. For instance, if we are interested in better understanding how mating groups form and persist, we may investigate how mating dynamics and movement between nest aggregations are impacted by sex-specific and/or density-dependent arrival and departure.

**Modelling mate choice:** as many models of sexual selection (Castellano, 2009), I made the assumption that individuals freely interact in the population (see previous paragraph), form standing mating pairs based on their competitive ability, and sequentially decide whether to mate or not following a threshold decision rule. I made this assumption because I wanted the pair formation and mate choice process to be symmetrical (Bergstrom and Real, 2000; Johnstone et al., 1996; Johnstone, 1997; Ramsey, 2011). However, as emphasized in section 5.2.2, lamprey mating behaviour is mainly based on males gaining access to females through their success in intra-sexual competition. An alternative decision rule to consider for males would therefore be a best-of-$n$ rule (Janetos, 1980) (also called "pooled comparison", e.g. Wittenberger, 1983; Uy et al., 2001). The most competitive male would sample $n$ females before choosing the most attractive one within this pool. Such mating rule relies on the assumption that males have the cognitive abilities to assess and order potential partners based on their quality. The decision to mate, on the other hand, would only rely on a female threshold decision rule. In **Chapter 3**, I pointed out a significant limitation of the model: the preference strength (or choosiness) does not vary according to the social environment faced by an individual. Implementing a best-of-$n$ strategy in males would enable us to take into consideration rapid within-season changes in female quality distribution, which would ultimately limit this bias. Through theoretical simulations, several studies have shown that the mate-sampling process chosen can indeed have consequences on the intensity of sexual

selection (Dechaume-Moncharmont et al., 2016; Chevalier et al., 2020; Janetos, 1980; Gibson and Langen, 1996). This additional investigation would therefore determine whether the patterns of sexual selection observed in **Chapter 3** are considerably dependent on the pairing process used.

**Integrating divergence in life histories:** the ABM also offers an opportunity to better understand under what conditions hybridisation between closely related species with divergent life histories may occur. Individual-based simulations of various scenarios of pre-mating barriers may be performed to explain the observed frequency of hybrids in the wild. Pre-mating barriers may include temporal isolation during the spawning season and patchiness of the breeding habitat. As mentioned in **Chapter 1** and **Chapter 4**, previous studies have indeed shown that the breeding season does not entirely overlap between anadromous and resident species living in sympatry (Docker, 2015). In Europe for instance, the spawning season of *L. planeri* occurs from March to April while *L. fluviatilis* tends to reproduce from April to May (Renaud, 2011). Similarly, previous observations in France suggested that *L. fluviatilis* tend to reproduce downstream, while *L. planeri* mainly occupy upstream sites (Lasne et al., 2010). In support of **Chapter 4** results, we could also test the relative effects of form-assortative mating and sneaking behaviours in preventing or promoting hybridisation, respectively. Post-mating barriers, on the other hand, have been recently investigated by Decanter et al. (under preparation) through an individual-based simulation software NEMO that incorporates several genetic modules (Guillaume and Rougemont, 2006). However, none of the simulated scenarios of hybrid viability explained the observed proportions of adult hybrids of first generation in the Oir population, France. It would be interesting to create an individual based-model that is both genetically and spatially explicit to represent the complex life histories of lampreys (i.e. a demo-genetic agent-based

model, see Appendix B). Modelling evolutionary processes (i.e. heritable traits transmission across generations) as well as spatial and temporal distribution of individuals based on their life cycle would unravel possible eco-evolutionary mechanisms behind lamprey speciation.

**Representing reproductive timing:** the hypothesis underlying my modelling approach was that reproductive timing depended solely on changes in environmental seasonality. However, several studies showed that reproductive timing also has biological determinants and can be caused by social interactions. In mammals, French and Stribley (1987) showed that reproductive synchrony can be achieved among group-living females through the exchange of pheromonal stimulation. Similarly, Jovani and Grimm (2008) demonstrated that social cues may influence the reproduction of conspecific individuals in birds and trigger reproductive synchrony. Therefore, individual reproductive timing might not solely rely on individual sensitivity to abiotic cues (climatic seasonality) but also on individual ability to sample potential mates and competitors and to adjust its activity to the current social environment. Individuals may indeed adapt their timing of sexual activity according to the perceived quality of competitors and potential mates as well as their own phenotype. This aligns with the approach used in **Chapter 2**, where I examined the potential sexual selection on the timing of reproductive activity with respect to sex and phenotype and showed, for instance, that females are selected to start early, especially if they are small. A more realistic modelling approach would therefore be to make reproductive timing dependent on an individual trait (e.g. social assessment ability) that could potentially evolve as part of a reproductive strategy to improve individual reproductive success (see Fig. 5.3). However, it may be complex to define the genetic basis of this trait and to model the interplay between genetic and environmental changes.

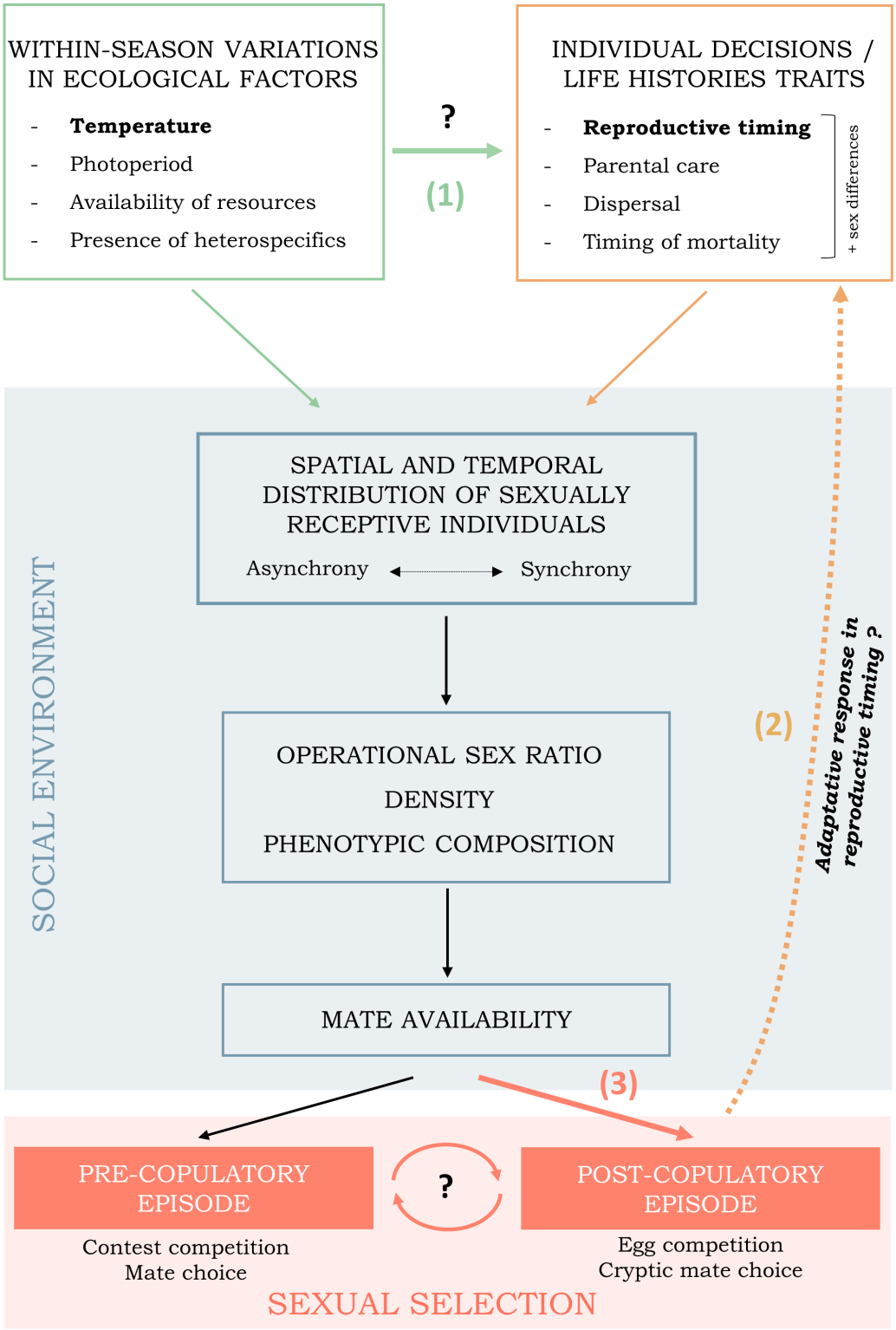


**Figure 5.3.** Abiotic (environmental) and biotic (ecological) factors that may affect mating system dynamics and ultimately the strength and direction of sexual selection. **(1)** represent the factor I had initially planned to test (see 5.3) while **(2)** and **(3)** rather shed light on mechanisms that should be explored (see 5.2.4 and 5.4, respectively).

### 5.2.5 Experimental approach

In light of the challenges associated with doing empirical work (notably monitoring natural populations), many scientists are increasingly opting for theoretical modelling (Scheiner, 2013) as an alternative to conducting experiments. Although I highlighted in the previous section the considerable opportunities offered by ABMs for studying ecological and evolutionary processes that would be difficult to explore in experimental settings, I am convinced that empirical research remains essential. While empirico-inductive methods are important when there is a lack of knowledge on the basic reproductive patterns of the species under study, hypothetico-deductive methods rather enable testing the validity of more theoretical hypotheses. For instance, the in situ observations of communal spawning between *L. planeri* and *L. fluviatilis* (Lasne et al., 2010) have been the foundation of many substantial works on stem-satellite species complexes. I, therefore, believe that theoretical work and empirical work should coexist closely and mutually stimulate each other in a feedback loop.

Across both the experimental approaches used in **Chapter 2** and **Chapter 4**, sexual network theory served as a conceptual tool to explore the role of the social environment in determining sexual selection. This implied doing experiments in a more realistic biological setting than is generally done, without interfering with mate choice rules. Studies on sexual selection and mate choice indeed generally use controlled copulations with very few partners (usually two in classical simultaneous choice experiments; Miller and Svensson, 2014; Dougherty, 2020). In such artificial situations, intra-sexual competition and inter-sexual preference are largely constrained as individuals are generally restricted to a limited number of mates. By creating relatively large mating groups of lampreys, I was therefore able to get experimental conditions that more closely reflected the demographic conditions of natural populations and are more suitable for testing how mate choice occurs.

However, one can argue the necessity to do experiments in even more natural conditions in order to measure the effects of selection in a completely realistic context. In the experimental conditions, I restricted mating to a single substrate area, which may have increased the probability of heteroform matings in **Chapter** 4 and, more generally, mating rates and the potential for polygynandry (**Chapter** 2, **Chapter** 3). In France, ECOBIOP's Lapitxuri experimental channel (INRAE, 2018) offers a nice opportunity to replicate these experiments in more realistic conditions. As the Lapitxuri channel is a derivation of a natural river (the Lapitxuri stream, in southwestern France), it offers environmental features close to natural conditions, including an unlimited substrate for nest construction, while enabling reproductive activity to be monitored. However, I am not totally convinced that the experimental settings have accentuated the level of polygynandry or intra-sexual competition as a few studies demonstrated high promiscuity in natural settings (for instance up to 70 individuals in a *L.fluviatilis/L.planeri* nest, Lasne et al., 2010) with similar sex-ratio.

### 5.2.6 Working on non-model organisms

A recent literature survey conducted by Zuk et al. (2014) emphasized that sexual selection studies primarily concentrate on insects (29%) and birds (27%) and to a lesser extent on fishes (16%). For the latter, the authors' search returned 161 empirical articles on sexual selection that concerned 81 different species. However, nearly 27% of studies using fish as a model species have been made on the three-spined stickleback *Gasterosteus aculeatus* and the guppy *Poecilia reticulata*. Although these two famous model species have contributed significantly to the understanding of sexual selection during recent decades (notably the role of colouration in mate choice), the large proportion of studies that are made on the two species reflects the lack of general knowledge about the evolution of reproductive behaviours in fishes.

Using lampreys as a biological model was therefore very stimulating as it gave me the opportunity to address many unexplored research questions, fuelled by previous studies on other organisms. In my opinion, working on non-model species, especially as part of a PhD thesis, greatly facilitates the development of original experimentation. One way lampreys deviate from most other model species is in terms of their lack of sexual dimorphism and conspicuous ornamentation. This, together with their polygynandrous mating system, made the strength of pre-copulatory sexual selection quite difficult to predict, making them a fascinating model to study. On the other hand, I was confronted with unexpected events (see 5.3) that make me realise that some species are perhaps little studied for certain logistic reasons. The first is the size and density of lampreys. Most popular model fish species in current research on sexual selection are quite small and occur at high densities. This makes laboratory work logistically easier and allows many more replicates to be carried out in parallel. Although this applies to *L. planeri*, the anadromous species are rather medium-sized and are increasingly difficult to observe in the field due to their general decline; e.g. in the Iberian peninsula for *L. fluviatilis* (Cabral et al., 2005) and in the Japanese Archipelago for *L. camschaticum* (Renaud, 1997; Yazawa, 1998). For these reasons, I was not able to do more than two replicates in **Chapter 4**. Additional difficulties inherent to the species under study were also faced. The first is the inability of identifying males from females, except just before spawning. The overall absence of sexual dimorphism until the period of reproduction is complicated to manage when it comes to manipulating sex ratio and densities. Second, it is a challenge to work on long-lived species exhibiting seasonal reproduction within the framework of a 3-year PhD project. As explained in the next section (5.3), the failure of my first experiment forced me to reconsider my thesis plan and postpone the new projects arising from this reflection until the following year. Working on species that breed approximately all over the year prevents such practical risks.

Despite difficulties linked to working with less-known species, I still encourage further studies to use new model systems to generate more meaningful theories about sexual selection. Fishes are incredibly diverse, not only in terms of species number but also in terms of sorts of mating systems represented (Forsgren et al., 2002). Restricting our focus on a few sets of model organisms may therefore limit our knowledge of the potential variation of patterns of selection across taxa.

## 5.3 The failed experiment: the missing piece

Numerous studies revealed the increase of heat waves in recent decades due to climate change (e.g. Easterling et al., 2000; Orlowsky and Seneviratne, 2012). Indeed, heat wave frequency, duration and intensity have been shown to increase in the northern hemisphere due to global warming. Although river water temperature may differ considerably among different rivers due to factors such as river size or flow velocity (Arismendi et al., 2012), the overall increase in air temperatures has been identified as the primary cause of the warming trend in European rivers (Webb and Nobilis, 1995). As most fishes are poikilotherms, rising water temperatures highly influence their reproductive synchrony, by altering the timing of maturation and spawning (Munro et al., 1990; McQueen and Marshall, 2017).

One aspect I omit to introduce until here is that the first experiment of my thesis project initially aimed to investigate whether a rapid and strong increase in water temperature rate in March (based on an extreme event observed in the Nivelle river, France) was sufficient to alter the onset of sexual maturation and induce inter-individual variations in maturation timing (see Fig. 5.3). I had hypothesized that (1) individual sexual maturity would respond to a thermal reaction norm (Hardisty and Potter, 1971), (2) a rapid rise in spring temperature would increase maturity synchrony compared with a slow rise (Clemens et al., 2009), and (3)

sex-differences in maturity timing to heatwave would occur (e.g. in squirrels Kucheravy et al., 2021). Ultimately, this experiment was intended to provide conditions and circumstances surrounding the research question presented in **Chapter 3**, and to justify the assumption that climate-driven changes in environmental seasonality would induce intra-and/or inter-sexual variations in the timing of reproduction in lampreys.

Unfortunately, all individuals died before reaching sexual maturity in both the test (i.e. rapid increase) and control (i.e. slow increase) conditions. This mortality may be explained by the environmental conditions in which individuals were maintained. They were kept in small individual tanks to exclude the effect of pheromones on sexual maturation synchrony and were manipulated daily to assess secondary sexual characteristics. The regular handling, lack of environmental enrichment, and absence of social contact likely contributed to increased stress in lampreys, ultimately leading to deleterious effects on their development and immune function. Although this experiment was unsuccessful, I still consider that this project was interesting overall for (1) contextualizing more clearly the theoretical assumption of the ABM used (**Chapter 2**), and for more broadly (2) testing the effect of climate change on population dynamics and sexual selection. However, it might be preferable to consider other species for which potential sources of stress are well known to tackle this specific research question.

## 5.4 But what happens after copulation?

A behavioural-based approach to mating success has its drawbacks, however. Although defining mating success as the number of matings performed by the focal individual allows us to approximate its reproductive success, the omission of mechanisms occurring after copulation prevents us from properly determining whether the observed covariance between a focal trait and mating success actually translates into real selection on this trait (i.e. whether the Bateman gradient would be positive). This is particularly true for group-spawning species with external fertilisation such as lampreys, for which there is a high potential for gamete competition and cryptic mate choice (Petersen and Warner, 1998; Stockley et al., 1997*a*; Fitzpatrick, 2020). In this part of the discussion, I will first investigate the potential of sperm competition and cryptic female choice in lampreys considering the available literature and some results of my thesis. Additionally, I will shed light on lesser-explored mechanisms, i.e. egg competition and cryptic male choice, which could also have an influence on how I assessed the strength of pre-copulatory sexual selection.

### 5.4.1 Sperm competition and cryptic female choice: what we know and what we could expect

Externally fertilising males are believed to exert limited control over paternity as they release their gametes externally, enabling group spawning and sneaking behaviours (Petersen and Warner, 1998; Stockley et al., 1997*a*). This high risk of sperm competition is expected to weaken the pre-copulatory sexual selection as behaviourally successful matings may not result in egg fertilisation. The main limitation of my thesis work is that I have not been able to access the overall reproductive fitness of lampreys through parentage analysis. To tackle this problem, I tried to estimate the potential level of sperm competition in *L. fluviatilis* (**Chapter 2**) via an additional networks analysis that took into consideration matings "shared" by multiple males (see Box 5.2 for details).

**Box 5.2.** Potential for sperm competition in *Lampetra fluviatilis* via a network approach

With polyandry, a male's reproductive success not only depends on the total number of mates and matings he has managed to acquire but also on the degree of polyandry of its partners as successful sperm release may not necessarily result in the fertilisation of ova under sperm competition. The relationship between males' mating success and the sperm competitive environment they face may be explained by the degree of *assortativity* of the overall population mating network. In a mating network characterised by positive assortativity (Fig. 5.4, a), males with the highest number of partners also tend to mate with females with the highest number of partners. As males that mate with many females face the most intense sperm competition, such mating pattern may ultimately reduce the strength of pre-copulatory sexual selection on mating success by flattening the relationship between reproductive success and mating success (i.e. a shallower Bateman gradient). Conversely, in a mating network characterised by negative assortativity (Fig. 5.4, b), males with the highest mating success display mate monopolisation, facing lower sperm competition than males with few partners. In such a case, the relation between reproductive success and mating success would be stronger (i.e. a steeper Bateman gradient). The assortativity of a mating network can be quantified through different network metrics such as Newman's assortativity (Newman, 2002), nestedness measurements (e.g. NODF, Almeida-Neto et al., 2008) or more recently the sperm competition intensity correlation (SCIC, McDonald and Pizzari, 2016).

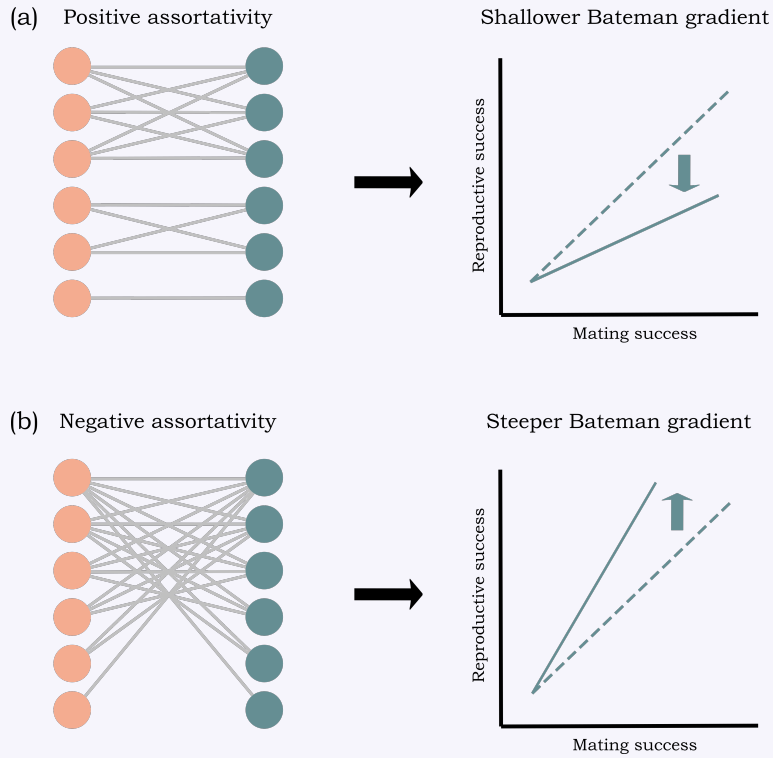


**Figure 5.4.** Relation between mating network assortativity and the Bateman gradient. A mating network characterised by positive assortativity is expected to weaken the relationship between reproductive success and mating success, resulting in a shallow Bateman gradient (a) while a mating network characterised by negative assortativity is expected to strengthen the relationship between reproductive success and mating success, resulting in a steeper Bateman gradient (b). Orange nodes represent females, blue nodes represent males. Grey ties indicate a mating pair. Adapted from Greenway et al. (2021)

However, applying these metrics to organisms with external fertilisation may be problematic. Unlike internal fertilisers, a male's reproductive success does not entirely depend on how polyandrous his partners are since there is, by definition, no sperm storage by females. Although a female may successfully mate with multiple males throughout a breeding season, these males may not compete with each other as their ejaculates may not overlap at the time of fertilisation (e.g. in the absence of sneaky matings). During the experimental study presented in **Chapter** 2 on *L. fluviatilis*, I have regularly observed successful matings involving two or more males at the same time. Under such circumstances, we may consider that the target female represents a resource shared by the different males acting simultaneously, inducing a high potential for sperm competition. In this context, I constructed a unique competitive environment for each male of the population, either on a daily basis or over the whole breeding season. Competitive networks were derived via matings networks constructed for each mating interaction where multiple males were active (Fig. 5.5). For instance, if both males were simultaneously mating with the same female, they both shared a competitive tie in their respective competitive network.

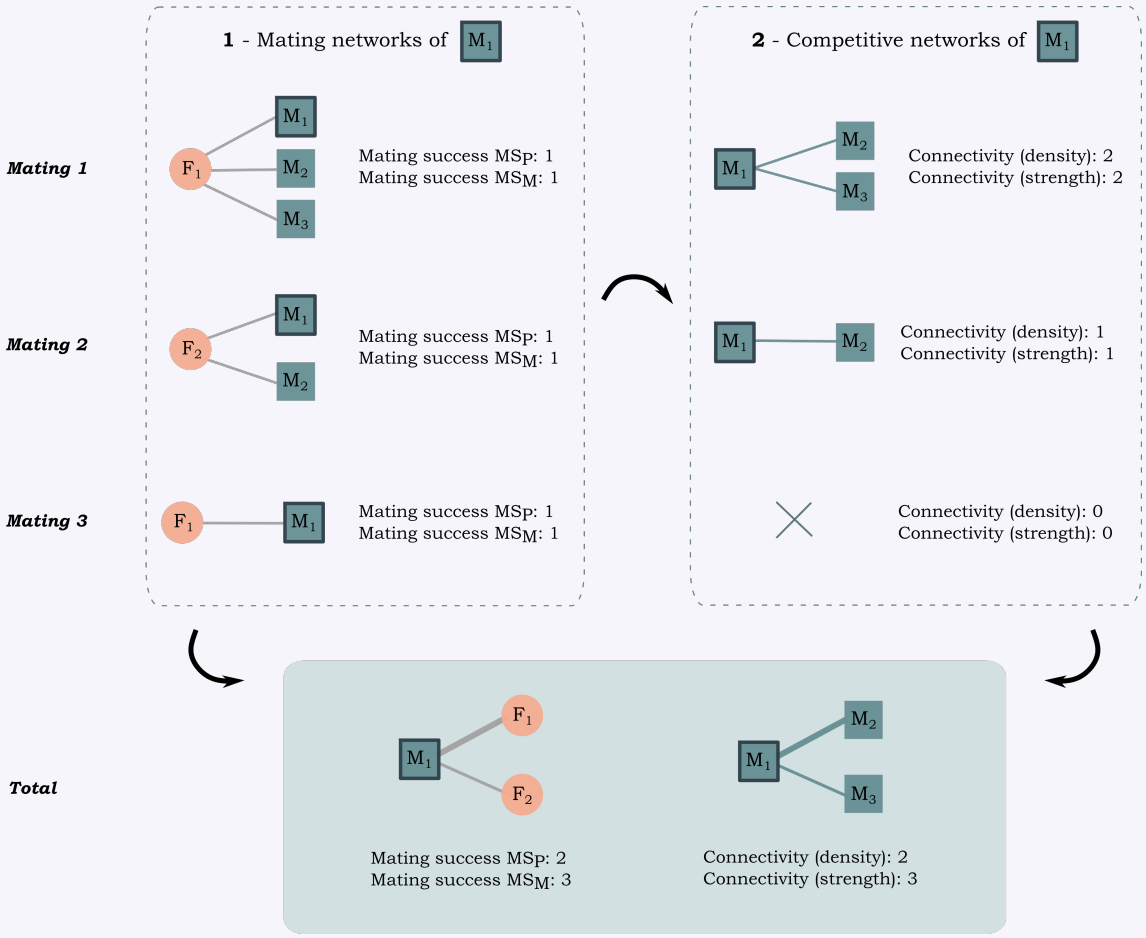


**Figure 5.5.** Representation of the network approach used to estimate the sperm competitive environments of males. Mating networks, where ties represent copulations, were constructed for each male and were projected into a competitive network, where ties represent indirect competitive interactions. The global mating and competitive network of each male was then constructed either daily or at the scale of the whole breeding season.

The overall mating success was calculated either as the number of mates $MS_P$ or the number of matings $MS_M$. Males' connectivity in their competitive network was characterised by the density of the network (i.e. the number of competitors) and the ties' strength (i.e. the number of competitive interactions). While the relationship between $MS_P$ and density metric reflects the level of assortativity of the network (Fig. 5.4), interpretation may be limited as it only quantifies binary ties, i.e. whether the pair either copulated/competed or not. Calculating both tie strength and its relation with $MS_M$ allows us to consider the frequency with which a male mated with females and competed with other males, giving clearer insight into the impact of having additional matings on reproductive success. The pairwise relationship between males mating success and their sperm competitive networks was assessed via Pearson correlation coefficient or Spearman's rank correlations tests.

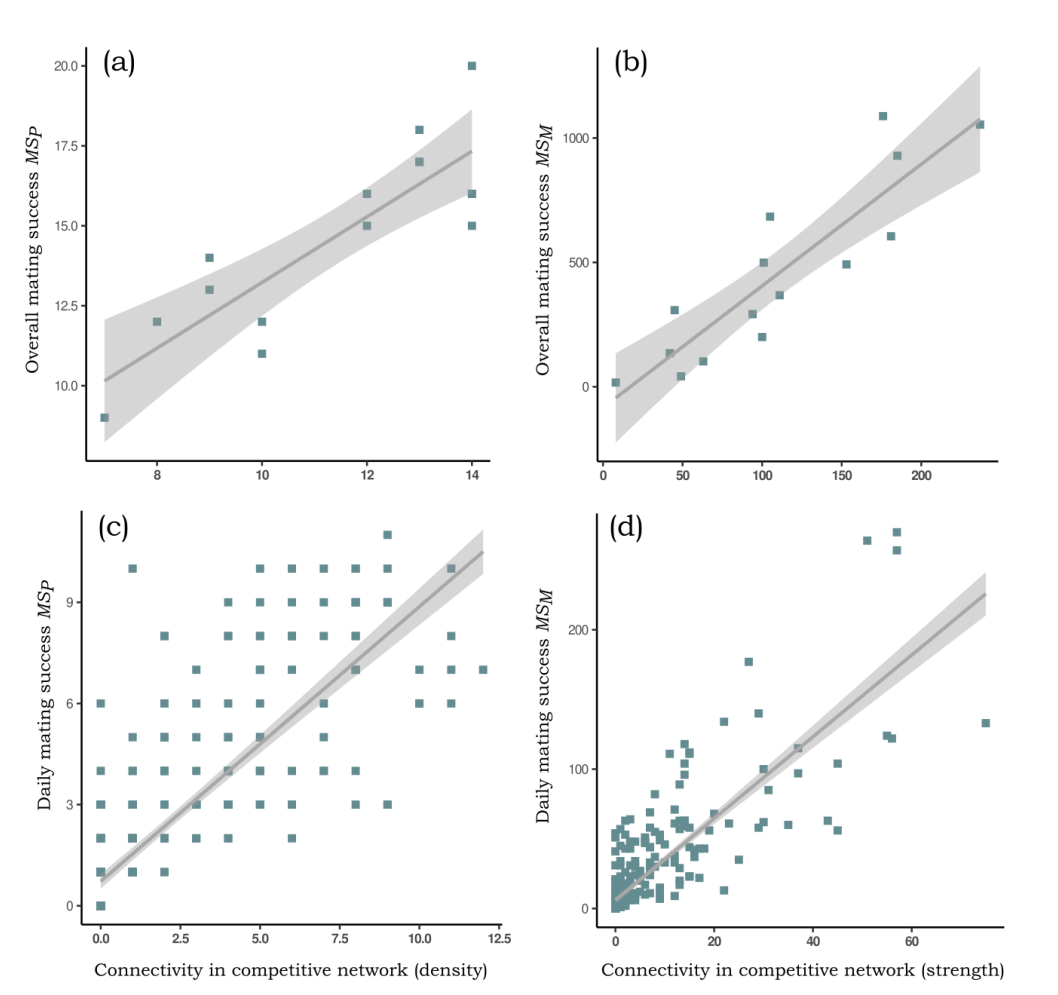


**Figure 5.6.** Relation between males mating success and their sperm competitive network. Male mating success was calculated either as the number of partners $MS_P$ (a,c) or the number of matings (b, d) and either daily (a, d) or over the whole season (a, b). Connectivity in the competitive network was characterised as the number of male competitors (density, a, c) or as the total number of indirect male competitive interactions (strength, b,d).

There was a strong correlation between mating success and connectivity when mating success was calculated over the whole season; either with $MS_P$ (r = 0.85, df = 13, $P < 0.01$) or with $MS_M$ (r = 0.89, df = 13, $P < 0.01$). Similarly, there was a

strong correlation between mating success and connectivity when mating success was calculated daily; both with $MS_P$ (r = 0.87, df = 328, $P < 0.01$) or with $MS_M$ (r = 0.88, df = 328, $P < 0.01$). The positive assortativity between $MS_P$ and density metric suggests that males with the higher number of partners constantly faced higher sperm competition as they mated with the most polyandrous females throughout the mating season. Similarly, the positive relationship between $MS_M$ and network strength implies that males with the highest re-mating rate mated with females with the highest re-mating rate. Such a pattern further suggests that the strength of pre-copulatory selection on mating success might be reduced in this mating system, as both the number of mates and the number of matings might be weakly or even not correlated to reproductive success.

Here, the scope and potential for sperm competition to operate in *L. fluviatilis* has only been estimated by analysing matings involving multiple males. However, the occurrence of sneaking behaviours is quite common in lampreys (see previous section and **Chapter** 4). Although ejaculates from sneaking individuals are likely subject to greater dilution than the ones of regular males, sneaky males may still succeed in fertilising ova, which may further limit the strength of pre-copulatory sexual selection on having additional mates by increasing the potential of sperm competition. As mentioned in the previous section of the discussion, genetic parentage analysis may be used in combination with behavioural observations to have a more comprehensive view of the relationship between mating success and reproductive success in lampreys.

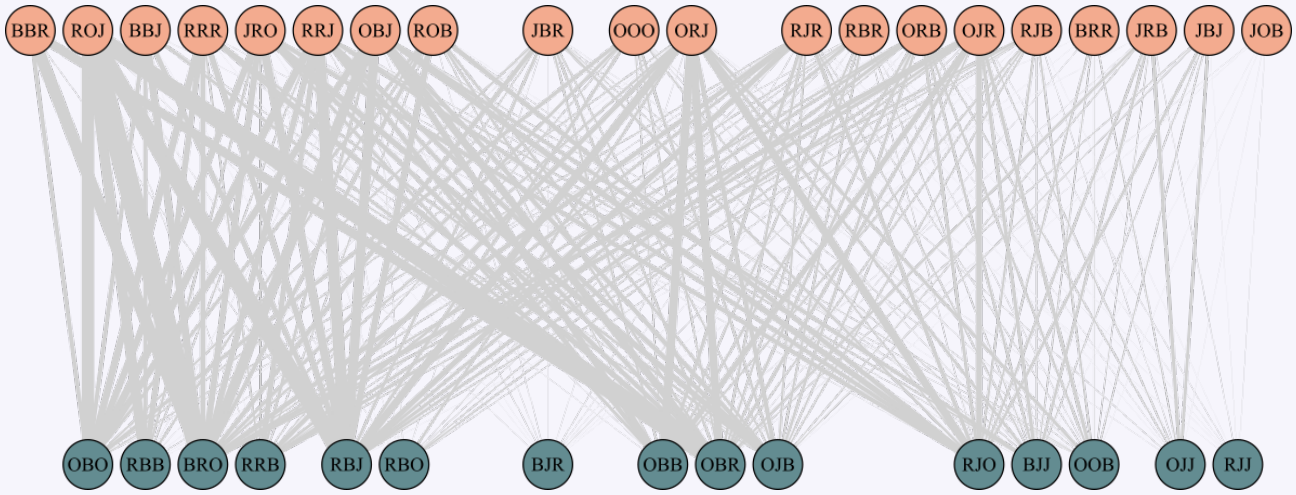


**Figure 5.7.** Overall mating network in the experiment from **Chapter** 2 on *Lampetra fluviatilis*. Males are in blue while females are in orange. A grey tie represents a mating interaction. The thickness of the tie reflects its weight i.e. the number of copulations between the mating pair.

Previous studies have shown that the duration of lamprey sperm motility is high in comparison with many other externally fertilising fish (Browne et al., 2015). For instance, Kobayashi (1993) and Ciereszko et al. (2002) demonstrated that Arctic and sea lamprey sperm were motile for 4 to 5 minutes following activation, while rainbow trout sperm are, for instance, motile about 30 seconds. As the time between egg emission and fertilisation by lamprey sperm may be relatively long, the occurrence of sneaking behaviours in males (**Chapter** 4) could further accentuate sperm competition risk. This is all the more important in light of the evolutionary context of lamprey speciation since a high proportion of sneak matings involved non-parasitic resident males and parasitic anadromous females.

In **Chapter** 4, I investigated how sexual selection may drive reproduction isolation through pre-copulatory mechanisms (male–male competition and mate choice) and showed that form-assortative mating does occur, but through mechanical isolation. Sexual selection may also drive lamprey speciation through post-mating, pre-zygotic processes that include cryptic female choice (Andersson, 1994; Hosken et al., 2002; Howard et al., 2009; Tyler et al., 2013; Yeates et al., 2013; Firman et al., 2017). Cryptic female choice may indeed facilitate speciation by favouring fertilisation of conspecific sperm in sympatric conditions where there is a risk of genetic incompatibility due to hybridisation (Yeates et al., 2013). Using a common garden experimental design that controls for direct parental effects, Rodríguez-Muñoz and Tregenza (2009) showed that male × female interactions had a highly significant effect on hatching success in sea lamprey, highlighting variation in male–female reproductive compatibility. These findings suggest that females may enhance their reproductive success by promoting those sperm conferring the highest offspring fitness to be the successful fertilisers. In this context, Decanter et al. (2023) recently investigated the potential of conspecific sperm precedence (CSP, Howard et al., 2009) as an enforcer of reproductive isolation (Firman et al.,

2017) between *L. fluviatilis* and *L. planeri*. Using sperm competition experiments either at equal semen volume or at equal sperm number, the authors found no evidence for cryptic female choice as there was no tendency of eggs to be fertilised by sperm of conspecific males. Additionally, Decanter et al. (2023) also demonstrated complete fertilisation compatibility between both species in no-choice fertilisation experiments, as previous studies on the *L. planeri*/*L. fluviatilis* species pair suggested (Hume et al., 2013*a*; Rougemont et al., 2015). This result further indicates that post-mating pre-zygotic barriers to reproductive isolation are weak in lampreys and that the sneaker males observed in **Chapter 4** might have achieved fertilisation of heteroform eggs.

Although lamprey females do not appear to display cryptic female choice through biased fertilisation (at least towards homospecifics), they could express their preference by controlling the release of their eggs. Yamazaki and Koizumi (2017) recently showed that female lampreys of five species (*P. marinus*, *L. planeri*, *Lethenteron appendix*, *Lethenteron kessleri* and *Entosphenus tridentatus*) engage in *sham mating*, a behaviour where they mate without releasing eggs. In *L. kessleri*, the authors demonstrated that the release of eggs was affected by the body size of both mating partners due to the physical constraint of lamprey's mating behaviour. Specifically, if a male is either too small or too large, its ability to squeeze eggs from the female is reduced. However, Yamazaki and Koizumi (2017) did not investigate a link between male potential quality (absolute body size) and the number of eggs emitted by the female. Interestingly, the authors also observed that the frequency of sham matings was higher in conditions of high male abundance (single female with three males) compared to conditions with low male abundance (single female with one male). Such observation suggests that female lampreys may also adopt post-mating strategies in response to changes in population demographics. Previous studies showed that overabundance of competing

sperm at high densities may induce reproductive failure in females due to polyspermy (i.e. fertilisation of an egg by more than one sperm that generally results in an unviable zygote) (Levitan, 1998, 2004; Okamoto, 2016). However, the absence of polyspermy in lampreys refutes the hypothesis that sperm saturation at high densities could be a factor promoting sham mating in females (Kobayashi et al., 1994). In **Chapter 2**, I showed that late-starting females attempt more matings with males active at the end of the season, but appear to be more selective towards them. As late-active males are more likely to be sperm-depleted, I suggested that females are probably more discriminating towards them to prevent costly matings. This hypothesis is supported by a recent study highlighting that sea lamprey females are attracted to spermine, a seminal plasma pheromone emitted by spermiating males (Scott et al., 2019). Considering the limited ability of female lampreys to avoid mating attempts (see section 5.2.2), I hypothesize that females may also exert post-mating control by exhibiting sham mating behaviours towards sperm-depleted males. Through no-choice test experiments, it would be interesting to explore whether females exposed to spermiating males with inhibited spermine production exhibit a higher occurrence of sham mating behaviours.

Interestingly, Decanter et al. (2023) also reported that *L. planeri* males have a higher sperm concentration than *L. fluviatilis* males. The authors proposed that differences in this sperm trait among species could be attributed to the sneaking strategy employed by *L. planeri*. Furthermore, they suggest that this tactic may not evolve in allopatric populations, indicating that the evolution of the sneaking strategy emerged as an alternative way to fertilise *L. fluviatilis* eggs. However, in **Chapter 4** I showed anadromous *L. camtschaticum* males also displayed sneaking behaviours towards anadromous females. Similarly, sneaking behaviours were also observed in both *L. fluviatilis* (**Chapter 2**) and *L.planeri* (**Chapter 3**). Moreover, males dis-

playing sneaking behaviours also engaged in typical spawning with females, highlighting that both behaviours are not mutually exclusive in male lampreys. These observations overall highlight that (1) sneaking also occurs at the intra-form/intra-specific scale and (2) male lampreys may switch back and forth between tactics. I therefore assume that the sneaking strategy did not evolve as the sole consequence of the presence of large heterospecifics (although relative body size may be a key factor) but may also be a conditional choice depending on additional social factors such as sex ratio and density at spawning aggregations (Taborsky and Brockmann, 2010; Lee, 2005). Based on the data of the experimental study presented in **Chapter 3**, I performed a chi-square test of independence to examine the relation between the breeding scenario and the ratio of the number of sneaking behaviours to the total number of successful matings. The relation between these variables was significant ($\chi^2$ (1, N = 200) = 1, P < 0.01). The occurrence of sneaking behaviours was higher in the AF-SM scenario, i.e. when the OSR was male-biased at the beginning of the experiment than in the SF-SM scenario, i.e. when the OSR was male-biased at the beginning of the experiment. This suggests that males are more likely to adopt a sneaking strategy when the level of competition is high. Further investigation is required to demonstrate whether fluctuations in mating opportunities and sexual selection intensity influence the expression of male alternative reproductive tactics in lampreys.

### 5.4.2 Egg competition and cryptic male choice: what we (mainly do not) know and what we could envisage

Although there has been a significant increase in interest regarding the impact of sexual selection on females in recent decades (mainly concerning cryptic female choice, e.g. Eberhard, 1996; Firman et al., 2017), research on sexual selection has rarely focused on female traits that may confer a competitive advantage for access to mates and male gametes (Hare and

Simmons, 2019). In **Chapter 2**, one of my wishes was to report symmetrically how sexual selection acts in both sexes to get more accurate knowledge on the mechanisms and effects of sexual selection in lampreys. By measuring the opportunity for sexual selection $Is_{bc}$ in both males and females, I showed that there was as much scope for pre-copulatory sexual selection in females as in males. Similarly, I demonstrated that sexual selection may also act on female body size and on female behaviours such as spawning time and duration. Such results made me think that sexual selection may also act on aspects of gamete morphology and post-mating behaviour through *egg competition*, where eggs from different females compete for fertilisation. However, this term is barely used, partly due to the difficulty of disentangling egg competition and cryptic female choice processes (although this difficulty also happens in males, and the term cryptic male choice is, on the other hand, rarely employed). To my knowledge, Berglund (1991) was the first to explicitly demonstrate egg competition in an externally fertilising fish. When small and young *Syngnathus typhle* females had unrestricted access to males but were simultaneously in the presence of a visibly larger female who was confined, they reduced their egg production and instead prioritized their growth. This behaviour differed from their response when they were in the presence of another small female or when no other female was present at all. One can argue that this outcome is a consequence of the larger female exerting intra-sexual dominance due to a male preference for larger females that can produce more and larger eggs.

Levitan (1998) then suggested that egg competition may strongly influence female reproductive success in sperm-limiting conditions e.g. when the OSR is too low. Since Levitan (1998) work, only two studies, to my knowledge, have explicitly tested the hypothesis that egg competition occurs (Marshall and Evans, 2005; Okamoto, 2016). In the sea urchin (*Strongylocentrotus purpuratus*), Okamoto (2016) showed that at low sperm densities, eggs compete for fertilisation by secreting sperm-chemoattractant while at high sperm densities,

eggs cooperate to mitigate the risk of polyspermy. Considering the degree to which the discovery of sperm competition mechanism reshaped the sexual selection landscape, this is highly surprising that egg competition has not been further investigated yet in taxa where the potential is high. In the previous section of the discussion (5.4.1), I introduced sham mating behaviours (Yamazaki and Koizumi, 2017) as a potential mechanism underlying female post-mating choice in lampreys. Alternatively, such a mechanism may result from female-female competition for gametes when mating opportunities are highly variable. However, Yamazaki and Koizumi (2017) were unable to determine whether the occurrence of sham mating behaviours was related to the competitive environment faced by females as only one female was present in their experimental setting.

Cryptic male choice, defined as the variation in the number of resources that males allocate to females of varying quality, is also expected to occur whenever there is sufficient variation in female quality and male mating costs are high (Reinhold et al., 2002). Under female-biased operational OSR or/and when sperm limits male reproductive success (e.g. in the absence of sperm renewal during the breeding season), the evolution of strategic sperm allocation for reproductively superior females is expected to occur. In several species, males have been shown to transfer more sperm when mating with large females (Engqvist and Sauer, 2001; Reinhold et al., 2002; Gage and Barnard, 1996; Gage, 1998; Cornwallis and O'Connor, 2009). Similarly, Pizzari et al. (2003) showed that male jungle fowl (*Gallus gallus*) deliver larger ejaculates to more elaborately ornamented females, especially when the risk of sperm competition is high. Males are therefore expected to choose cryptically by varying their investment when it pays them to do so. In lampreys, competitive males could mate with low-quality females to monopolise them without using too much sperm while investing more with high-quality females. While such a strategy limits gamete cost, it nevertheless entails an energy cost.

### 5.4.3 Exploring how changes in the social environment affect post-copulatory processes

The main objective of my thesis was to investigate how changes in the social environmental influence the strength of pre-copulatory sexual selection. In **Chapter** 2, I showed that the number of mating attempts in lampreys is affected by individual and competitive environment characteristics, highlighting their potential ability to access the number of competitors and potential mates present and adapt their sexual activity accordingly. Previous works I have presented in earlier sections of the discussion suggest that both males and females may also adopt post-mating strategies in response to changes in population demographics, by allocating gamete differently according to the gamete competition risk or the quality of potential partners.

I suggest that future studies focus on determining the relative importance of pre- versus post-copulatory processes in lampreys and more precisely investigate how different components of mating competition/mate choice change in response to changes in the social environment (see Fig. 5.3). Indeed, the pattern of pre-copulatory sexual selection highlighted in **Chapter** 2 may be biased if sexual selection acts independently on pre- and post-copulatory stages. For instance, the existence of a trade-off between pre- and post-copulatory competitive investment may weaken the estimated strength of pre-copulatory sexual selection on having additional mates (Simmons and Emlen, 2006; Pitcher et al., 2009; Klaus et al., 2011). In the Box 5.2, I also pointed out that males with higher mating success also tend to face a higher sperm competition risk as they overall share more matings with other males. In such conditions, the mean number of eggs emitted by females at each mating event is reduced, further limiting pre-copulatory sexual selection by flattening the relationship between reproductive success and mating success (i.e. by inducing a shallower Bateman gradient).

This relationship may be further weakened through sexual conflict. As a male-biased OSR is expected to increase sexual harassment of females by males (Clutton-Brock and Parker, 1995; Fitze and Le Galliard, 2008), females might change their post-copulatory mate choice behaviour by diminishing the numbers of eggs emitted if their ability to express their preference is limited at the pre-copulatory phase. Such strategy relates to the *convenience polyandry* hypothesis, which postulates that females increase their receptivity to mating based on the relative costs of resistance and mating. Females may indeed be more inclined to accept mating if resisting superfluous matings with persistent males is more energetically demanding. The convenience polyandry hypothesis is usually tested by comparing female mating activity (frequency and duration) under different OSRs as harassment of females is expected to be higher under a male-biased sex ratio. However, I did not find any significant correlation between OSR and female mating frequency (Spearman test; r = 0.19, df = 20, $P$ = 0.39) using the data from **Chapter 2**. The OSR also had no effect on the mean number of mating acts performed by *L. kessleri* females (Yamazaki and Koizumi, 2017). Still, the authors proposed sexual harassment as a possible explanation for the high frequency of sham mating in female lampreys. By combining both behavioural and molecular data, the statistical approach I used in **Chapter 2** (i.e. a Bayesian model decomposing mating success in two successive processes) could be developed further and include post-mating processes (i.e. gamete emission, fertilisation success) to ultimately determine whether post-copulatory episodes of sexual selection oppose or reinforce pre-copulatory sexual selection.

## 5.5 Conclusion

This thesis has demonstrated that taking into account within-season variations in the structure of the social environment is essential to gain a comprehensive understanding of the direction and strength of pre-copulatory sexual selection in a polygynandrous mating system.

Although this applies particularly to species that undergo important shifts in demography, such as lampreys, similar dynamics could be common in the wild as the social and physical environment changes over the breeding season in many species. I also believe that the methodological approaches used in this thesis could be useful in the field of sexual selection and could be further developed to incorporate post-mating processes. Overall, I hope that my work will encourage future empirical and theoretical studies to further examine the potential within-season variations in sexual selection across a wide range of mating systems and to determine the resulting evolutionary implications.

# Appendices

Appendix A

# Spawning preference in *Lampetra fluviatilis*

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This section corresponds to an article published in the ***Journal of Fish Biology***. This work has been designed, analyzed and written mainly in collaboration with a doctoral colleague from my research unit. As this work is not directly related to the thematic of my thesis project, I decided to introduce this paper in a Appendix section of my manuscript.

# Realistic variations in substrate composition affect spawning preference and egg retention in river lamprey (*Lampetra fluviatilis*)

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**Abstract**

Egg drift from the nest is clearly an important cause of mortality in lithophilic species; however, the effect of substrate composition on this process has been overlooked. Here, we investigated the role of substrate on the spawning preference and egg retention of river lamprey (Lampetra fluviatilis) during a whole breeding season in a two-option experimental setting. Despite no initial preference, the lamprey eventually favoured the most efficient substrate for

egg retention. The pebbly substrate hosted 12 times as many matings as the sandy one, while blurting 20% fewer eggs.

**Keywords:** spawning habitat, reproduction, habitat choice, South-West France

## A.1 Introduction

Among the 41 lamprey species (order: Petromyzontiformes; Potter et al., 2015), the European river lamprey *Lampetra fluviatilis* (Linnaeus, 1758), also known as the river lamprey, is a parasitic anadromous species that is widespread throughout Europe (Hardisty, 1986; Maitland, 1980). Although the river lamprey has been globally considered Least Concern according to the IUCN Red List of Threatened Species, the species is considered endangered in the Iberian Peninsula. In Spain, *L. fluviatilis* is considered Regionally Extinct (Doadrio et al., 2001) while in Portugal it is included in the Critically Endangered category of the red list of endangered species (Cabral et al., 2005). One of the main reasons for the general drop in population size is the loss of spawning and larval habitat due to river fragmentation induced by dredging, engineering works or impoundments (Lucas et al., 2021). Lampreys being lithophilic (i.e. they deposit eggs and sperm within the substrate in shallow water) (Jang and Lucas, 2005; Nika and Virbickas, 2010), such anthropic disturbances make the accessibility to suitable spawning grounds challenging. The river lamprey spawns in nests built by removing coarse substrate (pebbles) with their oral disc and fine substrate (sand and gravel) with their tail (Jang and Lucas, 2005). Egg drift from the nest is a major cause of mortality for rheophilic fishes (e.g. Gauthey et al., 2017), especially for lampreys. By comparing the number of eggs in nests of sea lamprey (*Petromyzon marinus L.*) with the number expected from the number and size of females, Manion and Hanson, 1980 estimated that 86% of the eggs were washed from the nest. In another study, Silva et al., 2015 placed drift nets downstream from nests of river lamprey in which dyed eggs were inserted, and caught from 1.5% to 86% of the inserted eggs, increasing with higher current speed to which the nests were exposed and decreasing with the distance from the spawning habitat (depth effect not considered here). Since egg survival is very high in the nest and virtually nil out of it, mainly because of predation (Manion and Hanson, 1980: survival rate in nest = 90%; Smith

and Marsden, 2009: no viable egg outside of nest), the ability of lamprey to choose nesting conditions that reduce the likelihood of egg drift must be under strong selection. Silva et al., 2015 highlighted an egg hatching success of solely 52.0% downstream from the nests with silt beds, generally found downstream of spawning areas. However, as their observation was made in the laboratory without egg predation, we therefore suspect that this percentage is overestimated.

Of all the environmental factors that could affect egg retention in the nest, substrate is probably, alongside current speed where the nest is built (Silva et al., 2015; Dhamelincourt et al., 2021), one of the most significant. Indeed, freshly laid lamprey eggs are coated with an adhesive structure that aggregates sand grains (Yorke and McMillan, 1979). Thus ballasted, the eggs sink in cavities between pebbles, where they nestle safe from drift and predators. Consistently, lampreys typically spawn in stream beds covered with a mixture of sand, gravel and pebbles (Jang and Lucas, 2005; Johnson et al., 2015). Although Smith and Marsden, 2009 showed that egg retention was better in gravel than in silt, lampreys rarely, if ever, spawn in silt, and one can wonder if more realistic variations in substrate composition can affect egg drift. If so, one would expect lampreys to prefer the substrate that better retains the eggs. Such assessment may help to understand the effects of substrate subtle modifications within spawning grounds. Hence, the objective of the present study was to accurately determine the role of the relative proportion of sand and pebbles on both the choice for spawning micro-habitat and the retention of river lamprey eggs during a whole breeding season. A gradual change from one substrate type to another may occur more frequently than a total switch, as such variation is prone to be found within real spawning grounds affected by environmental variations. To do this, we placed 35 adults of river lamprey in a large fish tank with two spawning patches containing a mixture of gravel (50%) and a large proportion of either sand

or pebbles (40% and 10%). The number of spawning acts performed on both substrate patches, and the number of eggs drifting from them was compared. If the factor limiting egg retention is the ballasting sand grains, egg drift should be less likely from the sandy patch, and lamprey should prefer to spawn on it. The expected outcome would be reversed if cavities between coarse particles are the limiting factor.

## A.2 Methods

### A.2.1 Study species

The *L. fluviatilis* used in this study were captured with drift nets in early spring 2019 (between March $15^{th}$ and $26^{th}$) during their upstream migration on the Garonne river (South-West France) by professional fishermen. A total of 35 individuals (15 males, total length: 28.3 ± 2.1 cm and mass: 45.2 ± 8.3 g; 20 females, total length: 28.4 ± 1.7 cm and mass: 51.6 ± 7.5 g) were sampled and transferred in an oxygenated and temperature-controlled tank with Garonne water (13°) to the INRAE experimental facilities in Saint-Pée-sur-Nivelle, France (INRAE, 2018). Individuals were acclimated for a few days in tanks (between 8 and 19 days depending on the capture date, 13.8 ± 0.8 °C in tanks) supplied with water from the Nivelle River (France) to avoid behavioural changes due to transportation and/or differences in water properties during the course of behavioural observations. The day before the experiment, we tagged each lamprey with a unique combination of three spots of UV-fluorescent visible implant elastomer (VIE) injected in the posterior dorsal fin to allow individual recognition under both white light and UV light. Tagging was performed after fish were anaesthetised with benzocaine (0.3ml/L).

### A.2.2 Experimental design

The experiment took place in a 4 $m^3$ (10 x 1 x 0.4 m) linear section of a 25 metres long circular aquarium, supplied with water from the Nivelle River in a semi-open circuit, with water replacement of 6 litres per minute. To define whether egg drift from nests was influenced by substrate size and the degree of activity of the spawners, spawning substrate was limited to two 0.48 $m^2$ (0.8 x 0.6 x 0.1 m) boxes placed 5 meters from each other, and filled with a mixture of sand, gravels and pebbles corresponding to the spawning habitat selected by river lampreys (Jang and Lucas, 2005; Figure 1). The first box, referred to as the "sandy patch", was filled with 50% (in volume) gravels (= 2-4 mm), 10% pebbles (4-64 mm) and 40% sand (0.125-2 mm) while the second box, referred to as the "pebbly patch" was filled with 50% gravels, 40% pebbles and 10% sand. Current speed was set to 0.6 m/s on both substrates and water temperature was monitored daily and followed that of the river (15.87 ± 0.95 °C). A net with a 0.5 mm nylon mesh size and 70 cm width was placed immediately downstream of each substrate box and covered the entire water column while being larger than the boxes. Nonetheless individuals could easily move around as the nets left a gap on the left side of the boxes. Eggs were recovered from nets at the same time each day and stored in Falcon® tubes with 90° ethanol up to the exhaustive count. Two video cameras (Basler acA1920-40gc) continuously recorded lampreys' activity in each spawning substrate throughout the experiment. The aquarium was lighted with white neon bulbs (1800 lx delivered at the water level) following the natural photoperiod (12:12 with 30 minutes of "dawn" from 8 to 8:30 AM and 30 minutes of "dusk" from 8:00 to 8:30 PM), but since river lamprey is also active at night during the spawning period (Sjoberg, 1977), we positioned UV light above each substrate box (20 lx delivered at the water level). Individuals were placed in the experimental tank on the $3^{rd}$ of April and the experiment ended on the $3^{rd}$ of May, at the death of the last individual. Individuals were only removed from the aquarium once they died. Recorded videos were analysed using BORIS software (Fri-

ard and Gamba, 2016) and the number of spawning acts occurring each day during the entire spawning season was exhaustively noted by the observer. A spawning act was identified as body entwinement and vibration (Hardisty and Potter, 1971) of at least one male and one female, the species being polygynandrous (Jang and Lucas, 2005). During the spawning act, the female is usually attached to a pebble with her oral disk, and her cloaca is in contact with the substrate in order to lay the eggs in it, so the body vibration associated with spawning often results in substrate movement. The first and last mating acts occurred on April $9^{th}$ and $30^{th}$ respectively, making the spawning season 22 days long.

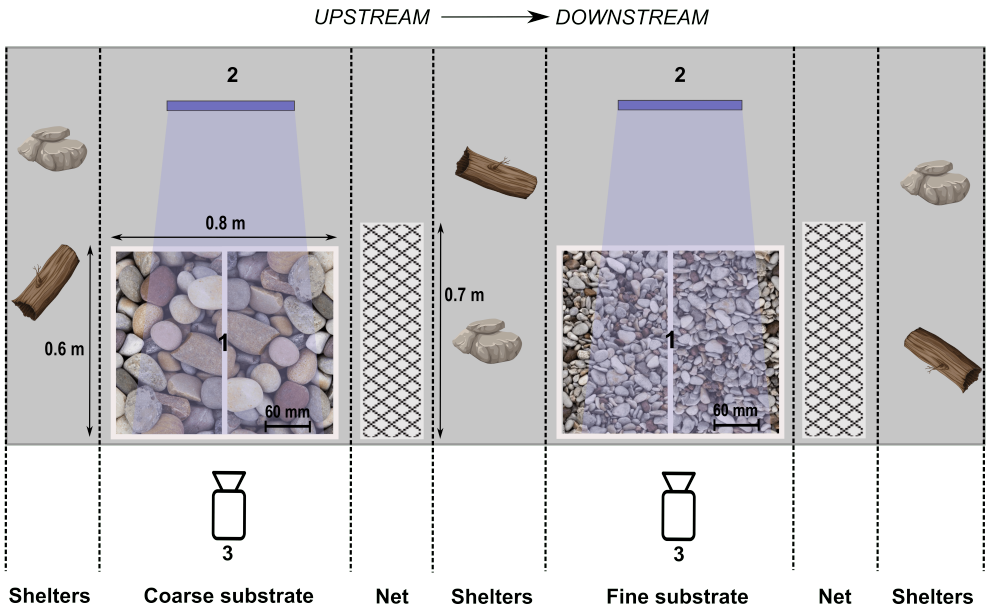


**Figure A.1.** Experimental setup used for the experiment. 1: substrate boxes (0.8 x 0.6 x 0.1 meter) with either fine or coarse substrate; 2: UV light used during the night, replaced by white light during the day; 3: cameras recording spawning activity. Current speed was set to 0.6 m/s on both substrates. The scale in each box refers only to the substrate size.

### A.2.3 Statistical analysis

All analyses were performed using R software version 4.1.0 (R Core Team, 2022) and using a significance level of 0.05. Non-parametric Kruskal-Wallis test was used to test whether

the daily recorded number of spawning acts differed between the coarse and fine substrate patches. A binomial test was used to test whether the first spawning act performed by each individual was more likely to occur on either substrate. A Generalized Linear Model (GLM) was applied to test whether the number of eggs caught downstream from a spawning patch on a given day depended on 1) substrate size, 2) the number of spawning acts performed on it on that day, and 3) the cumulated number of spawning acts performed on it over the last twelve days. While the number of spawning acts on a given day is an indicator of both the number of eggs laid on that day, the cumulated number of spawning acts over the last twelve days was used to indicate the number of eggs buried in the substrate and possibly dislodged from it. Indeed, eggs of river lamprey hatch after 200 degree.days (Moser et al., 2019), which corresponded to twelve days in our experimental conditions. The GLM assumed a negative binomial distribution to account for data overdispersion, and a Log link function. The three independent variables and their interactions were included in an initial full model, which was reduced through a model selection procedure based on the minimization of Akaike Information Criterion (function stepAIC in MASS package for R; Venables and Ripley, 2002).

### A.2.4 Ethical statement

The care and use of experimental animals complied with the French animal welfare laws, guidelines and policies as approved by the ethical committee for birds and fishes in the French region Nouvelle Aquitaine (authorization #2019021009248986).

## A.3 Results

A total number of 6815 matings occurred during the breeding season, among which 515 (7.5%) took place on the sandy patch and 6300 (92.5%) on the pebbly patch. An average (± SD) of 23.41 (± 58.11) matings per day occurred on the sandy patch while an average of 286.36 (± 367.76)

took place on the pebbly patch (Figure 2a). The number of mating acts differed significantly between the substrate types (Kruskal-Wallis test: $\chi^2$ = 15.51, P < 0.001). A total of 16 females and 14 males spawned at least once on the sandy patch (between 1 and 149 acts per female; between 1 and 93 acts per male), whereas 18 females and all 15 males spawned at least once on the pebbly patch (between 2 and 803 acts per female; between 10 and 1054 acts per male). Six (30%) females and 10 (67%) males spawned first on the sandy patch, indicating no initial preference for either substrate (Binomial test; P = 0.1153 for females, P = 0.3018 for males, P = 0.7353 for pooled females and males), when individuals did not experience any patch by digging on it. Overall, 5900 eggs drifted during the experiment, among which 3277 (55.5%) were found downstream of the sandy patch and 2623 (44.5%) downstream of the pebbly patch. An average (±SD) of 148.95 (±180.49) eggs drifted per day on the sandy patch while an average of 119.23 (±277.59) eggs drifted from the pebbly patch (Figure 2b). The final model after the AIC-based selection procedure indicated a negative effect of pebbly patch (z value = -3.862, P < 0.001) and a positive effect of the number of spawning acts observed during the current day (z value = 3.731, P < 0.001) on egg drifting from the spawning patch. Hence, the sandy substrate and an increase in the number of spawning acts influence negatively the retention in the nest. Table 1 summarises the results for the number of mating acts and number of eggs that drifted.

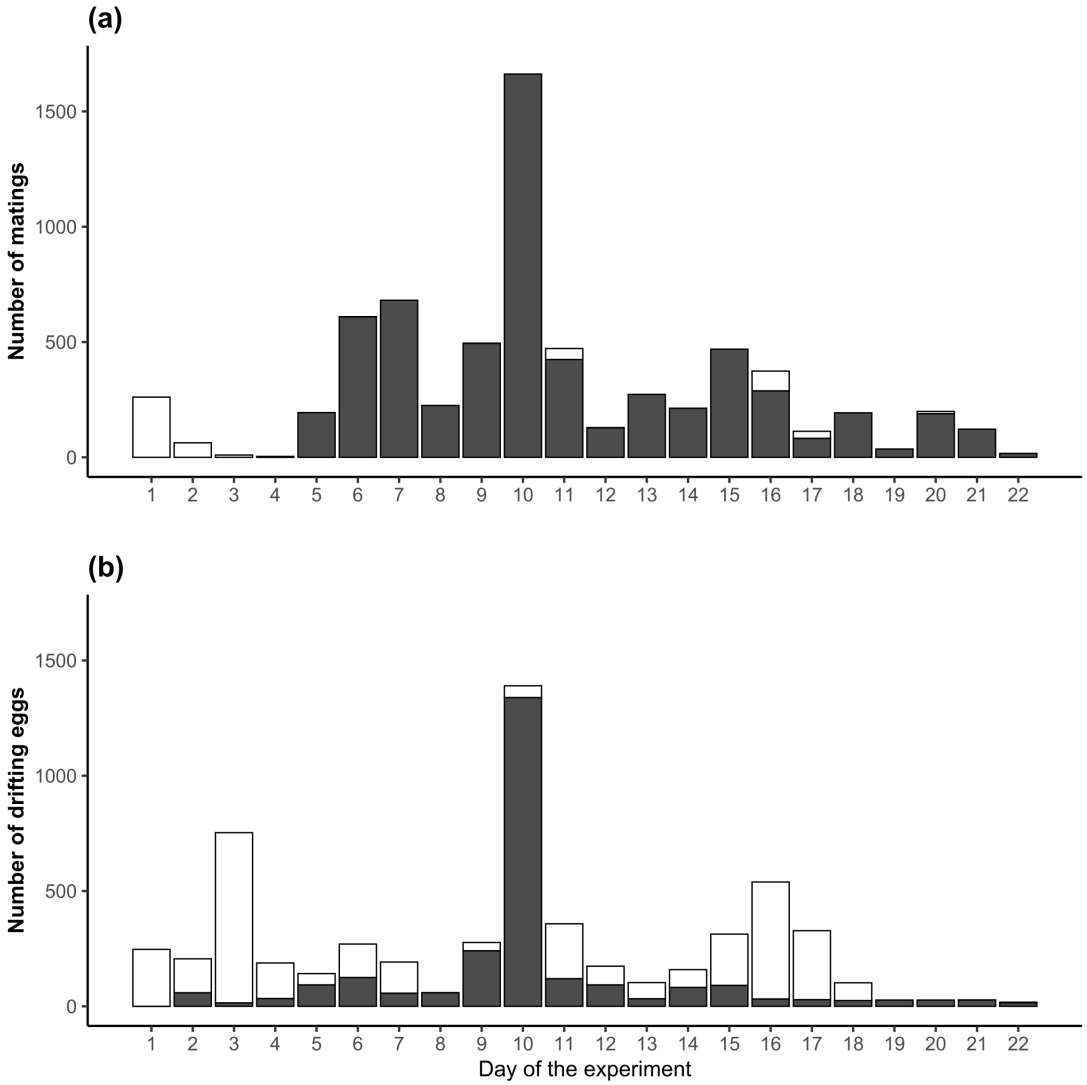


**Figure A.2.** Daily number of mating acts (a) and eggs drifting (b) from the pebbly (grey bars) and sandy (white bars, stacked on grey bars) substrate patches, placed in an aquarium containing 20 females and 15 males of river lamprey (*Lampetra fluviatilis*). The first and last mating acts occurred on April $9^{th}$ and $30^{th}$ respectively, making the breeding season 22 days long.

**Table A.1.** Comparison of the results for the number of mating acts and the number of eggs that drifted between pebbly and sandy substrate.

| Variable | Sandy substrate | Pebbly substrate |
|---|---|---|
| Number of matings | 515 (7.5%) | 6300 (92.5%) |
| Number of matings per day | 23.41 ± 54.66 | 286.36 ± 370.19 |
| Number of females | 16 | 18 |
| Number of males | 14 | 15 |
| Number of mating acts for females | 1-149 | 2-803 |
| Number of mating acts for males | 1-93 | 10-1054 |
| First spawning act (females) | 6 (30%) | 14 (70%) |
| First spawning act (males) | 10 (67%) | 5 (33%) |
| Total egg drift | 3277 (55.5%) | 2623 (44.5%) |
| Daily egg drift | 148.95 ± 180.49 | 119.23 ± 277.59 |

## A.4 Discussion

The pebbly substrate was clearly better at retaining eggs, and river lamprey clearly preferred to spawn on it. Their preference seems to emerge from a sampling process, as the probability of choosing either substrate on the first spawning occasion was balanced considering the binomial test results - showing no preference of one substrate for each sex independently or with all individuals pooled - whereas the proportion of total spawning acts performed on the pebbly substrate was 12 times higher than on the sandy substrate. Lampreys are certainly able to assess substrate composition during nest-building, using their mouth and tail to build the nest. Moreover, lampreys can spawn hundreds of times (here, on average 341 for females and 454 for males) within a few days in the same or different sites (Dhamelincourt et al., 2021; Jang and Lucas, 2005), reinforcing the idea that they may be able to sample their environment and choose their spawning site accordingly. Gardner et al., 2012 observed a negative association between the abundance of sea lamprey nests and substrate cover by fine sediment, and suggested that this result could be due to lampreys either preferring coarser substrate, or coarsening the substrate through repeated nest-building in the same spots, or both. Here, we showed that river lamprey deliberately selected a suitable spawning habitat by preferring pebbly substrate over sandy substrate, from which eggs were more likely to drift, suggesting that an excess of fine particles on nesting sites was detrimental to egg retention in the substrate. The coarsening effect of spawning activity on substrate size suggested by Gardner et al., 2012 is unlikely to have occurred in our study: a priori, heavy scouring was prevented by the moderate current speed and the containment of substrate in boxes; a posteriori, no accumulation of substrate was observed on the bare concrete surrounding the boxes. Substrate size in the nest may affect egg survival through exposure to low-oxygenated water, fungal contamination or predators (Silva et al., 2015; Smith and Marsden, 2009). While coarse particles offer shelter from predators, fine particles may

cause suffocation but also limit the contact surface for fungus propagation. The optimal response to this trade-off certainly depends on the prevalence of each source of mortality at the spawning site, and echoes the trade-off faced by all nest-building animals when choosing a nesting site (Lissåker and Kvarnemo, 2006; Mayer et al., 2009; Tieleman et al., 2008).

Although the great risk of egg drift documented in the field was not even approached in our experimental setup, our results highlight substrate composition and over digging as two realistic sources of variation in the risk of egg drift. Assuming that female fecundity ranges from 16 000 to 37 000 eggs (Docker, 2019), the 5 903 eggs that drifted from both substrate patches only represent 0.8% to 1.8% of the number of eggs produced. Several features of our setup could explain this low proportion, among which the constant and moderate water flow (0.6 m/s) and the fact that the substrate was contained in boxes that prevented heavy scouring. However, one commonality between our setup and natural conditions in the field was that lamprey repeatedly spawned on the same patch, so eggs previously laid on it could have been resuspended and drift downstream. However, the number of eggs drifting on a day was positively linked to the number of matings occurring on that day, not on the twelve previous days. This initial failure to sink in the substrate may be the main cause of drift, and eggs that managed to sink in the substrate may be not disturbed by subsequent spawning activity. The deleterious effect of overdigging documented in salmonids (Fleming, 1996), can however not be completely ruled out: Although we were not able to determine the precise age of eggs to check if eggs older than one day still drifted, some prolarvae (from stages prior to their natural downstream migration; Piavis, 1961) were caught in the nets. In the field, overdigging can be accentuated by obstacles to migration and habitat loss that lead to spawning aggregation in suboptimal (e.g. sandy) habitat. Overall, our results confirm the necessity to consider the spawning-site substrate as an important factor influencing lamprey egg retention in the nest

and therefore egg survival and larvae hatching. As advocated by Lucas et al., 2021, attention should be paid to the preservation or restoration of adequate substrate in areas suitable for lamprey spawning.

Appendix B

# The benefits of eco-evolutionary agent based modelling approaches

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This section is related to a paper that was published in the ***Evolutionary applications*** journal and presents models that address the difficulties that have previously been noted in the investigation of population eco-evolutionary responses. This paper is the outcome of a team effort and is a component of a scientific network that brings together researchers interested in this modeling approach. As this work was not part as my thesis project, I chose to include this paper as an Appendix.

# Importance of interindividual interactions in eco-evolutionary population dynamics: the rise of demo-genetic agent-based models

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**Abstract**

The study of eco-evolutionary dynamics, that is of the intertwinning between ecological and evolutionary processes when they occur at comparable time scales, is of growing interest in the current context of global change. However, many eco-evolutionary studies overlook the role of interindividual interactions, which are hard to predict and yet central to selective values. Here, we aimed at putting forward models that simulate interindividual interactions in an eco-evolutionary framework: the demo-genetic agent-based models (DG-ABMs). Being demo-genetic, DG-ABMs consider the feedback loop between ecological and evolutionary processes. Being agent-based, DG-ABMs follow populations of interacting individuals with sets of traits that vary among the individuals. We argue that the ability of DG-ABMs to take into account the genetic heterogeneity — that affects individual decisions/traits related to

local and instantaneous conditions — differentiates them from analytical models, another type of model largely used by evolutionary biologists to investigate eco-evolutionary feedback loops. Based on the review of studies employing DG-ABMs and explicitly or implicitly accounting for competitive, cooperative or reproductive interactions, we illustrate that DG-ABMs are particularly relevant for the exploration of fundamental, yet pressing, questions in evolutionary ecology across various levels of organization. By jointly modelling the effects of management practices and other eco-evolutionary processes on interindividual interactions and population dynamics, DG-ABMs are also effective prospective and decision support tools to evaluate the short-and long-term evolutionary costs and benefits of management strategies and to assess potential trade-offs. Finally, we provide a list of the recent practical advances of the ABM community that should facilitate the development of DG-ABMs.

**Keywords:** agent-based models, demo-genetic models, DG-ABMs, eco-evolutionary dynamics, eco-genetic models

## B.1 Introduction

Understanding and anticipating populations' response to changes in environmental and anthropogenic pressures requires conceptual and modelling approaches coupling ecological and evolutionary processes. This is largely motivated by the increasing realisation that ecological and evolutionary responses of populations can occur on similar temporal scales, with potential consequences on dynamics from gene to ecosystem (Carroll et al., 2007). The burgeoning literature investigating eco-evolutionary dynamics illustrates this growing interest (Dunlop et al., 2009; Schoener, 2011; Romero-Mujalli et al., 2019; Bassar et al., 2021).

The conceptual framework of eco-evolutionary dynamics depicts feedback loops between response processes at different levels of biological organisation in a contemporary time scale (Pelletier et al., 2009; Hendry, 2016; Govaert et al., 2019). These feedback loops acknowledge that (1) genetic diversity and its architecture determine the demographic structure and population dynamics through phenotypic expression; (2) demographic structure and population dynamics determine evolutionary processes, i.e., genetic drift, selection and gene flow, which in turn (3) determine genetic diversity. As an illustration of such feedback, the competition between trees within a forest results in a selection process contributing to genetic evolution, while the genetic composition of the tree population drives interindividual competition and forest productivity (Pretzsch, 2021). To account for feedback loops, eco-evolutionary models must integrate inheritance mechanisms and the multiple driving forces controlling the dynamics of the distributions of heritable traits across generations (Bassar et al., 2021).

One of these key drivers of selection is the interactions between individuals within populations, as they directly or indirectly affect individual fitness at the core of any evolutionary dynamics (Maynard Smith, 1974; Webber and Vander Wal, 2018). We focus here on

*within*-population interindividual interactions (i.e., competition, cooperation, and mating) affecting the demographic dynamics (growth, reproduction, mortality) and ultimately individual fitness or even inclusive fitness (Box 7.1). In essence, the outcome of such interactions is eminently stochastic and context-dependent, and population structure itself is part of the context. It is now recognised that the structure of social networks within a population may affect natural selection and traits evolution through indirect genetic effects (traits affected by genes in other individuals, Wade et al., 2010; Kazancıoğlu et al., 2012). Additionally, these networks are themselves dynamic, since changing the social environment may influence an individual's later decisions in a social interaction, leading to rapid shifts in networks' structures (Farine and Whitehead, 2015). For instance, individuals are able to modify their mating tactics, which diminushes the selection they endure (Oh and Badyaev, 2010) and thus affects selection at the population level. Likewise, the distribution of phenological traits (e.g., flowering or maturation time) shapes mating opportunities within plant and animal populations, and possibly leads to assortative mating (here, the positive correlation of phenology between mates). Compared with random mating, assortative mating can either deplete or increase the genetic variance available for selection depending on whether the environment is stable or changing, with contrasted consequences on genetic adaptation (Godineau et al., 2022). Unfortunately, the interindividual interactions are usually little appreciated in eco-evolutionary models, with potential consequences on our understanding of the full range of eco-evolutionary responses.

Our objectives here are to put forward models that explicitly or implicitly account for variable within-population interindividual interactions in an eco-evolutionary framework: the demo-genetic agent-based models (DG-ABMs). After defining these models, we survey the literature to illustrate how DG-ABMs can be used to investigate fundamental issues in

evolutionary ecology, as well as to assist the management of natural populations facing environmental changes.

**Box B.1.** Interindividual interactions involved in eco-evolutionary dynamics

Here, we focus on interactions between conspecific individuals within a population - mainly competition, cooperation, and mating - which directly drive the processes of mortality, growth, and reproduction (e.g., A, C, D below) and whose variations subsequently induce evolutionary changes. This also includes the variety of ecological interactions indirectly impacting demography, such as exchange of information (e.g., on predator, or resource availability), movement (e.g. to escape predation or competition) or group behaviour (e.g. affecting predator's avoidance or resistance, A, B below).

The major reason why we focus on local (i.e., within-population), variable, conspecific interactions is that evolution is a population-specific process, primarily fuelled by differences in individual fitness arising from the response to abiotic and biotic environments, the latter including the social context. Interspecific interactions may also shape the within-population social context and contribute to evolution: for instance, the existence and strength of plant-pollinator interactions define the social context within which selfing may evolve (Katsuhara et al., 2021). Trophic interactions may contribute to the resource context within which functional traits related to resource acquisition may evolve (Kang and Thibert-Plante, 2017). On a macroevolutionary timescale, intra- and inter-specific competition for resources can drive speciation (Gavrilets et al., 2007; Weber et al., 2017). However, considering interspecific interactions without genetic variation in at least one of the partners of the interaction is not enough to model the dynamic feedback loop between ecological interactions, fitness, and the genetic composition of the population. This is particularly why predation was not considered as a focal interaction in this review: indeed, when predation is investigated from the point of view of the variation of a prey's trait conferring variable avoidance ability from the predator, or from the variation of a predator's trait conferring variable ability to catch prey, then it becomes a trait involved in competition among prey to escape predators, or among predators to optimize prey foraging and selection (e.g., Kelly and Phillips, 2019; Labonne and Hendry, 2010).


**A**: School of common minnow (*Phoxinus phoxinus*) individuals maintained in an experimental tank at INRAE, Saint-Pée-sur-Nivelle, France. Schooling behaviour in this species is supposed to be both an anti-predator and a foraging optimisation strategy (Photo: ©INRAE - Stéphane Glise).

**B**: Fifth instar hoppers of gregarious desert locust basking in the morning sun within herbaceous plants of the Mauritanian desert; grouping behaviours and bright coloration in desert locust (*Schistocerca gregaria*) are supposed to be an anti-predator strategy (Photo: © JIRCAS - Koutaro Ould Maeno).

**C**: Sea lamprey (*Petromyzon marinus*) spawning in the Nive River (South-western France). Species from the Petromyzontidae family are semelparous, but the number of mates is highly variable among species (Photo: ©INRAE - Stéphane Glise).

**D**: Beech (*Fagus sylvatica*) trees with late and early phenologies on Mont-Ventoux, France. Phenological mismatch limits male more than female reproductive success (Photo: ©INRAE – Frédéric Jean)

## B.2 How to model eco-evolutionary feedback loops: from analytical models to DG-ABMs

At the very core of the eco-evolutionary models is the need of specifying the genetically variable and heritable traits, their impact on the focal organism's life history and the ecological embedding that determines how life-history traits affect and are affected by environmental conditions and the demographic context (Dieckmann and Ferrière, 2004). This can be achieved by various approaches (Fig. B.1). First, there is a long tradition in evolutionary ecology to rely on analytical models (differential-equation and difference equation models), which offer elegant solutions and provide general knowledge on elementary eco-evolutionary feedback loops, generally at the cost of simplifying hypotheses. Among the most common analytical formalisms of eco-evolutionary feedback loops are (1) adaptive dynamics models (Dieckmann and Ferrière, 2004), which incorporate ecological realism, in particular, the notion that the success of any given strategy depends on its frequency within the population, but often bypass the complexity of genotype–phenotype relationship (for instance by assuming asexual reproduction, clonal inheritance); (2) evolutionary quantitative genetics models (Kirkpatrick and Barton, 1997; Pease et al., 1989; Slatkin, 1978), which integrate the genotype–phenotype map with population demography (e.g. density-dependence) but where other ecological changes remain independent from the population dynamics; and (3) integral projection models (Smallegange and Coulson, 2013), which use population models classically developed in population dynamics to describe the evolution of continuous characters in a quantitative genetics framework. We purposely do not mention traditional optimisation models, such as stochastic dynamic programming used to represent individual behaviour (e.g. life-history decisions) and development (e.g. growth and sexual maturity) and their consequences for population dynamics (Mangel, 2015), as these models do not specify the genetic architecture of traits, which is yet mandatory for eco-evolutionary feedback to emerge. The main limitation of the above-

listed analytical approaches is that they consider evolutionary and ecological processes (be they deterministic or stochastic) to be homogeneous within groups of individuals (the population or life stages), whereas group composition constantly varies in terms of phenotypes and genotypes, affecting individual decisions, linked to local and instant conditions, and their outcome at the group level (i.e. emerging effects).

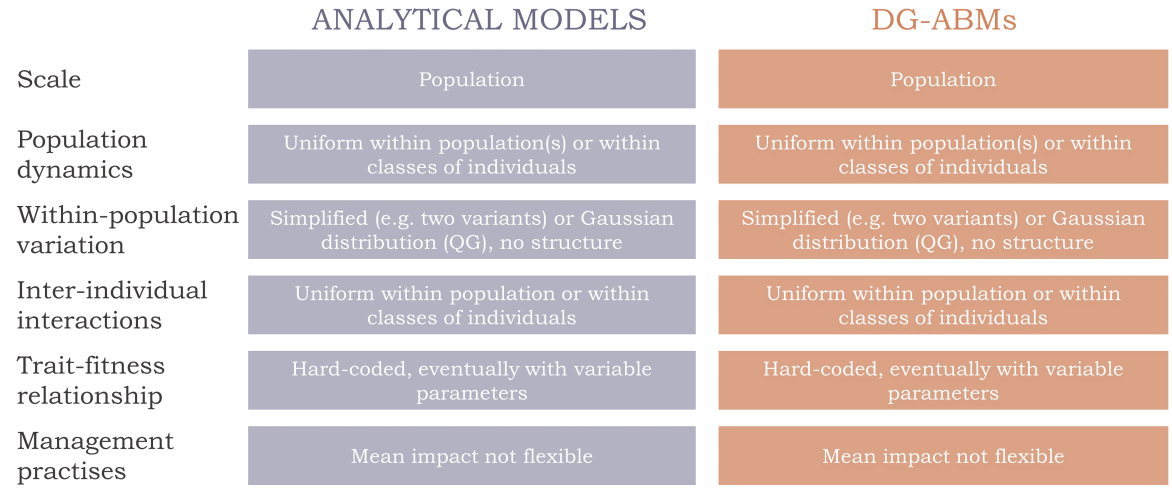


**Figure B.1.** Different approaches to model eco-evolutionary feedback loops. This scheme summarises the main differences between two major modelling approaches used to investigate eco-evolutionary dynamics: analytical models on the left and Demo-Genetic Agent-Based Models (DG-ABMs) on the right. Their main difference is that analytical models consider evolutionary and/or ecological processes to be homogeneous within groups of individuals (the population or life-stages), whereas DG-ABMs can account for phenotypic and genotypic variation in groups of individuals, its effects on individual decisions/traits linked to local and instant conditions, and their outcome at the group level (i.e., emerging effects). In particular, some (although not all) DG-ABMs model interindividual interactions, and their effects on individual fitness, which emerge in part from these interactions.

Yet the question of individual heterogeneity and its effects has long preoccupied eco-evolutionary ecologists. For several decades, simulations using agent-based models (ABMs, also called individual-based models or IBMs in ecology) were used to investigate more complex scenarios and explore unexpected eco-evolutionary feedback loops, with approaches spreading on a spectrum of complexity well-described by DeAngelis and Mooij (2005). On

the one side of the spectrum, some ABMs were developed to validate and/or explore the predictions made with analytical models, replace these models and/or eventually nurture their future development. To keep these ABMs as simple as possible, individuals usually have a minimum number of attributes and fitness does not depend on interindividual interactions. For instance, by coupling a niche-based model with individual-based demo-genetic simulations, Cotto et al. (2020) investigated the evolutionary constraints related to alpine plant response to a changing climate. The key originality of their approach is to model individuals as spatial points across a complex climatic landscape, where the individual phenotypes are explicitly linked to climatic variables and where the optimal phenotype is prescribed by the niche-based model and varies through time. They use a classical multistage life cycle model (from seeds to adults) where individual survival and ultimately fitness increases when the multivariate phenotype is close to the optimal phenotype but is independent of the phenotype of other individuals. This typical top-down approach aims at extending classic analytical models into more complex domains with the assistance of ABMs.

On the other side of the spectrum, some ABMs employ a specific bottom-up approach to fully integrate individual interactions and their outcome over time and space within a population, the result of which will dictate the strength and direction of evolutionary processes at the population level (DeAngelis and Mooij, 2005; Huston et al., 1988). These ABMs acknowledge that individuals have inherently nonuniform interactions with each other, and that the consequences of the variation in traits mediating interindividual interactions are better described by rule-based simulations than by mathematical models. Accordingly, these approaches depict the interactions between individuals and their effects on individual fitness, accounting for the social context, and observe the resulting dynamics in terms of distributions of heritable traits and demography. We hereafter refer to these ABMs as DG-ABMs, DG-ABMs (another

possible acronym would be eco-genetic ABMs). DG-ABMs can be defined as individual-based (meta) population dynamics models with heritable trait variation and phenotype-dependent interactions between individuals (Box 7.2). A key feature of DG-ABMs is that fitness variation emerges mechanically from interactions between individuals (as opposed to assuming an a priori fitness function) and gives rise to the evolution of patterns structuring the population diversity and its dynamics (e.g. genetic architecture and spatial genetic structure). Typical examples of emerging fitness variation are spatially structured individual-based models focusing on dispersal evolution (Bach et al., 2006; Kubisch et al., 2013; Poethke et al., 2007). Indeed, these studies demonstrated that genetic structure and kin competition emerge from the spatial design of their DG-ABMs, when the genetic architecture of dispersal and competition is included (here implicitly). Hence, dispersal evolves to reduce kin competition and increase inclusive fitness, ultimately driving back kin structure within populations. This is radically different from assuming a prescribed relationship between traits and fitness, as done in analytical models and some ABMs (e.g. Cotto et al., 2020). We argue here that this bottom-up construction of fitness in DG-ABMs provides different and new insights into various fundamental and applied questions in ecology and evolution, and illustrate further our point of view by a review of the literature.

**Box B.2.** AN OVERVIEW OF DG-ABMS

**Modelling interindividual interactions**: ABMs have the general capacity to represent both *direct* interactions among agents (i.e., when one agent identifies one or more other agents and directly affects them, e.g., by having some kind of contest with them, eating them, or choosing them to mate) and *mediated/indirect* interactions (when one agent affects others indirectly by producing or consuming a shared resource).

The choice to model these interactions *explicitly* or *implicitly* in DG-ABMs depends on the interaction type, the degree of realism/complexity desired, and on the focal, evolvable trait(s) involved in the interaction (see Table B.1 for examples of these traits). Direct reproductive interactions are most often explicitly modelled, through variable mate preference or competitiveness among potential mates (e.g., Chevalier et al., 2022), or assortative mating for a variable phenological trait (e.g., Soularue and Kremer, 2014). This is also the case of direct cooperative interactions, where the mechanisms involved (e.g., in grouping behaviour) are usually explicitly represented (de Jager et al., 2020; van der Post et al., 2015).

Indirect interactions such as competition for resources can be implicitly modelled through density-dependence functions. For instance, most DG-ABMs investigating fisheries-induced evolution assume that increasing density will lead to increasing competition, the competition strength also depending on individual size (Ivan and Höök, 2015; Piou and Prévost, 2012). By contrast, some DG-ABMs consider competition in an explicit prey-predator (Costa et al., 2015) or consumer-resource (Kang and Thibert-Plante, 2017) system; in these cases, the level of the resource and the consumption process at each time step are explicitly modelled, and the traits involved in the interaction can be more realistically represented (e.g., gill-raker count in Kang and Thibert-Plante, 2017).

**DG-ABMs applications**: DG-ABMs also offer the opportunity to study eco-evolutionary dynamics at multiple levels of organisation and spatio-temporal scales. At population scale, habitat structuring and variation in the abiotic environment can be included to account for selection, stochastic events and subdivision of the social environment. These models also allow simulations of several populations' dynamics connected through dispersal with potential gene flow, such as in a metapopulation case. At a higher level, community dynamics can be modelled through interspecific interactions between individuals from directly or indirectly interacting species.

**Figure B.2.** Individuals (or agents) are characterised by their phenotypic traits, determined by their genotype, the environment, and interactions between them (denoted GxE). The agents together define the population, hence determining its diversity and structure, where interindividual interactions shape the social environment. This social environment influences population dynamics, which ultimately drives evolutionary processes (drift, selection, gene flow). Fitness variations (e.g., survival, fecundity variation) emerge from different outcomes of interindividual interactions (e.g., mating, competition, cooperation, information exchange) and give rise to evolution of traits via the trans-generational response to selection. This framework, highlighting the feedback loop central to eco-evolutionary approaches, is the core part of DG-ABMs and is identified by solid (units) / dashed (units' properties) line boxes and bold arrows.

**Table B.1.** Interindividual interactions and associated evolvable traits modelled in DG-ABMs. To illustrate the categories of traits considered as evolvable in the reviewed DG-ABMs, we listed some examples depending on the interaction type considered (IT): competition, reproduction or cooperation.

| IT | Evolvable traits category | Examples | Examples of references (species/kingdom) |
|---|---|---|---|
| Competition | (1) Growth/ maturation | Size at emergence | Fielding, 2004 (grasshopper); Ayllón et al., 2016, 2018 (trout) |
| | | Threshold for size at migration | Piou and Prévost, 2012, 2013 (salmon) |
| | | Growth rate | Kang and Thibert-Plante, 2017 (alewife); Moya-Laraño, 2011 (generic); Travis et al., 2010 |
| | (2) Abstract trait | Competitive abilities | Gascuel et al., 2015; Pontarp et al., 2015; Ward and Collins, 2022 (all generic for species community) |
| | (4) Dispersal trait | Prospecting of habitat quality | Fronhofer and Altermatt, 2017 (generic) |
| | | Dispersal distance | LaRue et al., 2019 (sea rocket); Leidinger et al., 2021 (plant) |
| | (5) Behaviour | Movement preference | Hrycik et al., 2019 (perch) |
| | | Drifting | Mazzucco et al., 2015 (shrimps) |
| | (6) Energy, allocation | Functional traits related to energy acquisition | Ivan and Höök, 2015 (perch); Mollet et al., 2016 (plaice) |
| | (7) Defence | Toxin production | de la Peña et al., 2011 (plant-herbivores) |
| | | Abstract defence | Costa et al., 2015; Urban et al., 2019 (generic) |
| | (8) Virulence | Pathogen virulence | Papaïx et al., 2018; Rimbaud et al., 2018 (plant pathogen) |
| Reproduction | (1) Growth/ maturation | Threshold for size at maturity | Ayllón et al., 2016, 2018 (trout); Piou and Prévost, 2012, 2013 (salmon); Kane et al., 2022 (trout) |
| | | Slope/intercept of the maturation reaction norm | Dunlop et al., 2007 (bass) |
| | (3) Mating | Selfing or self-incompatibility | Kirchner et al., 2006; Katsuhara et al., 2021 (plant) |
| | | Mate choice (preference, competitiveness), mate search | Berec et al., 2018; Chevalier et al., 2022 (generic) ; Labonne and Hendry, 2010 (guppy) ; Nathan et al., 2019 (trout) |
| Cooperation | (2) Abstract trait | Mutualistic or antagonistic trait | Maliet et al., 2020 (generic) |
| | (5) Cognitive behaviour | Grouping, schooling behaviour | van der Post et al., 2015 (generic); Reuter et al., 2016 (fish) |
| | | Attachment density | de Jager et al., 2020 (mussel) |

## B.3 Objective & method for the literature review

In their recent review of individual-based modelling of eco-evolutionary dynamics, Romero-Mujalli et al. (2019) illustrated how ABMs have been applied to assess organisms' and populations' responses to environmental change, but overlooked whether these ABMs accounted or not for interindividual interactions. Here, we specifically reviewed DG-ABMs in which fitness variation emerges mechanically from interactions between individuals. To that aim, we searched the Web of Science Core Collection between 1955 and 2022 for various combinations of keywords (Appendix.). A first query using (Individual-based model* OR IBM*) AND (eco-evol*OR demo-genet*OR demogenet* OR ecogenet*OR eco-genet*) returned 138 publications. Using the terms (Agent-based model OR ABM) instead of (Individual-based model*OR IBM*), we obtained 15 publications indicating that the eco-evolutionary community has not appropriated the term ABM despite its broader meaning (e.g. Railsback and Grimm, 2019). Of all these 153 publications, only 54 included the terms ([interindivid* OR inter-individ*OR individ*] AND interact*). After excluding reviews, technical publications, book chapters, preprint and duplicated studies (Table S2), we retained 120 publications. Finally, as we were interested in studies using a DG-ABM approach, we checked whether these 120 remaining publications (1) use an IBM; (2) simulate dynamics over multiple generations; (3) represent (direct or indirect) interactions between conspecific individuals; (4) represent individual variation in the interaction-related trait(s); and (5) consider that part of this variation is heritable. With this method, we filtered out 45 additional publications that did not satisfy these five criteria, resulting in a total of 75 publications using DG-ABMs where interindividual interactions affect fitness. Using a nonexhaustive snowball approach, we found 14 additional references cited in or citing the 75 selected publications. Note that the difficulties we encountered in selecting studies using DG-ABMs with interindividual interactions from the WOS illustrate the need for clearer referencing based on keywords better shared by the community.

## B.4 Synthesis of the literature review

In the selected 89 studies, competition was by far the most considered interaction (79 studies), followed by reproductive interactions (38 studies) and cooperative interactions (four studies only). We found 32 studies accounting for two types of interaction simultaneously.

On average, 1.9 traits (between 1 and 19 traits) per study were considered as evolvable. The nature of evolvable trait(s) depended on the interaction type, the species/kingdom considered and the level of generality/realism/precision of the model (following the classification of models properties of Levins, 1966). We distinguished eight categories of evolvable traits (Tables B.1, B.2): (1) traits related to growth and/or maturation thresholds (36 studies); (2) traits related to mating (12 studies); (3) dispersal traits (12 studies); (4) traits related to cognitive behaviour and information exchange (six studies); (5) traits related to energy acquisition or allocation (six studies); traits related to (6) defence (five studies) or (7) virulence (two studies); (8) and finally, abstract traits—meaning that they do not correspond directly to a measurable trait—generally related to competitive ability or/and assortative mating (17 studies). We found seven studies considering two types of traits simultaneously. While some of these traits directly mediate interindividual interactions (e.g. mating traits for reproduction, behavioural traits for cooperation), most of them indirectly impact interactions. For instance, dispersal traits or movement preferences are often associated with avoidance of competition and/or predation, or mate search for reproduction (Fronhofer and Altermatt, 2017; Travis et al., 2012). Traits related to growth, maturation and energy acquisition or allocation, influence individual size, which often plays a major role in the outcome of competition.

These evolvable traits are at the core of the eco-evolutionary feedback loops in DG-ABMs, since fitness variation emerges from interactions among individuals that differ in these traits,

giving rise to population dynamics in terms of both distribution of evolvable traits and demography. We distinguished five main types of eco-evolutionary feedback in the reviewed DG-ABMs (Table B.2). We found 17 'Ecology-focussed' DG-ABMs, with a high level of realism in the demographic and ecological processes, and incorporating a 'dose' of evolutionary processes to gain a better understanding of the ecological/demographic behaviour. In these DG-ABMs, evolvable traits were most often growth/maturation traits, but six other trait categories were considered. Then, we found 19 'Microevolution-focussed' DG-ABMs, with a high level of generality in the evolutionary processes, and incorporating a 'dose' of demographic and ecological processes to gain a better understanding of the evolutionary behaviour at a contemporary timescale. Similarly, there were also 13 'Macroevolution-focussed' DG-ABMs, dedicated to the understanding of speciation at a macroevolutionary timescale. In these 'Micro-or macroevolution-focussed' DG-ABMs, the evolvable trait was most often abstract, but mating traits were also often considered. Then, we identified 24 'Management-focussed' DG-ABMs, used to address how management practices interfere with eco-evolutionary feedbacks; in these DG-ABMs, evolvable traits were most often growth/maturation traits. Finally, we found 16 'Spatial-focussed' DG-ABMs, used to investigate eco-evolutionary feedback loops in a spatially explicit context (e.g. metapopulation). These DG-ABMs investigated in particular the evolution of dispersal traits.

Another characteristic of DG-ABMs is the type of inheritance framework used to model genetic variation in the evolvable traits. We found that 64 studies (71.9%) used a Mendelian inheritance process either in a population genetic framework (one locus, possibly multi-allelic, which directly determines the phenotype) or combined with a quantitative genetic framework (several loci, together with the environment, which govern trait variation). Besides, 22 studies (24.7%) used an infinitesimal quantitative genetic framework (where each offspring inherits

the mean of the two parent's genetic values), and two studies (2.2%) tested for population versus quantitative genetic framework. Note that our definition of DG-ABM is larger than the one suggested by some authors (e.g. Frank and Baret, 2013), who proposed to reserve the term 'eco-genetic' to models based on a quantitative genetics framework, and the term 'demo-genetic' to models based on a population genetics framework. Beyond these general typologies, we illustrate below the main applications of the reviewed DG-ABMs, through selected examples.

**Table B.2.** Association between the category of evolvable traits considered in each DG-ABM, and the type of eco-evolutionary feedback considered.

| Trait category | Type of eco-evolutionary feedback | | | | | |
|---|---|---|---|---|---|---|
| | **Ecology-focused** | **Microevolution-focused** | **Macroevolution-focused** | **Management-focused** | **Spatial-focused** | **Number of studies** |
| Growth/Maturation | 5 | 2 | 3 | 16 | 3 | 29 |
| Abstract trait | 2 | 7 | 8 | | | 17 |
| Dispersal | 2 | | | | 9 | 11 |
| Mating | 2 | 5 | | 1 | | 8 |
| Cognitive behaviour | 2 | 1 | 1 | | 2 | 6 |
| Defence | 1 | 2 | | | 1 | 4 |
| Energy acquisition or allocation | 2 | 1 | | 1 | | 4 |
| Virulence | | | | 2 | | 2 |
| Mating & growth/mat | | | 1 | 2 | | 3 |
| Mating & Energy acq. or allocat. | | 1 | | | | 1 |
| Growth/mat. & Defence | | | | 1 | | 1 |
| Growth/mat. & Dispersal | | | | | 1 | 1 |
| Growth/mat. & Energy acq. or allocat. | | | | 1 | | 1 |
| *Number of studies* | 16 | 19 | 13 | 24 | 16 | **88** |

## B.5 DG-ABMs to better understand eco-evolutionary feedback loops

Accounting for variable within-population inter-individual interactions in a bottom-up approach allows DG-ABMs to better investigate the emergence of fitness variation resulting from several complex eco-evolutionary processes and the interactions between them. Accounting for the stochastic and context-dependent outcomes of competitive, cooperative or reproductive interactions can change the predicted evolution of life-history traits compared with an approach where the relationship between traits and fitness is prescribed. Below, we emphasize relevant studies from our literature review which investigate these three types of interaction.

We start with examples of DG-ABMs considering explicit competitive interactions within species. Fielding (2004) investigated competition in grasshoppers and showed that contrasted optimal values of life-history traits can emerge from different types of localized interindividual interactions, that is exploitative or size-based competition. In their DG-ABM of trout population, Ayllón et al. (2016) observed the emergence of different eco-evolutionary outcomes due to explicit competitive interactions for food in a changing environment. These two DG-ABMs with explicit competitive interactions were built from well-tested demographic models, and additionally considered that the same traits (size at emergence and maturity size threshold) could evolve and interact with the spatial distribution of food resources to shape population dynamics. Most often in the reviewed DG-ABMs focussing on single species adaptive dynamics, competition is implicitly considered, for example through a density-dependence function. In a perch species, Ivan and Höök (2015) showed variable patterns of energy allocation along individual ontogeny, resulting from the interplay between plastic and adaptive responses to selection and density-dependent competition for food.

Using a DG-ABM representing competition among individuals choosing different life-history tactics, Piou and Prévost (2012, 2013) showed that climate change may modify salmon population dynamics through plastic responses of individual size. These two DG-ABMs acknowledge the main role of individual size on competition, and incorporate both genetic and plastic variation into this trait to gain a better understanding of the adaptive population dynamics in future, changing environments.

Integrating behavioural interactions between individuals and eco-evolutionary feedback is logically critical to understand the evolution of sociality and cooperation. van der Post et al. (2015) investigated how grouping, a taxonomically widespread social process, co-evolved with two cooperative social behaviours: anti-predator vigilance and foraging. In a simulation experiment where behavioural processes were specified through 19 variable traits, but not the cost and benefits of each decision strategy, they showed eco-evolutionary interactions between group size and vigilance with an evolutionary trajectory towards bigger groups and less vigilance, eventually leading to fission into small groups with high vigilance and back. Accounting for heritable interindividual differences and environmental heterogeneity in resource distribution, Reuter et al. (2016) were able to relate landscape structuration to the evolution of schooling behaviour and collective foraging in fish. Although these studies mostly focussed on how cooperation can emerge in models where costs and benefits are not explicitly specified but related to other behavioural traits, reverse strategy, where cooperation is the evolvable trait, could also be used to investigate adaptive dynamics.

*Reproductive interactions* are an obvious major driver of demographic dynamics, and 'Ecology-focussed' DG-ABMs are particularly suitable to investigate this issue in an eco-evolutionary framework. For instance, to explore how mating behaviour and population size

jointly affect fitness components or population growth rate through Allee effects, Berec et al. (2018) considered the rate of mate search as evolvable and found different optimal values of search rates for populations at different densities, resulting in lower Allee thresholds in populations kept at lower densities. DG-ABMs are also relevant to examine the interplay between demographic processes and the mating system when self-incompatibility (Kirchner et al., 2006) or sterility (Nonaka and Kaitala, 2020) occur as a direct consequence of the genotype.

*Reproductive interactions* are also known to drive evolutionary dynamics (Maan and Seehausen, 2011), and explicit representation of mating interactions is important as sexual selection can sometimes oppose natural selection (Labonne and Hendry, 2010), or eventually reinforce it (Soularue and Kremer, 2014). Mate choice strongly depends on the population structure, making the outcome challenging to predict yet rarely random (Klug and Stone, 2021). DG-ABMs, by allowing to represent explicitly sexual interactions, are particularly adapted to explore the evolution of traits considering the dynamic aspects of mating systems, such as when sexual preference and competition over mating partners occur, while still accounting for natural selection (Chevalier et al., 2022; Nathan et al., 2019). In this context, growth traits, or traits related to life-history decisions such as migration or maturation, are often chosen as key traits to jointly consider size-dependent survival and reproductive interaction and their possible interactions (Ayllón et al., 2019; Piou et al., 2015). Another application is the investigation of sexual dimorphism, which can arise when a given trait is subject to different selection pressures in males versus females (or even opposing pressures in the case of sexual conflict), but has a shared genetic basis between the sexes. Höök et al. (2021) showed how sex-specific plasticity for size could evolve by looking at perch evolutionary response to environment. Kane et al. (2022) showed that optimal migration propensity differed among males

and females in trout, and that populations could adapt to environmental change across a range of intersex genetic correlations for migration propensity, which influence the magnitude of sexual conflict.

## B.6 Extending in space, time and levels of organisation

In most examples detailed above, eco-evolutionary dynamics are modelled within a non-spatially explicit population. However, the spatial arrangement of habitats shapes animal movements or gametes propagation, and therefore also shapes social interactions and sexual networks (He et al., 2019). Since they allow fine-scale explicit representation of habitats as well as individual movements, DG-ABMs are well-suited to represent spatial evolutionary dynamics. Focussing on the evolution of dispersal, Fronhofer and Altermatt (2017) showed how eco-evolutionary feedback can emerge from a simple spatially explicit DG-ABM. Depending on network topology and connectivity, variable evolutionary stable dispersal strategies emerged from their model via kin competition, and lead to eco-evolutionary feedback by changing back the network's demography and genetic structure. Hrycik et al. (2019) explored the importance of environmental cues in perch vertical movement. By allowing movement rules in response to these cues to evolve, they illustrated the role of DG-ABMs in determining appropriate movement rules in spatially explicit ecological modelling. Travis et al. (2010) used a mechanistic DG-ABM approach to model the evolution of seed dispersal in plant populations, accounting for likely trade-offs between traits in a patchy landscape. Additionally, sexual selection can determine the reproductive success of immigrants in populations and thus the strength and direction of demo-genetic consequences of dispersal (e.g. demographic rescue, evolutionary rescue vs. gene swamping). For instance, Soularue and Kremer (2014) highlighted the major importance of gene flow and assortative mating in

shaping the genetic differentiation between populations in a heterogeneous environment.

Interactions between conspecific individuals are at the core of DG-ABMs. In addition, considering explicitly higher levels of organization (e.g. community level) to represent interspecific interactions may ultimately change the evolutionary outcomes expected from single species systems (terHorst et al., 2018; Weber et al., 2017). We found examples of such multispecies DG-ABMs used to investigate mating interactions: for instance, using an ABM in which two plant species share the same pollinators, Katsuhara et al. (2021) highlighted that the evolution of selfing without pollinator assistance (autonomous selfing) may increase population growth rates of inferior competitors and consequently favour long-term coexistence via an evolutionary rescue. Furthermore, McDonald et al. (2019) showed that the strength of intraspecific competition for mates may result from sexual interactions with heterospecifics, which may interfere with sexual selection (i.e. interspecific reproductive interference).

Most of the reviewed multispecies DG-ABMs focussed on competitive interactions, in an explicit prey–predators' or community context. For instance, Kang and Thibert-Plante (2017) illustrated that considering trophic interactions and the genetic basis of functional traits within a single model could improve the understanding of evolutionary morphological changes in fish. Hillaert et al. (2020) showed that in a fragmented habitat, the presence of predators selects for increased herbivore movement and hence larger herbivore size. Demo-genetic models of plant-virus interactions allowed to investigate the emergence of plant viral genotypes breaking down plant qualitative resistance genes (Fabre et al., 2009). Ecological interactions at the community level may drive selection within species, and selection may affect in return the processes of species assembly at a community scale (Leidinger et al., 2021). Finally, as multispecies DG-ABMs represent both intra-and interspecific complexity,

they are especially suited to address macroevolutionary consequences of interspecific interactions, such as speciation (Gavrilets et al., 2007; Weber et al., 2017). We found several examples of macroevolution-focussed DG-ABMs developed to investigate adaptive radiation, that is the rapid diversification of a single lineage into many species with a great diversity of ecological strategies (Gascuel et al., 2015; Pontarp et al., 2015; Ward and Collins, 2022). These models generally consider a limited number of abstract, phenotypic traits reflecting the competitive ability of the focal individual with all the other individuals of the local patch. The distance between these ecological phenotypes within a patch drives exploitative competition, while heritable variation of the ecological phenotype fuels the processes of local adaptation and speciation.

Overall, it appears that DG-ABMs have a large potential to address fundamental eco-evolutionary questions accounting for multiple drivers of fitness, and are increasingly used in an integrative way, allowing effects to flow up and down between organization levels.

## B.7 DG-ABMs to assist management strategies

Another key feature of DG-ABMs is their capacity to model the effects of management practices on individuals and their interactions, together with that of other eco-evolutionary processes. Hence, by allowing emerging effects, DG-ABMs can also be efficient prospective tools to elaborate and assess management strategies. When management consists of *demographic control of populations*, in particular through individual phenotype-based choices, it can deeply impact all demographic processes and population genetic composition, and therefore the intensity and direction of the evolutionary processes (Lefèvre et al., 2014). For example, selective fishing (or harvesting) directly affects competition among surviving fish (or trees), while genetic composition determines optimal fishing (or harvesting) patterns. In particular, different DG-ABMs were used to understand how selective fishing can affect

the demography and evolution of fish populations (fisheries-induced evolution), through cascading and sometimes counterintuitive effects on population demographic structure, growth and maturation thresholds (Ayllón et al., 2018; Piou et al., 2015; Wang et al., 2017; Wang and Höök, 2009). By simultaneously modelling the plastic and genetic responses of individuals, DG-ABMs can also disentangle the role of selective fishing and environment in the observed and predicted population declines and phenotypic changes (Piou et al., 2015).

When evolutionary dynamics and *land use planning decisions* are linked, DG-ABMs also represent valuable decision support tools. For example, Papaïx et al. (2018) and Rimbaud et al. (2018) used a spatially explicit demo-genetic model to assess the joint effect of crop cultivar deployment strategies in space and time and key pathogen life-history traits on epidemiological dynamics, resistance durability and long-term evolutionary control. Using a DG-ABM, Mims et al. (2019) found strong effects of spatial connectivity on demo-genetic outcomes in reintroduced bull trout populations, and allowed identification of watershed areas with higher persistence probabilities. In the case of *hybridization* between native/wild and introduced/domesticated gene pools, DG-ABMs allow to study the impact of management on the dynamics of crossing within and between gene pools, which depends on differential social interactions (e.g. mating preference) and genetic performances (e.g. local adaptation) between gene pools (Castellani et al., 2015; Nathan et al., 2019). In this context, DG-ABMs are an effective means of developing genetic enrichment strategies in a prospective approach (which genetic resources and which deployment modalities for which risks?), and conversely of evaluating strategies aimed at preserving the local gene pool from unwanted introgression.

In these different case studies, DG-ABMs offer a relevant framework to evaluate the short- and long-term evolutionary costs and benefits of management actions and to assess potential

trade-offs between them. For example, they allow to address the issue of exploiting a population or a metapopulation (e.g. fishing and wood production) while preserving its genetic value and diversity, or to determine how to minimize the risks of demo-genetic collapses of populations facing climate change. Furthermore, by controlling the social context of populations, management drives the overall ecological processes and thus affects biotic and abiotic stressors, the susceptibility of populations to these stressors, and selection intensity (Jactel et al., 2009).

## B.8 Taking advantage of ABMs for DG-ABMs

The above-listed examples from our literature review illustrate the diversity of interindividual interactions, adaptive traits and ecological processes that can be investigated using DG-ABMs. This diversity is a strength but requires active strategies to better identify possible links between similar models developed to answer different questions, and to structure the community of developers and users of these models. Identified as ABMs, DG-ABMs can benefit from multiple advances in the ABM community. The flexibility of the approach ranges from very simple and generic models to very complex and specific models, depending on model assumptions and objectives (Edmonds and Moss, 2005). A wide panel of tools and methodologies are available to explore DG-ABMs (Thiele et al., 2014). The exponential increase in genomic databases should help in the calibration/validation of DG-ABMs (Rudman et al., 2018). The use of description protocols such as Overview, Design concepts and Details protocol ensures the replicability and enhances the understanding of the models (Grimm et al., 2020). The TRACE framework (Grimm et al., 2014) is also a powerful tool for planning, documenting and assessing model development, analysis and application. Software for ABM development have increased in simplicity, quality, speed of computation and reliability and allow sharing pieces of code easily (Dufour-Kowalski et al.,

2012); in particular, quantitative genetic libraries can be plugged into existing population dynamic models to describe the genetic architecture of adaptive traits (e.g. 'Genetics' library in CAPSIS Dufour-Kowalski et al., 2012; Oddou-Muratorio and Davi, 2014). Software for complex model exploration have been proposed (Reuillon et al., 2013). Complex and multi-authored models may use modelling notebooks to keep trace of all steps of conceptualisation, model development, implementation and exploration in order to enhance the confidence of end-users of DG-ABMs in the management communities (Ayllón et al., 2021). Finally, the publication of model codes on specific dissemination platforms is encouraged in the ABM community (e.g. *https://www.comses.net/codebases/*). All these recommendations should benefit the development of DG-ABMs.

Intrinsically, DG-ABMs conception requires a multidisciplinary approach integrating multiple levels of knowledge and can be used in interdisciplinary research projects as a tool of interaction among disciplines. ABMs are also used as frontier objects in several contexts (Le Page and Perrotton, 2018; Reilly et al., 2021). As such, DG-ABMs are important tools in interacting with management or other end-user communities that need to incorporate evolutionary processes in their decisions. Although this has not been done so far, DG-ABMs could even be developed as part of a participatory modelling approach (Le Page et al., 2012) to integrate the knowledge of a diverse community of experts that need to manage constantly evolving ecosystems. Finally, they should become essential to adaptive management with an evolutionary perspective (Groot and Rossing, 2011).

### Conclusion

In complement to the analytical models traditionally employed by evolutionary ecologists to investigate eco-evolutionary feedback loops, this review puts forward DG-ABMs, which are individual-based (meta)population dynamics models with heritable trait variation and

phenotype-dependent interactions between individuals. Our literature review illustrates how the bottom-up construction of fitness in these DG-ABMs allows them to provide new insights into various fundamental and applied questions in ecology and evolution.

Previous reviews of the literature have indicated that ABMs in general are not used to address general questions in ecology and evolution, but have a more 'narrow' or 'pragmatic' scope (DeAngelis and Grimm, 2014). We advise modellers working on eco-evolutionary processes to carefully consider the benefits of accounting for the effects of interactions between individuals on fitness in their approach, since it might significantly affect the direction and magnitude of evolution. This is true for theoretical investigations and for more applied objectives, since these eco-evolutionary mechanisms also operate on rather short timescales (a handful of generations). Using a dedicated term—such as DG-ABM—would facilitate a distinction between categories of modelling approaches, highlighting the specifics of eco-evolutionary models accounting for interindividual interactions and their variations, and the potential differences in their respective predictions.

## B.9 Appendix

Additional supporting information can be found online in the Supporting Information section at the end of the article *https://doi.org/10.1111/eva.13508*. The database of the 89 original research studies using DG-ABMs with interindividual interactions affecting fitness is available at: *https://doi.org/10.57745/FUQGSG*.

# Bibliography

Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239. (Cited on page 188.)

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, NJ. (Cited on pages 1, 2, 7, 8, 47, 142 and 192.)

Anthes, N., P. David, J. Auld, J. Hoffer, P. Jarne, J. Koene, H. Kokko, M. Lorenzi, B. Pélissié, D. Sprenger, A. Staikou, and L. Schärer. 2010. Bateman Gradients in Hermaphrodites: An Extended Approach to Quantify Sexual Selection. The American Naturalist 176:249–263. (Cited on pages 2 and 48.)

Anthes, N., I. K. Häderer, N. K. Michiels, and T. Janicke. 2017. Measuring and interpreting sexual selection metrics: evaluation and guidelines. Methods in Ecology and Evolution 8:918–931. (Cited on pages 16, 20 and 96.)

Applegate, V. C. 1950. Natural history of the sea lamprey, Petromyzon marinus, in michigan. Ph.D. thesis. Great Lakes Science Center. (Cited on pages 33, 34, 35, 36 and 177.)

Arismendi, I., S. L. Johnson, J. B. Dunham, R. Haggerty, and D. Hockman-Wert. 2012. The paradox of cooling streams in a warming world: Regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. Geophysical Research Letters 39. (Cited on page 185.)

Arnold, K. E., A. Adam, K. J. Orr, R. Griffiths, and I. Barber. 2003. Sex-specific survival and parasitism in three-spined sticklebacks: seasonal patterns revealed by molecular analysis. Journal of Fish Biology 63:1046–1050. (Cited on page 27.)

Arnold, S. J., and D. Duvall. 1994. Animal Mating Systems: A Synthesis Based on Selection Theory. The American Naturalist 143:317–348. (Cited on page 15.)

Arnold, S. J., and M. J. Wade. 1984. On the Measurement of Natural and Sexual Selection: Theory. Evolution 38:709–719. (Cited on page 13.)

Avila, F. W., L. K. Sirot, B. A. LaFlamme, C. D. Rubinstein, and M. F. Wolfner. 2011. Insect Seminal Fluid Proteins: Identification and Function. Annual Review of Entomology 56:21–40. (Cited on page 26.)

Ayllón, D., S. F. Railsback, A. Almodovar, G. G. Nicola, S. Vincenzi, B. Elvira, and V. Grimm. 2018. Eco-evolutionary responses to recreational fishing under different harvest regulations. Ecology and Evolution 8:9600–9613. (Cited on pages 232 and 244.)

Ayllón, D., S. F. Railsback, C. Gallagher, J. Augusiak, H. Baveco, U. Berger, S. Charles, R. Martin, A. Focks, N. Galic, C. Liu, E. E. van Loon, J. Nabe-Nielsen, C. Piou, J. G. Polhill, T. G.

Preuss, V. Radchuk, A. Schmolke, J. Stadnicka-Michalak, P. Thorbek, and V. Grimm. 2021. Keeping modelling notebooks with TRACE: Good for you and good for environmental research and management support. Environmental Modelling & Software 136:104932. (Cited on page 246.)

Ayllón, D., S. F. Railsback, B. C. Harvey, I. García Quirós, G. G. Nicola, B. Elvira, and A. Almodóvar. 2019. Mechanistic simulations predict that thermal and hydrological effects of climate change on Mediterranean trout cannot be offset by adaptive behaviour, evolution, and increased food production. Science of The Total Environment 693:133648. (Cited on page 240.)

Ayllón, D., S. F. Railsback, S. Vincenzi, J. Groeneveld, A. Almodóvar, and V. Grimm. 2016. InSTREAM-Gen: Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change. Ecological Modelling 326:36–53. (Cited on pages 232 and 238.)

Bach, L. A., R. Thomsen, C. Pertoldi, and V. Loeschcke. 2006. Kin competition and the evolution of dispersal in an individual-based model. Ecological Modelling 192:658–666. (Cited on page 229.)

Bassar, R. D., T. Coulson, J. Travis, and D. N. Reznick. 2021. Towards a more precise – and accurate – view of eco-evolution. Ecology Letters 24:623–625. (Cited on page 222.)

Bateman, A. J. 1948. Intra-sexual selection in Drosophila. Heredity 2:349–368. (Cited on pages 15 and 108.)

Beamish, R. J. 1985. Freshwater Parasitic Lamprey on Vancouver Island and a Theory of the Evolution of the Freshwater Parasitic and Nonparasitic Life History Types. Pages 123–140 *in* R. E. Foreman, A. Gorbman, J. M. Dodd, and R. Olsson, eds. Evolutionary Biology of Primitive Fishes, NATO ASI Series. Springer US, Boston, MA. (Cited on page 140.)

———. 1987. Evidence that Parasitic and Nonparasitic Life History Types are Produced by One Population of Lamprey. Canadian Journal of Fisheries and Aquatic Sciences . (Cited on page 140.)

Beamish, R. J., and C.-E. M. Neville. 1992. The Importance of Size as an Isolating Mechanism in Lampreys. Copeia 1992:191–196. Publisher: American Society of Ichthyologists and Herpetologists (ASIH), Allen Press. (Cited on pages 38 and 141.)

Berec, L., A. M. Kramer, V. Bernhauerová, and J. M. Drake. 2018. Density-dependent selection on mate search and evolution of Allee effects. Journal of Animal Ecology 87:24–35. (Cited on pages 232 and 240.)

Berglund, A. 1991. Egg Competition in a Sex-Role Reversed Pipefish: Subdominant Females Trade Reproduction for Growth. Evolution 45:770. (Cited on pages 8 and 196.)

Bergstrom, C., and L. Real. 2000. Towards a theory of mutual mate choice: Lessons from two-sided matching. Evolutionary Ecology Research 2:493–508. (Cited on page 178.)

Binder, T. R., and D. G. McDonald. 2008*a*. The role of dermal photoreceptors during the sea lamprey (Petromyzon marinus) spawning migration. Journal of Comparative Physiology A 194:921–928. (Cited on page 147.)

———. 2008*b*. The role of temperature in controlling diel activity in upstream migrant sea lampreys (Petromyzon marinus). Canadian Journal of Fisheries and Aquatic Sciences 65:1113–1121. (Cited on pages 96 and 147.)

Bird, D., D. Ellis, and I. Potter. 1993. Comparisons between the fatty acid compositions of the muscle and ovary of the nonparasitic lamprey Lampetra planeri (bloch) and their counterparts in the anadromous and parasitic Lampetra fluviatilis (L.). Comparative Biochemistry and Physiology Part B: Comparative Biochemistry 105:327–332. (Cited on page 157.)

Blanckenhorn, W. U. 2000. The Evolution of Body Size: What Keeps Organisms Small? The Quarterly Review of Biology 75:385–407. Publisher: The University of Chicago Press. (Cited on page 49.)

Both, C., M. Van Asch, R. G. Bijlsma, A. B. Van Den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology 78:73–83. (Cited on page 94.)

Bracken, F. S. A., A. R. Hoelzel, J. B. Hume, and M. C. Lucas. 2015. Contrasting population genetic structure among freshwater-resident and anadromous lampreys: the role of demographic history, differential dispersal and anthropogenic barriers to movement. Molecular Ecology 24:1188–1204. (Cited on page 160.)

Bradshaw, W. E., and C. M. Holzapfel. 2007. Evolution of Animal Photoperiodism. Annual Review of Ecology, Evolution, and Systematics 38:1–25. (Cited on page 24.)

Brooks, S. P., and A. Gelman. 1998. General Methods for Monitoring Convergence of Iterative Simulations. Journal of Computational and Graphical Statistics 7:434–455. Publisher: Taylor & Francis. (Cited on page 58.)

Browne, R. K., S. A. Kaurova, V. K. Uteshev, N. V. Shishova, D. McGinnity, C. R. Figiel, N. Mansour, D. Agnew, M. Wu, E. N. Gakhova, B. Dzyuba, and J. Cosson. 2015. Sperm motility of externally fertilizing fish and amphibians. Theriogenology 83:1–13.e8. (Cited on page 192.)

Bulmer, M. G. 1983. Models for the evolution of protandry in insects. Theoretical Population Biology 23:314–322. (Cited on page 122.)

Burrows, M. T., D. S. Schoeman, L. B. Buckley, P. Moore, E. S. Poloczanska, K. M. Brander, C. Brown, J. F. Bruno, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, W. Kiessling, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. B. Schwing, W. J. Sydeman, and A. J. Richardson.

2011. The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. Science 334:652–655. (Cited on page 96.)

Bush, G. L. 1994. Sympatric speciation in animals: new wine in old bottles. Trends in Ecology & Evolution 9:285–288. (Cited on page 139.)

Butlin, R. K., J. Galindo, and J. W. Grahame. 2008. Sympatric, parapatric or allopatric: the most important way to classify speciation? Philosophical Transactions of the Royal Society B: Biological Sciences 363:2997–3007. (Cited on page 141.)

Cabral, M., J. Almeida, P. R. Almeida, T. Dellinger, N. Ferrand de Almeida, M. Oliveira, J. Palmeirim, A. Queiros, L. Rogado, and M. Santos-Reis. 2005. Livro Vermelho dos Vertebrados de Portugal. Tech. rep., Instituto da Conservação da Natureza. (Cited on pages 184 and 206.)

Calabrese, J., and W. Fagan. 2004. Lost in Time, Lonely, and Single: Reproductive Asynchrony and the Allee Effect. The American Naturalist 164:25–37. (Cited on page 123.)

Carleial, R., T. Pizzari, D. S. Richardson, and G. C. McDonald. 2023. Disentangling the causes of temporal variation in the opportunity for sexual selection. Nature Communications 14:1006. (Cited on pages 20, 96 and 169.)

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: A Probabilistic Programming Language. Journal of Statistical Software 76:1–32. (Cited on page 58.)

Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. Functional Ecology 21:387–393. (Cited on page 222.)

Case, B. 1970. Spawning Behaviour of the Chestnut Lamprey (Ichthyomyzon castaneus). Journal of the Fisheries Research Board of Canada 27:1872–1874. Publisher: NRC Research Press. (Cited on pages 53, 99 and 146.)

Castellani, M., M. Heino, J. Gilbey, H. Araki, T. Svåsand, and K. A. Glover. 2015. IBSEM: An Individual-Based Atlantic Salmon Population Model. PLOS ONE 10:e0138444. Publisher: Public Library of Science. (Cited on page 244.)

Castellano, S. 2009. Towards an information-processing theory of mate choice. Animal Behaviour 78:1493–1497. (Cited on page 178.)

Chapman, T. 2001. Seminal fluid-mediated fitness traits in Drosophila. Heredity 87:511–521. Publisher: Nature Publishing Group. (Cited on page 26.)

Chevalier, L., F. De Coligny, and J. Labonne. 2022. A demogenetic individual based model for the evolution of traits and genome architecture under sexual selection. Peer Community Journal 2:e8. (Cited on pages 230, 232 and 240.)

Chevalier, L., J. Labonne, M. Galipaud, and F.-X. Dechaume-Moncharmont. 2020. Fluctuating Dynamics of Mate Availability Promote the Evolution of Flexible Choosiness in Both Sexes. The American Naturalist 196:730–742. Publisher: The University of Chicago Press. (Cited on pages 122 and 179.)

Ciereszko, A., K. Dabrowski, G. P. Toth, S. A. Christ, and J. Glogowski. 2002. Factors Affecting Motility Characteristics and Fertilizing Ability of Sea Lamprey Spermatozoa. Transactions of the American Fisheries Society 131:193–202. Publisher: Taylor & Francis. (Cited on page 192.)

Cleland, E., I. Chuine, A. Menzel, H. Mooney, and M. Schwartz. 2007. Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22:357–365. (Cited on page 94.)

Clemens, B. J., S. van de Wetering, J. Kaufman, R. A. Holt, and C. B. Schreck. 2009. Do summer temperatures trigger spring maturation in Pacific lamprey, *Entosphenus tridentatus* ? Ecology of Freshwater Fish 18:418–426. (Cited on pages 37 and 185.)

Clobert, J., E. Danchin, A. A. Dhondt, J. D. Nichols, J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, eds. 2001. Dispersal. Oxford University Press, Oxford, New York. (Cited on page 27.)

Clutton-Brock, T., and G. Parker. 1995. Sexual coercion in animal societies. Animal Behaviour 49:1345–1365. (Cited on page 199.)

Clutton-Brock, T. H., and G. A. Parker. 1992. Potential Reproductive Rates and the Operation of Sexual Selection. The Quarterly Review of Biology 67:437–456. Publisher: The University of Chicago Press. (Cited on page 12.)

Cochran, P. A., D. D. Bloom, and R. J. Wagner. 2008. Alternative Reproductive Behaviors in Lampreys and Their Signifcance. Journal of Freshwater Ecology 23:437–444. (Cited on pages 34, 38, 141, 158 and 159.)

Cockburn, A., H. L. Osmond, and M. C. Double. 2008. Swingin' in the rain: condition dependence and sexual selection in a capricious world. Proceedings of the Royal Society B: Biological Sciences 275:605–612. Publisher: Royal Society. (Cited on page 18.)

Cornwallis, C. K., and E. A. O'Connor. 2009. Sperm: seminal fluid interactions and the adjustment of sperm quality in relation to female attractiveness. Proceedings of the Royal Society B: Biological Sciences 276:3467–3475. Publisher: Royal Society. (Cited on page 197.)

Costa, M., C. Hauzy, N. Loeuille, and S. Méléard. 2015. Stochastic eco-evolutionary model of a prey-predator community. Journal of Mathematical Biology 72:573–622. (Cited on pages 230 and 232.)

Cotto, O., M. Schmid, and F. Guillaume. 2020. Nemo-age: Spatially explicit simulations of eco-evolutionary dynamics in stage-structured populations under changing environments. Methods in Ecology and Evolution 11:1227–1236. (Cited on pages 228 and 229.)

Crow, J. F. 1989. Some Possibilities for Measuring Selection Intensities in Man. Human Biology 61:763–775. Publisher: Wayne State University Press. (Cited on pages 49 and 175.)

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection. Murray, London. (Cited on pages 1 and 139.)

———. 1871. The Descent of Man, and Selection in Relation to Sex, vol. 1. Murray, London. (Cited on page 1.)

Daupagne, L., M. Dhamelincourt, A. Michaud, J. Rives, S. Sebihi, and C. Tentelier. 2022. Realistic variations in substrate composition affect spawning preference and egg retention in river lamprey ( *Lampetra fluviatilis* ). Journal of Fish Biology page jfb.15164. (Cited on pages 98 and 145.)

Davies, B., and N. Bromage. 2002. The effects of fluctuating seasonal and constant water temperatures on the photoperiodic advancement of reproduction in female rainbow trout, Oncorhynchus mykiss. Aquaculture 205:183–200. (Cited on page 24.)

Davies, N. B. 1991. Mating system. Behavioural ecology-An evolutionary approach pages 263–294. Publisher: Blackwell. (Cited on pages 3 and 7.)

de Jager, M., J. van de Koppel, E. J. Weerman, and F. J. Weissing. 2020. Patterning in Mussel Beds Explained by the Interplay of Multi-Level Selection and Spatial Self-Organization. Frontiers in Ecology and Evolution 8. (Cited on pages 230 and 232.)

De Jong, M. C. M., and M. W. Sabelis. 1991. Limits to runaway sexual selection: The wallflower paradox. Journal of Evolutionary Biology 4:637–655. (Cited on page 122.)

de la Peña, E., B. D'hondt, and D. Bonte. 2011. Landscape structure, dispersal and the evolution of antagonistic plant-herbivore interactions. Ecography 34:480–487. (Cited on page 232.)

DeAngelis, D. L., and V. Grimm. 2014. Individual-based models in ecology after four decades. F1000Prime Reports 6:39. (Cited on pages 97 and 247.)

DeAngelis, D. L., and W. M. Mooij. 2005. Individual-Based Modeling of Ecological and Evolutionary Processes. Annual Review of Ecology, Evolution, and Systematics 36:147–168. (Cited on pages 227 and 228.)

Decanter, N., R. Normand, A. Souissi, C. Labbé, E. Edeline, and G. Evanno. 2023. Sperm competition experiments reveal low prezygotic postmating isolation between parasitic and non-parasitic lamprey ecotypes. Ecology and Evolution 13:e9970. (Cited on pages 192, 193 and 194.)

Dechaume-Moncharmont, F.-X., T. Brom, and F. Cézilly. 2016. Opportunity costs resulting from scramble competition within the choosy sex severely impair mate choosiness. Animal Behaviour 114:249–260. (Cited on page 179.)

Dey, C. J., A. R. Reddon, C. M. O'Connor, and S. Balshine. 2013. Network structure is related to social conflict in a cooperatively breeding fish. Animal Behaviour 85:395–402. (Cited on page 23.)

Dhamelincourt, M., M. Buoro, J. Rives, S. Sebihi, and C. Tentelier. 2021. Individual and group characteristics affecting nest building in sea lamprey ( *Petromyzon marinus* L. 1758 ). Journal of Fish Biology 98:557–565. (Cited on pages 35, 69, 177, 207 and 215.)

Dieckmann, U., and R. Ferrière. 2004. Adaptive Dynamics and Evolving Biodiversity. Pages 188–224 *in* R. Ferrière, U. Dieckmann, and D. Couvet, eds. Evolutionary Conservation Biology, 1st ed. Cambridge University Press. (Cited on page 226.)

Doadrio, I., J. I. D. Villarejo, E. D. G. d. C. d. l. Naturaleza, and M. N. d. C. Naturales. 2001. Atlas y libro rojo de los peces continentales de España. Museo Nacional de Ciencias Naturales, Dirección General de Conservación de la Naturaleza. (Cited on page 206.)

Docker. 2019. Lampreys: Biology, Conservation and Control: Volume 2. Springer Netherlands, Dordrecht. (Cited on pages 30, 31, 38, 49, 51, 72, 96, 102, 139, 140, 143, 146, 160 and 216.)

Docker, M. F., ed. 2015. Lampreys: Biology, Conservation and Control: Volume 1. Springer Netherlands, Dordrecht. (Cited on pages 30, 31, 53, 99, 146, 157 and 179.)

Dougherty, L. R. 2020. Designing mate choice experiments. Biological Reviews 95:759–781. (Cited on page 182.)

Dougherty, L. R., and D. M. Shuker. 2015. The effect of experimental design on the measurement of mate choice: a meta-analysis. Behavioral Ecology 26:311–319. (Cited on page 172.)

Dufour-Kowalski, S., B. Courbaud, P. Dreyfus, C. Meredieu, and F. de Coligny. 2012. Capsis: an open software framework and community for forest growth modelling. Annals of Forest Science 69:221–233. (Cited on pages 245 and 246.)

Dunlop, E. S., M. Heino, and U. Dieckmann. 2009. Eco-genetic modeling of contemporary life-history evolution. Ecological Applications 19:1815–1834. (Cited on pages 97 and 222.)

Dunlop, E. S., B. J. Shuter, and U. Dieckmann. 2007. Demographic and Evolutionary Consequences of Selective Mortality: Predictions from an Eco-Genetic Model for Smallmouth Bass. Transactions of the American Fisheries Society 136:749–765. (Cited on page 232.)

Dunn, P. 2004. Breeding Dates and Reproductive Performance. Pages 69–87 *in* Advances in Ecological Research, vol. 35. Elsevier. (Cited on page 94.)

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate Extremes: Observations, Modeling, and Impacts. Science 289:2068–2074. (Cited on page 185.)

Eberhard, W. 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press. (Cited on pages 8 and 195.)

Edmonds, B., and S. Moss. 2005. From KISS to KIDS – An 'Anti-simplistic' Modelling Approach. Pages 130–144 *in* P. Davidsson, B. Logan, and K. Takadama, eds. Multi-Agent and Multi-Agent-Based Simulation. Lecture Notes in Computer Science. Springer, Berlin, Heidelberg. (Cited on page 245.)

Emlen, S. T., and L. W. Oring. 1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. Science 197:215–223. (Cited on pages 3, 4, 10, 11, 19, 47, 49, 54, 70, 95, 96, 120 and 174.)

Endler, J. A. 1986. Natural Selection in the Wild. Princeton University Press. (Cited on pages 2, 3 and 17.)

Engqvist, L., and K. P. Sauer. 2001. Strategic male mating effort and cryptic male choice in a scorpionfly. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:729–735. (Cited on pages 8 and 197.)

Evans, T. M., and K. E. Limburg. 2019. Parasitism offers large rewards but carries high risks: Predicting parasitic strategies under different life history conditions in lampreys. Journal of Evolutionary Biology page 12. (Cited on pages 30 and 140.)

Fabre, F., C. Bruchou, A. Palloix, and B. Moury. 2009. Key determinants of resistance durability to plant viruses: Insights from a model linking within- and between-host dynamics. Virus Research 141:140–149. (Cited on page 242.)

Farine, D. R., and H. Whitehead. 2015. Constructing, conducting and interpreting animal social network analysis. Journal of Animal Ecology 84:1144–1163. (Cited on page 223.)

Fielding, D. J. 2004. Intraspecific competition and spatial heterogeneity alter life history traits in an individual-based model of grasshoppers. Ecological Modelling 175:169–187. (Cited on pages 232 and 238.)

Fine, J. M., L. A. Vrieze, and P. W. Sorensen. 2004. Evidence That Petromyzontid Lampreys Employ a Common Migratory Pheromone That Is Partially Comprised of Bile Acids. Journal of Chemical Ecology 30:2091–2110. (Cited on page 37.)

Firman, R. C., C. Gasparini, M. K. Manier, and T. Pizzari. 2017. Postmating Female Control: 20 Years of Cryptic Female Choice. Trends in Ecology & Evolution 32:368–382. (Cited on pages 192 and 195.)

Fisher, R. A. 1930. The genetical theory of natural selection. The genetical theory of natural selection. Clarendon Press, Oxford, England. (Cited on pages 9 and 47.)

Fitze, P. S., and J.-F. Le Galliard. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. Ecology Letters 11:432–439. (Cited on pages 10, 11 and 199.)

Fitzpatrick, J. L. 2020. Sperm competition and fertilization mode in fishes. Philosophical Transactions of the Royal Society B: Biological Sciences 375:20200074. (Cited on page 187.)

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379–416. (Cited on page 216.)

Formica, V., H. Donald, H. Marti, Z. Irgebay, and E. Brodie. 2021. Social network position experiences more variable selection than weaponry in wild subpopulations of forked fungus beetles. Journal of Animal Ecology 90:168–182. (Cited on page 23.)

Forsgren, E., J. D. Reynolds, A. Berglund, and R. Mooi. 2002. Behavioural Ecology of Reproduction in Fish. Pages 225–247 *in* Handbook of Fish Biology and Fisheries. John Wiley & Sons, Ltd. (Cited on page 185.)

Fox, C. W., and C. M. Rauter. 2003. Bet-hedging and the evolution of multiple mating. Evolutionary Ecology Research page 14. (Cited on page 72.)

Frank, B. M., and P. V. Baret. 2013. Simulating brown trout demogenetics in a river/nursery brook system: The individual-based model DemGenTrout. Ecological Modelling 248:184–202. (Cited on page 236.)

French, J. A., and J. A. Stribley. 1987. Synchronization of ovarian cycles within and between social groups in golden lion tamarins (Leontopithecus rosalia). American Journal of Primatology 12:469–478. (Cited on page 180.)

Friard, O., and M. Gamba. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution 7:1325–1330. (Cited on pages 53, 99, 146 and 209.)

Fronhofer, E. A., and F. Altermatt. 2017. Classical metapopulation dynamics and eco-evolutionary feedbacks in dendritic networks. Ecography . (Cited on pages 232, 234 and 241.)

Gage, A. R., and C. J. Barnard. 1996. Male crickets increase sperm number in relation to competition and female size. Behavioral Ecology and Sociobiology 38:349–353. (Cited on page 197.)

Gage, M. 1998. Influences of sex, size, and symmetry on ejaculate expenditure in a moth. Behavioral Ecology 9:592–597. (Cited on page 197.)

Garcia-Gonzalez, F., Y. Yasui, and J. P. Evans. 2015. Mating portfolios: bet-hedging, sexual selection and female multiple mating. Proceedings of the Royal Society B: Biological Sciences 282:20141525. (Cited on page 72.)

Gardner, C., S. M. Coghlan, and J. Zydlewski. 2012. Distribution and Abundance of Anadromous Sea Lamprey Spawners in a Fragmented Stream: Current Status and Potential Range

Expansion Following Barrier Removal. Northeastern Naturalist 19:99–110. (Cited on pages 35 and 215.)

Gascuel, F., R. Ferriere, R. Aguilee, and A. Lambert. 2015. How Ecology and Landscape Dynamics Shape Phylogenetic Trees. Systematic Biology 64:590–607. (Cited on pages 232 and 243.)

Gaulin, S. J. C., and R. W. Fitzgerald. 1989. Sexual selection for spatial-learning ability. Animal Behaviour 37:322–331. (Cited on page 122.)

Gauthey, Z., C. Tentelier, O. Lepais, A. Elosegi, L. Royer, S. Glise, and J. Labonne. 2017. With our powers combined: integrating behavioral and genetic data to estimate mating success and sexual selection. preprint, Evolutionary Biology. (Cited on pages 55, 70 and 206.)

Gavrilets, S., A. Vose, M. Barluenga, W. Salzburger, and A. Meyer. 2007. Case studies and mathematical models of ecological speciation. 1. Cichlids in a crater lake: MODELLING SPECIATION IN A LAKE. Molecular Ecology 16:2893–2909. (Cited on pages 224 and 243.)

Gelman, A., A. Jakulin, M. G. Pittau, and Y.-S. Su. 2008. A weakly informative default prior distribution for logistic and other regression models. The Annals of Applied Statistics 2. (Cited on page 58.)

Gelman, A., and D. B. Rubin. 1992. Inference from Iterative Simulation Using Multiple Sequences. Statistical Science 7:457–472. Publisher: Institute of Mathematical Statistics. (Cited on page 58.)

Ghiselin, M. T. 1969. The Evolution of Hermaphroditism Among Animals. The Quarterly Review of Biology 44:189–208. Publisher: The University of Chicago Press. (Cited on page 2.)

Gibson, R. M., and T. A. Langen. 1996. How do animals choose their mates? Trends in Ecology & Evolution 11:468–470. (Cited on page 179.)

Gillet, C. 1991. Egg production in an Arctic charr ( *Salvelinus alpinus* L.) brood stock: effects of temperature on the timing of spawning and the quality of eggs. Aquatic Living Resources 4:109–116. (Cited on page 25.)

Gillott, C. 2003. Male Accessory Gland Secretions: Modulators of Female Reproductive Physiology and Behavior. Annual Review of Entomology 48:163–184. (Cited on page 26.)

Gochfeld, M. 1980. Mechanisms and Adaptive Value of Reproductive Synchrony in Colonial Seabirds. Pages 207–270 *in* J. Burger, B. L. Olla, and H. E. Winn, eds. Behavior of Marine Animals: Current Perspectives in Research. Marine Birds. Springer US, Boston, MA. (Cited on page 26.)

Godineau, C., O. Ronce, and C. Devaux. 2022. Assortative mating can help adaptation of flowering time to a changing climate: Insights from a polygenic model. Journal of Evolutionary Biology 35:491–508. (Cited on page 223.)

Govaert, L., E. A. Fronhofer, S. Lion, C. Eizaguirre, D. Bonte, M. Egas, A. P. Hendry, A. De Brito Martins, C. J. Melián, J. A. M. Raeymaekers, I. I. Ratikainen, B.-E. Saether, J. A. Schweitzer, and B. Matthews. 2019. Eco-evolutionary feedbacks—Theoretical models and perspectives. Functional Ecology 33:13–30. (Cited on page 222.)

Grant, P. R., and B. R. Grant. 2002. Unpredictable Evolution in a 30-Year Study of Darwin's Finches. Science 296:707–711. (Cited on page 17.)

Greenway, E. V., J. A. Hamel, and C. W. Miller. 2021. Exploring the effects of extreme polyandry on estimates of sexual selection and reproductive success. Behavioral Ecology 32:1055–1063. (Cited on page 188.)

Grimm, V., J. Augusiak, A. Focks, B. M. Frank, F. Gabsi, A. S. Johnston, C. Liu, B. T. Martin, M. Meli, V. Radchuk, P. Thorbek, and S. F. Railsback. 2014. Towards better modelling and decision support: Documenting model development, testing, and analysis using TRACE. Ecological Modelling 280:129–139. (Cited on page 245.)

Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, G. Huse, A. Huth, J. U. Jepsen, C. Jørgensen, W. M. Mooij, B. Müller, G. Pe'er, C. Piou, S. F. Railsback, A. M. Robbins, M. M. Robbins, E. Rossmanith, N. Rüger, E. Strand, S. Souissi, R. A. Stillman, R. Vabø, U. Visser, and D. L. DeAngelis. 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198:115–126. (Cited on page 101.)

Grimm, V., and S. F. Railsback. 2005. Individual-based Modeling and Ecology. *In* Individual-based Modeling and Ecology. Princeton University Press. (Cited on page 101.)

Grimm, V., S. F. Railsback, C. E. Vincenot, U. Berger, C. Gallagher, D. L. DeAngelis, B. Edmonds, J. Ge, J. Giske, J. Groeneveld, A. S. Johnston, A. Milles, J. Nabe-Nielsen, J. G. Polhill, V. Radchuk, M.-S. Rohwäder, R. A. Stillman, J. C. Thiele, and D. Ayllón. 2020. The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism. Journal of Artificial Societies and Social Simulation 23:7. (Cited on page 245.)

Groot, J. C. J., and W. A. H. Rossing. 2011. Model-aided learning for adaptive management of natural resources: an evolutionary design perspective. Methods in Ecology and Evolution 2:643–650. (Cited on page 246.)

Gross, M. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. Fish Reproduction pages 35–75. Publisher: Adademic Press. (Cited on page 158.)

Guillaume, F., and J. Rougemont. 2006. Nemo: an evolutionary and population genetics programming framework. Bioinformatics 22:2556–2557. (Cited on page 179.)

Hagelin, L.-O. 1959. Further Aquarium Observations on the Spawning Habits of the River Lamprey (Petromyzon fluviatilis). Oikos 10:50–64. Publisher: Nordic Society Oikos, Wiley. (Cited on pages 33, 34 and 51.)

Hagelin, L.-O., and N. Steffner. 1958. Notes on the Spawning Habits of the River Lamprey (Petromyzon fluviatilis). Oikos 9:221–238. Publisher: Nordic Society Oikos, Wiley. (Cited on pages 33, 34, 144 and 145.)

Halliday, T., and S. J. Arnold. 1987. Multiple mating by females: A perspective from quantitative genetics. Animal Behaviour 35:939–941. Publisher: Elsevier Science. (Cited on page 6.)

Halupka, L., and K. Halupka. 2017. The effect of climate change on the duration of avian breeding seasons: a meta-analysis. Proceedings of the Royal Society B: Biological Sciences 284:20171710. Publisher: Royal Society. (Cited on page 94.)

Hardisty, M. W. 1961. Studies on an Isolated Spawning Population of the Brook Lamprey (Lampetra planeri). Journal of Animal Ecology 30:339–355. Publisher: Wiley, British Ecological Society. (Cited on page 35.)

———. 1986. General introduction to lampreys. The freshwater fishes of Europe, Petromyzontiformes Publisher: AULA-Verlag. (Cited on page 206.)

———. 2006. Lampreys: Life Without Jaws. Forrest. (Cited on page 140.)

Hardisty, M. W., and I. C. Potter. 1971. The biology of lampreys, vol. 1-4. Hardisty, m.w., potter, i.c. (eds.) ed. Academic Press, London. Publisher: Academic Press. (Cited on pages 30, 36, 37, 38, 49, 50, 51, 52, 96, 97, 98, 140, 141, 143, 145, 185 and 210.)

Hare, R. M., and L. W. Simmons. 2019. Sexual selection and its evolutionary consequences in female animals. Biological Reviews 94:929–956. (Cited on page 195.)

He, P., A. A. Maldonado-Chaparro, and D. R. Farine. 2019. The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behavioral Ecology and Sociobiology 73:9. (Cited on page 241.)

Hendry, A. P. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: An empirical demonstration using introduced sockeye salmon | SpringerLink. (Cited on page 139.)

———. 2016. Eco-evolutionary Dynamics. Princeton University Press. (Cited on page 222.)

Hendry, A. P., E. B. Taylor, and J. D. McPhail. 2002. ADAPTIVE DIVERGENCE AND THE BALANCE BETWEEN SELECTION AND GENE FLOW: LAKE AND STREAM STICKLEBACK IN THE MISTY SYSTEM. Evolution 56:1199–1216. (Cited on page 139.)

Henshaw, J. M., M. D. Jennions, and L. E. B. Kruuk. 2018. How to quantify (the response to) sexual selection on traits. Evolution 72:1904–1917. (Cited on page 16.)

Henshaw, J. M., A. T. Kahn, and K. Fritzsche. 2016. A rigorous comparison of sexual selection indexes via simulations of diverse mating systems. Proceedings of the National Academy of Sciences 113:E300–E308. (Cited on page 16.)

Higashi, M., G. Takimoto, and N. Yamamura. 1999. Sympatric speciation by sexual selection. Nature 402:523–526. (Cited on page 139.)

Hillaert, J., M. L. Vandegehuchte, T. Hovestadt, and D. Bonte. 2020. Habitat loss and fragmentation increase realized predator–prey body size ratios. Functional Ecology 34:534–544. (Cited on page 242.)

Holcik. 1986. The freshwater fishes of Europe. Volume 1, Part 1: Petromyzontiformes. (Cited on page 140.)

Hosken, D. J., W. U. Blanckenhorn, and T. W. J. Garner. 2002. Heteropopulation males have a fertilization advantage during sperm competition in the yellow dung fly (Scathophaga stercoraria). Proceedings of the Royal Society B: Biological Sciences 269:1701–1707. (Cited on page 192.)

Houston, McNamara, and Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences page 23. (Cited on page 139.)

Howard, D. J., S. R. Palumbi, L. M. Birge, and M. K. Manier. 2009. Sperm and speciation. Pages 367–403 *in* T. R. Birkhead, D. J. Hosken, and S. Pitnick, eds. Sperm Biology. Academic Press, London. (Cited on page 192.)

Hrycik, A. R., P. D. Collingsworth, T. M. Sesterhenn, D. Goto, and T. O. Höök. 2019. Movement rule selection through eco-genetic modeling: Application to diurnal vertical movement. Journal of Theoretical Biology 478:128–138. (Cited on pages 232 and 241.)

Huggins, R. J., and A. Thompson. 1970. Communal spawning of brook and river lampreys, Lampetra planeri Bloch and Lampetra fluviatilis L. Journal of Fish Biology 2:53–54. (Cited on pages 36, 53, 99, 146 and 159.)

Hume, J. B. 2011. Adult lamprey survey of the Endrick Water SSSI and SAC 2009-2010. Tech. Rep. 480, Scottish Natural Heritage Commissioned. (Cited on page 29.)

Hume, J. B., C. E. Adams, B. Mable, and C. Bean. 2013*a*. Post-zygotic hybrid viability in sympatric species pairs: a case study from European lampreys: Hybridization in Lamprey Species Pairs. Biological Journal of the Linnean Society 108:378–383. (Cited on pages 158 and 193.)

Hume, J. B., C. E. Adams, B. Mable, and C. W. Bean. 2013*b*. Sneak male mating tactics between lampreys (Petromyzontiformes) exhibiting alternative life-history strategies: INTERSPECIFIC SNEAK MATING BETWEEN LAMPREYS. Journal of Fish Biology 82:1093–1100. (Cited on pages 141 and 160.)

Hunt, J., C. J. Breuker, J. A. Sadowski, and A. J. Moore. 2009. Male-male competition, female mate choice and their interaction: determining total sexual selection. Journal of Evolutionary Biology 22:13–26. (Cited on page 50.)

Huston, M., D. DeAngelis, and W. Post. 1988. New Computer Models Unify Ecological Theory. BioScience 38:682–691. (Cited on page 228.)

Härdling, R., and H. Kokko. 2005. The evolution of prudent choice. Evolutionary Ecology Research page 21. (Cited on page 143.)

Höök, T. O., R. Svanbäck, and P. Eklöv. 2021. Sex-specific plasticity in a trophic polymorphic aquatic predator: a modeling approach. Oecologia 195:341–354. (Cited on page 240.)

Ims, R. A. 1990. The ecology and evolution of reproductive synchrony. Trends in Ecology & Evolution 5:135–140. (Cited on page 26.)

INRAE. 2018. ECP, INRAE. (Cited on pages 98, 183 and 208.)

Ivan, L. N., and T. O. Höök. 2015. Energy allocation strategies of young temperate fish: an ecogenetic modeling approach. Canadian Journal of Fisheries and Aquatic Sciences 72:1243–1258. (Cited on pages 230, 232 and 238.)

Iwata, A. 1989. Petromyzontidae. Freshwater Fishes of Japan pages 33–40. Publisher: Yamakei Publishers. (Cited on page 144.)

Iwata, A., and K. Hamada. 1986. A Dwarf Male of the Arctic Lamprey, Lethenteron japonicum from the Assabu River, Hokkaido, Japan. Bull. Fac. Fish. Hokkaido Univ. page 7. (Cited on pages 32, 38 and 144.)

Jactel, H., B. C. Nicoll, M. Branco, J. R. Gonzalez-Olabarria, W. Grodzki, B. Långström, F. Moreira, S. Netherer, C. Orazio, D. Piou, H. Santos, M. J. Schelhaas, K. Tojic, and F. Vodde. 2009. The influences of forest stand management on biotic and abiotic risks of damage. Annals of Forest Science 66:701–701. Publisher: BioMed Central. (Cited on page 245.)

Janetos, A. C. 1980. Strategies of female mate choice: A theoretical analysis. Behavioral Ecology and Sociobiology 7:107–112. (Cited on pages 106, 178 and 179.)

Jang, M.-H., and M. C. Lucas. 2005. Reproductive ecology of the river lamprey. Journal of Fish Biology 66:499–512. (Cited on pages 35, 49, 51, 52, 98, 145, 206, 207, 209, 210 and 215.)

Janicke, T., and E. H. Morrow. 2018. Operational sex ratio predicts the opportunity and direction of sexual selection across animals. Ecology Letters 21:384–391. (Cited on pages 11, 13, 54, 70, 108 and 175.)

Jennions, M. D., H. Kokko, and H. Klug. 2012. The opportunity to be misled in studies of sexual selection: The opportunity to be misled in studies of sexual selection. Journal of Evolutionary Biology 25:591–598. (Cited on pages 54 and 100.)

Jirotkul, M. 1999. Operational sex ratio influences female preference and male–male competition in guppies. Animal Behaviour 58:287–294. (Cited on page 19.)

Johnson, N. S., T. J. Buchinger, and W. Li. 2015. Reproductive Ecology of Lampreys. Pages 265–303 *in* M. F. Docker, ed. Lampreys: Biology, Conservation and Control. Springer Netherlands, Dordrecht. (Cited on pages 106 and 207.)

Johnstone, R. A. 1997. The tactics of mutual mate choice and competitive search. Behavioral Ecology and Sociobiology 40:51–59. (Cited on page 178.)

Johnstone, R. A., J. D. Reynolds, and J. C. Deutsch. 1996. Mutual Mate Choice and Sex Differences in Choosiness. Evolution 50:1382–1391. Publisher: Society for the Study of Evolution, Wiley. (Cited on page 178.)

Jones, A. G. 2009. On the Opportunity for Sexual Selection, the Bateman Gradient and the Maximum Intensity of Sexual Selection. Evolution 63:1673–1684. (Cited on pages 14 and 15.)

Jones, A. G., and J. Avise. 2001. Mating Systems and Sexual Selection in Male-Pregnant Pipefishes and Seahorses: Insights from Microsatellite-Based Studies of Maternity. Journal of Heredity 92:150–158. (Cited on page 16.)

Jones, A. G., G. I. Moore, C. Kvarnemo, D. Walker, and J. C. Avise. 2003. Sympatric speciation as a consequence of male pregnancy in seahorses. Proceedings of the National Academy of Sciences 100:6598–6603. (Cited on page 140.)

Jones, A. G., and N. L. Ratterman. 2009. Mate choice and sexual selection: What have we learned since Darwin? Proceedings of the National Academy of Sciences 106:10001–10008. (Cited on page 99.)

Jovani, R., and V. Grimm. 2008. Breeding synchrony in colonial birds: from local stress to global harmony. Proceedings of the Royal Society B: Biological Sciences 275:1557–1564. (Cited on pages 26 and 180.)

Kane, A., D. Ayllón, R. J. O'Sullivan, P. McGinnity, and T. E. Reed. 2022. Escalating the conflict? Intersex genetic correlations influence adaptation to environmental change in facultatively migratory populations. Evolutionary Applications 15:773–789. (Cited on pages 232 and 240.)

Kang, J. k., and X. Thibert-Plante. 2017. Eco-evolution in size-structured ecosystems: simulation case study of rapid morphological changes in alewife. BMC Evolutionary Biology 17:58. (Cited on pages 224, 230, 232 and 242.)

Kasumovic, M. M., M. J. Bruce, M. C. B. Andrade, and M. E. Herberstein. 2008. Spatial and Temporal Demographic Variation Drives Within-Season Fluctuations in Sexual Selection. Evolution 62:2316–2325. (Cited on pages 19, 21 and 48.)

Katsuhara, K. R., Y. Tachiki, R. Iritani, and A. Ushimaru. 2021. The eco-evolutionary dynamics of prior selfing rates promote coexistence without niche partitioning under conditions of reproductive interference. Journal of Ecology 109:3916–3928. (Cited on pages 224, 232 and 242.)

Kazancıoğlu, E., H. Klug, and S. H. Alonzo. 2012. The Evolution of Social Interactions Changes Predictions About Interacting Phenotypes. Evolution 66:2056–2064. (Cited on page 223.)

Keast, A. 1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environmental Biology of Fishes 3:7–31. (Cited on page 139.)

Kelly, E., and B. Phillips. 2019. How many and when? Optimising targeted gene flow for a step change in the environment. Ecology Letters 22:447–457. (Cited on page 224.)

Kirchner, F., A. Robert, and B. Colas. 2006. Modelling the dynamics of introduced populations in the narrow-endemic Centaurea corymbosa: a demo-genetic integration. Journal of Applied Ecology 43:1011–1021. (Cited on pages 232 and 240.)

Kirkpatrick, M., and N. Barton. 1997. Evolution of a Species' Range. The American Naturalist 150:1–23. (Cited on page 226.)

Klaus, S. P., L. P. Fitzsimmons, T. E. Pitcher, and S. M. Bertram. 2011. Song and Sperm in Crickets: A Trade-off between Pre- and Post-copulatory Traits or Phenotype-Linked Fertility?: Mating Behaviour and Sperm Traits in House Crickets. Ethology 117:154–162. (Cited on page 198.)

Klug, H., J. Heuschele, M. D. Jennions, and H. Kokko. 2010*a*. The mismeasurement of sexual selection. Journal of Evolutionary Biology 23:447–462. (Cited on pages 10, 13, 19, 54 and 100.)

Klug, H., K. Lindström, and H. Kokko. 2010*b*. Who to include in measures of sexual selection is no trivial matter. Ecology Letters 13:1094–1102. (Cited on pages 16 and 96.)

Klug, H., and L. Stone. 2021. More than just noise: Chance, mating success, and sexual selection. Ecology and Evolution 11:6326–6340. (Cited on page 240.)

Kobayashi, W. 1993. Effect of osmolality on the motility of sperm from the lamprey, Lampetra japonica. Zoological Science (Tokyo) pages 281–285. (Cited on page 192.)

Kobayashi, W., Y. Baba, T. Shimozawa, and T. S. Yamamoto. 1994. The Fertilization Potential Provides a Fast Block to Polyspermy in Lamprey Eggs. Developmental Biology 161:552–562. (Cited on page 194.)

Koizumi, I., and I. K. Shimatani. 2016. Socially induced reproductive synchrony in a salmonid: an approximate Bayesian computation approach. Behavioral Ecology 27:1386–1396. (Cited on page 26.)

Kokko, H. 2021. The tired copepod and the definition of sexual selection: a comment on Shuker and Kvarnemo. Behavioral Ecology 32:795–796. (Cited on pages 3 and 9.)

Kokko, H., R. Brooks, J. M. McNamara, and A. I. Houston. 2002. The sexual selection continuum. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:1331–1340. (Cited on page 142.)

Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. Journal of Evolutionary Biology 21:919–948. (Cited on pages 12 and 47.)

Kokko, H., M. D. Jennions, and R. Brooks. 2006. Unifying and Testing Models of Sexual Selection. Annual Review of Ecology, Evolution, and Systematics 37:43–66. (Cited on pages 1 and 47.)

Kokko, H., H. Klug, and M. D. Jennions. 2012. Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. Ecology Letters 15:1340–1351. (Cited on page 96.)

Kokko, H., and J. Mappes. 2005. Sexual selection when fertilizations is not guarenteed. Evolution 59:1876–1885. (Cited on page 122.)

Kovach, R. P., J. E. Joyce, J. D. Echave, M. S. Lindberg, and D. A. Tallmon. 2013. Earlier Migration Timing, Decreasing Phenotypic Variation, and Biocomplexity in Multiple Salmonid Species. PLoS ONE 8:e53807. (Cited on page 123.)

Krakauer, A. H., M. S. Webster, E. H. Duval, A. G. Jones, and S. M. Shuster. 2011. The opportunity for sexual selection: not mismeasured, just misunderstood: Opportunity for selection. Journal of Evolutionary Biology 24:2064–2071. (Cited on pages 14, 54 and 100.)

Kubisch, A., E. A. Fronhofer, H. J. Poethke, and T. Hovestadt. 2013. Kin Competition as a Major Driving Force for Invasions. The American Naturalist 181:700–706. (Cited on page 229.)

Kucheravy, C. E., J. M. Waterman, E. A. C. dos Anjos, J. F. Hare, C. Enright, and C. N. Berkvens. 2021. Extreme climate event promotes phenological mismatch between sexes in hibernating ground squirrels. Scientific Reports 11:21684. Publisher: Nature Publishing Group. (Cited on page 186.)

Kucheryavyi, A. V., K. A. Savvaitova, D. S. Pavlov, M. A. Gruzdeva, K. V. Kuzishchin, and J. A. Stanford. 2007. Variations of life history strategy of the arctic lamprey Lethenteron camtschaticum from the Utkholok River (Western Kamchatka). Journal of Ichthyology 47:37–52. (Cited on pages 36, 140, 157 and 159.)

Labonne, J., and A. Hendry. 2010. Natural and Sexual Selection Giveth and Taketh Away Reproductive Barriers: Models of Population Divergence in Guppies. The American Naturalist 176:26–39. (Cited on pages 224, 232 and 240.)

Lamarins, A., V. Fririon, D. Folio, C. Vernier, L. Daupagne, J. Labonne, M. Buoro, F. Lefèvre, C. Piou, and S. Oddou-Muratorio. 2022. Importance of interindividual interactions in eco-evolutionary population dynamics: The rise of demo-genetic agent-based models. Evolutionary Applications 15:1988–2001. (Cited on pages 97 and 101.)

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. Proceedings of the National Academy of Sciences 78:3721–3725. (Cited on page 139.)

Lande, R., and S. J. Arnold. 1983. The Measurement of Selection on Correlated Characters. Evolution 37:1210–1226. Publisher: Society for the Study of Evolution, Wiley. (Cited on pages 14, 47 and 55.)

Lande, R., and M. Kirkpatrick. 1988. Ecological speciation by sexual selection. Journal of Theoretical Biology 133:85–98. (Cited on page 139.)

Larsen, L. O. 1980. Physiology of Adult Lampreys, with Special Regard to Natural Starvation, Reproduction, and Death after Spawning. Canadian Journal of Fisheries and Aquatic Sciences 37:1762–1779. (Cited on page 30.)

LaRue, E. A., N. C. Emery, L. Briley, and M. R. Christie. 2019. Geographic variation in dispersal distance facilitates range expansion of a lake shore plant in response to climate change. Diversity and Distributions 25:1429–1440. (Cited on page 232.)

Lasne, E., M.-R. Sabatié, and G. Evanno. 2010. Communal spawning of brook and river lampreys (Lampetra planeri and L. fluviatilis) is common in the Oir River (France). Ecology of Freshwater Fish 19:323–325. (Cited on pages 25, 35, 36, 51, 159, 179, 182 and 183.)

Le Page, C., N. Becu, P. Bommel, and F. Bousquet. 2012. Participatory agent-based simulation for renewable resource management: the role of the Cormas simulation platform to nurture a community of practice. Journal of Artificial Societies and Social Simulation . (Cited on page 246.)

Le Page, C., and A. Perrotton. 2018. KILT: A Modelling Approach Based on Participatory Agent-Based Simulation of Stylized Socio-Ecosystems to Stimulate Social Learning with Local Stakeholders. Pages 156–169 *in* G. P. Dimuro and L. Antunes, eds. Multi-Agent Based Simulation XVIII. Lecture Notes in Computer Science. Springer International Publishing, Cham. (Cited on page 246.)

Lee, J. S. 2005. Alternative reproductive tactics and status-dependent selection. Behavioral Ecology 16:566–570. (Cited on page 195.)

Lefèvre, F., T. Boivin, A. Bontemps, F. Courbet, H. Davi, M. Durand-Gillmann, B. Fady, J. Gauzere, C. Gidoin, M.-J. Karam, H. Lalagüe, S. Oddou-Muratorio, and C. Pichot. 2014. Considering evolutionary processes in adaptive forestry. Annals of Forest Science 71:723–739. (Cited on page 243.)

Legrand, M., C. Briand, L. Buisson, T. Besse, G. Artur, D. Azam, A. Baisez, D. Barracou, N. Bourré, L. Carry, A.-L. Caudal, J. Corre, E. Croguennec, S. Der Mikaélian, Q. Josset, L. Le Gurun, F. Schaeffer, R. Toussaint, and P. Laffaille. 2021. Diadromous fish modified timing of upstream migration over the last 30 years in France. Freshwater Biology 66:286–302. (Cited on page 94.)

Lehtonen, T. K., and K. Lindström. 2008. Density-dependent sexual selection in the monogamous fish *Archocentrus nigrofasciatus*. Oikos 117:867–874. (Cited on page 19.)

Leidinger, L., D. Vedder, and J. S. Cabral. 2021. Temporal environmental variation may impose differential selection on both genomic and ecological traits. Oikos 130:1100–1115. (Cited on pages 232 and 242.)

Levins, R. 1966. The Strategy of Model Building in Population Biology. American Scientist 54:421–431. (Cited on page 234.)

Levitan, D. 1998. Sperm Limitation, Gamete Competition, and Sexual Selection in External Fertilizers. Page 175 *in* Sperm Competition and Sexual Selection. Elsevier. (Cited on pages 194 and 196.)

———. 2004. Density-Dependent Sexual Selection in External Fertilizers: Variances in Male and Female Fertilization Success along the Continuum from Sperm Limitation to Sexual Conflict in the Sea Urchin Strongylocentrotus franciscanus. The American Naturalist 164:298–309. (Cited on page 194.)

Li, W., A. P. Scott, M. J. Siefkes, H. Yan, Q. Liu, S.-S. Yun, and D. A. Gage. 2002. Bile Acid Secreted by Male Sea Lamprey That Acts as a Sex Pheromone. Science 296:138–141. (Cited on page 37.)

Lissåker, M., and C. Kvarnemo. 2006. Ventilation or nest defense—parental care trade-offs in a fish with male care. Behavioral Ecology and Sociobiology 60:864–873. (Cited on page 216.)

Liu, S., Z. Xie, B. Liu, Y. Wang, J. Gao, Y. Zeng, J. Xie, Z. Xie, B. Jia, P. Qin, R. Li, L. Wang, and S. Chen. 2020. Global river water warming due to climate change and anthropogenic heat emission. Global and Planetary Change 193:103289. (Cited on page 24.)

Lucas, M. C., J. B. Hume, P. R. Almeida, K. Aronsuu, E. Habit, S. Silva, C. J. Wang, and B. Zampatti. 2021. Emerging conservation initiatives for lampreys: Research challenges and opportunities. Journal of Great Lakes Research 47:S690–S703. (Cited on pages 206 and 217.)

Maan, M. E., and O. Seehausen. 2011. Ecology, sexual selection and speciation: Ecology, sexual selection and speciation. Ecology Letters 14:591–602. (Cited on page 240.)

Madsen, T., and R. Shine. 1993. Temporal Variability in Sexual Selection Acting on Reproductive Tactics and Body Size in Male Snakes. The American Naturalist 141:167–171. (Cited on page 18.)

Maitland, P. S. 1980. Review of the Ecology of Lampreys in Northern Europe. Canadian Journal of Fisheries and Aquatic Sciences 37:1944–1952. (Cited on pages 33, 36 and 206.)

Maliet, O., N. Loeuille, and H. Morlon. 2020. An individual-based model for the eco-evolutionary emergence of bipartite interaction networks. Ecology Letters 23:1623–1634. (Cited on page 232.)

Malmquist, H. J., S. S. Snorrason, S. Skúlason, B. Jonsson, O. T. Sandlund, and P. M. Jonasson. 1992. Diet Differentiation in Polymorphic Arctic Charr in Thingvallavatn, Iceland. Journal of Animal Ecology 61:21–35. (Cited on page 139.)

Malmqvist, B. 1983. Breeding Behaviour of Brook Lampreys Lampetra planeri: Experiments on Mate Choice. Oikos 41:43–48. (Cited on pages 33, 34, 35, 38, 50, 52, 53, 69, 71, 98, 99, 109, 142, 145, 146 and 158.)

Mangel, M. 2015. Stochastic Dynamic Programming Illuminates the Link Between Environment, Physiology, and Evolution. Bulletin of Mathematical Biology 77:857–877. (Cited on page 226.)

Mangel, M., and J. Stamps. 2002. Trade-offs between growth and mortality and the maintenance of individual variation in growth. Evolutionary Ecology Research page 12. (Cited on page 139.)

Manion, P. J., and L. H. Hanson. 1980. Spawning Behavior and Fecundity of Lampreys from the Upper Three Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 37:1635–1640. Publisher: NRC Research Press. (Cited on pages 33, 35, 177 and 206.)

Marshall, D. J., and J. P. Evans. 2005. Does egg competition occur in marine broadcast-spawners? Journal of Evolutionary Biology 18:1244–1252. (Cited on page 196.)

Mayer, P. M., L. M. Smith, R. G. Ford, D. C. Watterson, M. D. McCutchen, and M. R. Ryan. 2009. Nest construction by a ground-nesting bird represents a potential trade-off between egg crypticity and thermoregulation. Oecologia 159:893–901. (Cited on page 216.)

Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. Journal of Theoretical Biology 47:209–221. (Cited on page 222.)

Mazzucco, R., T. Van Nguyen, D.-H. Kim, T.-S. Chon, and U. Dieckmann. 2015. Adaptation of aquatic insects to the current flow in streams. Ecological Modelling 309-310:143–152. (Cited on page 232.)

McDonald, G. C., A. Gardner, and T. Pizzari. 2019. Sexual selection in complex communities: Integrating interspecific reproductive interference in structured populations. Evolution 73:1025–1036. (Cited on pages 25 and 242.)

McDonald, G. C., and T. Pizzari. 2016. Why patterns of assortative mating are key to study sexual selection and how to measure them. Behavioral Ecology and Sociobiology 70:209–220. (Cited on page 188.)

McKinnon, J. S., S. Mori, B. K. Blackman, L. David, D. M. Kingsley, L. Jamieson, J. Chou, and D. Schluter. 2004. Evidence for ecology's role in speciation. Nature 429:294–298. (Cited on page 140.)

McLain, D. K. 1982. Density Dependent Sexual Selection and Positive Phenotypic Assortative Mating in Natural Populations of the Soldier Beetle, Chauliognathus pennsylvanicus. Evolution 36:1227–1235. (Cited on pages 19 and 47.)

———. 1992. Population density and the intensity of sexual selection on body length in spatially or temporally restricted natural populations of a seed bug. Behavioral Ecology and Sociobiology 30:347–356. (Cited on page 19.)

McLean, B. S., N. Barve, and R. P. Guralnick. 2022. Sex-specific breeding phenologies in the North American deer mouse (Peromyscus maniculatus). Ecosphere 13:e4327. (Cited on page 95.)

McQueen, K., and C. T. Marshall. 2017. Shifts in spawning phenology of cod linked to rising sea temperatures. ICES Journal of Marine Science 74:1561–1573. (Cited on pages 94 and 185.)

Miller, C. W., and E. I. Svensson. 2014. Sexual Selection in Complex Environments. Annual Review of Entomology 59:427–445. (Cited on page 182.)

Mills, S. C., and J. D. Reynolds. 2003. Operational sex ratio and alternative reproductive behaviours in the European bitterling, Rhodeus sericeus. Behavioral Ecology and Sociobiology 54:98–104. (Cited on page 10.)

Mims, M. C., C. C. Day, J. J. Burkhart, M. R. Fuller, J. Hinkle, A. Bearlin, J. B. Dunham, P. W. DeHaan, Z. A. Holden, and E. E. Landguth. 2019. Simulating demography, genetics, and spatially explicit processes to inform reintroduction of a threatened char. Ecosphere 10:e02589. (Cited on page 244.)

Mollet, F. M., U. Dieckmann, and A. D. Rijnsdorp. 2016. Reconstructing the effects of fishing on life-history evolution in North Sea plaice Pleuronectes platessa. Marine Ecology Progress Series 542:195–208. (Cited on page 232.)

Morbey, Y. E., and R. C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. Ecology Letters 4:663–673. (Cited on page 73.)

Morita, K., T. Tamate, M. Kuroki, and T. Nagasawa. 2014. Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish. Journal of Animal Ecology 83:1268–1278. (Cited on page 123.)

Moser, M. L., J. B. Hume, K. K. Aronsuu, R. T. Lampman, and A. D. Jackson. 2019. Lamprey Reproduction and Early Life History: Insights from Artificial Propagation. Pages 187–245 *in* M. F. Docker, ed. Lampreys: Biology, Conservation and Control: Volume 2, Fish & Fisheries Series. Springer Netherlands, Dordrecht. (Cited on page 211.)

Moura, R., and P. E. C. Peixoto. 2013. The effect of operational sex ratio on the opportunity for sexual selection: a meta-analysis. Animal Behaviour 86:675–683. (Cited on pages 11 and 13.)

Moya-Laraño, J. 2011. Genetic variation, predator–prey interactions and food web structure. Philosophical Transactions of the Royal Society B: Biological Sciences 366:1425–1437. Publisher: Royal Society. (Cited on page 232.)

Munro, A. D., A. P. Scott, and T. J. Lam. 1990. Reproductive Seasonality in Teleosts: Environmental Influences. CRC Press, Boca Raton. (Cited on pages 24 and 185.)

Myhre, L. C., E. Forsgren, and T. Amundsen. 2013. Effects of habitat complexity on mating behavior and mating success in a marine fish. Behavioral Ecology 24:553–563. (Cited on page 47.)

Mönkkönen, M., R. Härdling, J. T. Forsman, and J. Tuomi. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. Evolutionary Ecology 13:93–106. (Cited on page 25.)

Nagel, L., and D. Schluter. 1998. BODY SIZE, NATURAL SELECTION, AND SPECIATION IN STICKLEBACKS. Evolution 52:209–218. (Cited on page 140.)

Nathan, L. R., N. Mamoozadeh, H. R. Tumas, S. Gunselman, K. Klass, A. Metcalfe, C. Edge, L. P. Waits, P. Spruell, E. Lowery, E. Connor, A. R. Bearlin, M.-J. Fortin, and E. Landguth.

2019. A spatially-explicit, individual-based demogenetic simulation framework for evaluating hybridization dynamics. Ecological Modelling 401:40–51. (Cited on pages 232, 240 and 244.)

Newman, M. E. J. 2002. Assortative mixing in networks. Physical Review Letters 89:208701. (Cited on page 188.)

Nika, N., and T. Virbickas. 2010. Brown trout Salmo trutta redd superimposition by spawning Lampetra species in a lowland stream. Journal of Fish Biology 77:2358–2372. (Cited on page 206.)

Nonaka, E., and V. Kaitala. 2020. The effects of functional response and host abundance fluctuations on genetic rescue in parasitoids with single-locus sex determination. Ecology and Evolution 10:13030–13043. (Cited on page 240.)

Oddou-Muratorio, S., and H. Davi. 2014. Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model. Evolutionary Applications 7:453–467. (Cited on page 246.)

Oh, K., and A. Badyaev. 2010. Structure of Social Networks in a Passerine Bird: Consequences for Sexual Selection and the Evolution of Mating Strategies. The American Naturalist 176:E80–E89. Publisher: The University of Chicago Press. (Cited on page 223.)

Okamoto, D. K. 2016. Competition among Eggs Shifts to Cooperation along a Sperm Supply Gradient in an External Fertilizer. The American Naturalist 187:E129–E142. (Cited on pages 194 and 196.)

Okasha, S. 2004. Multilevel Selection and the Partitioning of Covariance: A Comparison of Three Approaches. Evolution 58:486–494. (Cited on page 55.)

Orlowsky, B., and S. I. Seneviratne. 2012. Global changes in extreme events: regional and seasonal dimension. Climatic Change 110:669–696. (Cited on page 185.)

Pankhurst, N. W., and H. R. King. 2010. Temperature and salmonid reproduction: implications for aquaculture. Journal of Fish Biology 76:69–85. (Cited on page 24.)

Pankhurst, N. W., and P. L. Munday. 2011. Effects of climate change on fish reproduction and early life history stages. Marine and Freshwater Research 62:1015. (Cited on page 24.)

Papaïx, J., L. Rimbaud, J. J. Burdon, J. Zhan, and P. H. Thrall. 2018. Differential impact of landscape-scale strategies for crop cultivar deployment on disease dynamics, resistance durability and long-term evolutionary control. Evolutionary Applications 11:705–717. (Cited on pages 232 and 244.)

Parker, G. A. 1992. Snakes and female sexuality. Nature 355:395–396. (Cited on page 6.)

Parker, G. A., and P. Courtney. 1983. Seasonal incidence: Adaptive variation in the timing of life history stages. Journal of Theoretical Biology 105:147–155. (Cited on page 122.)

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics 37:637–669. (Cited on page 94.)

Pease, C. M., R. Lande, and J. J. Bull. 1989. A Model of Population Growth, Dispersal and Evolution in a Changing Environment. Ecology 70:1657–1664. (Cited on page 226.)

Pelletier, F., D. Garant, and A. Hendry. 2009. Eco-evolutionary dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 364:1483–1489. (Cited on page 222.)

Petersen, C. W., and R. R. Warner. 1998. Sperm Competition in Fishes. Pages 435–463 *in* T. R. Birkhead and A. P. Møller, eds. Sperm Competition and Sexual Selection. Academic Press, San Diego. (Cited on page 187.)

Piavis, G. 1961. Embryological stages in the sea lamprey and effects of temperature on development. Washington, DC: US Fish and Wildlife Service. pages 111–143. (Cited on page 216.)

Pinter-Wollman, N., E. A. Hobson, J. E. Smith, A. J. Edelman, D. Shizuka, S. de Silva, J. S. Waters, S. D. Prager, T. Sasaki, G. Wittemyer, J. Fewell, and D. B. McDonald. 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behavioral Ecology 25:242–255. (Cited on page 23.)

Piou, C., and E. Prévost. 2012. A demo-genetic individual-based model for Atlantic salmon populations: Model structure, parameterization and sensitivity. Ecological Modelling 231:37–52. (Cited on pages 230, 232 and 239.)

———. 2013. Contrasting effects of climate change in continental vs. oceanic environments on population persistence and microevolution of Atlantic salmon. Global Change Biology 19:711–723. (Cited on pages 232 and 239.)

Piou, C., M. H. Taylor, J. Papaïx, and E. Prévost. 2015. Modelling the interactive effects of selective fishing and environmental change on Atlantic salmon demogenetics. Journal of Applied Ecology 52:1629–1637. (Cited on pages 240 and 244.)

Pischedda, A., and W. R. Rice. 2012. Partitioning sexual selection into its mating success and fertilization success components. Proceedings of the National Academy of Sciences 109:2049–2053. Publisher: Proceedings of the National Academy of Sciences. (Cited on page 16.)

Pitcher, T. E., S. M. Doucet, J.-M. J. Beausoleil, and D. Hanley. 2009. Secondary sexual characters and sperm traits in coho salmon *Oncorhynchus kisutch*. Journal of Fish Biology 74:1450–1461. (Cited on page 198.)

Pizzari, T., C. K. Cornwallis, H. Løvlie, S. Jakobsson, and T. R. Birkhead. 2003. Sophisticated sperm allocation in male fowl. Nature 426:70–74. (Cited on page 197.)

Platt, T., C. Fuentes-Yaco, and K. T. Frank. 2003. Spring algal bloom and larval fish survival. Nature 423:398–399. Publisher: Nature Publishing Group. (Cited on page 94.)

Pletcher, F. T. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. Ph.D. thesis. University of British Columbia. (Cited on page 35.)

Poethke, H. J., B. Pfenning, and T. Hovestadt. 2007. The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. Evolutionary Ecology Research . (Cited on page 229.)

Pontarp, M., J. Ripa, and P. Lundberg. 2015. The Biogeography of Adaptive Radiations and the Geographic Overlap of Sister Species. The American Naturalist 186:565–581. Publisher: The University of Chicago Press. (Cited on pages 232 and 243.)

Potter, I. C., H. S. Gill, C. B. Renaud, and D. Haoucher. 2015. The Taxonomy, Phylogeny, and Distribution of Lampreys. Pages 35–73 *in* M. F. Docker, ed. Lampreys: Biology, Conservation and Control. Springer Netherlands, Dordrecht. (Cited on pages 32 and 206.)

Pretzsch, H. 2021. Genetic diversity reduces competition and increases tree growth on a Norway spruce (Picea abies [L.] Karst.) provenance mixing experiment. Forest Ecology and Management 497:119498. (Cited on page 222.)

Pröhl, H. 2002. Population differences in female resource abundance, adult sex ratio, and male mating success in Dendrobates pumilio. Behavioral Ecology 13:175–181. (Cited on pages 19 and 47.)

Pélissié, B., P. Jarne, and P. David. 2012. Sexual selection without sexual dimorphism: bateman gradients in a simultaneous hermaphrodite. Evolution 66:66–81. (Cited on pages 2 and 48.)

Pélissié, B., P. Jarne, V. Sarda, and P. David. 2014. DISENTANGLING PRECOPULATORY AND POSTCOPULATORY SEXUAL SELECTION IN POLYANDROUS SPECIES: SEXUAL SELECTION IN A POLYANDROUS SPECIES. Evolution 68:1320–1331. (Cited on page 16.)

Pörtner, H., D. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, and N. Weyer. 2019. The Ocean and Cryosphere in a Changing Climate: Special Report of the Intergovernmental Panel on Climate Change. 1st ed. Cambridge University Press. (Cited on page 24.)

R Core Team. 2022. R: A language and environment for statistical computing. (Cited on pages 58, 100, 148, 151, 161, 163 and 210.)

Rafferty, N. E., P. J. CaraDonna, and J. L. Bronstein. 2015. Phenological shifts and the fate of mutualisms. Oikos 124:14–21. (Cited on page 94.)

Railsback, S. F., and V. Grimm. 2019. Agent-Based and Individual-Based Modeling: A Practical Introduction, Second Edition. Princeton University Press. (Cited on page 233.)

Ramsey, D. M. 2011. Mutual Mate Choice with Multiple Criteria. Pages 337–355 *in* M. Breton and K. Szajowski, eds. Advances in Dynamic Games: Theory, Applications, and Numerical Methods for Differential and Stochastic Games, Annals of the International Society of Dynamic Games. Birkhäuser, Boston. (Cited on page 178.)

Reilly, A. C., R. L. Dillon, and S. D. Guikema. 2021. Agent-Based Models as an Integrating Boundary Object for Interdisciplinary Research. Risk Analysis 41:1087–1092. (Cited on page 246.)

Reinhold, K., J. Kurtz, and L. Engqvist. 2002. Cryptic male choice: sperm allocation strategies when female quality varies. Journal of Evolutionary Biology 15:201–209. (Cited on page 197.)

Renaud. 2011. Lampreys of the world. An annotated and illustrated catalogue of lamprey species known to date. FAO page 118. (Cited on pages 36, 144 and 179.)

Renaud, C. B. 1997. Conservation status of Northern Hemisphere lampreys (Petromyzontidae). Journal of Applied Ichthyology 13:143–148. (Cited on page 184.)

Reuillon, R., M. Leclaire, and S. Rey-Coyrehourcq. 2013. OpenMOLE, a workflow engine specifically tailored for the distributed exploration of simulation models. Future Generation Computer Systems 29:1981–1990. (Cited on page 246.)

Reuter, H., M. Kruse, A. Rovellini, and B. Breckling. 2016. Evolutionary trends in fish schools in heterogeneous environments. Ecological Modelling 326:23–35. (Cited on pages 232 and 239.)

Rimbaud, L., J. Papaïx, L. G. Barrett, J. J. Burdon, and P. H. Thrall. 2018. Mosaics, mixtures, rotations or pyramiding: What is the optimal strategy to deploy major gene resistance? Evolutionary Applications 11:1791–1810. (Cited on pages 232 and 244.)

Rodríguez-Muñoz, R., and T. Tregenza. 2009. Genetic compatibility and hatching success in the sea lamprey ( *Petromyzon marinus* ). Biology Letters 5:286–288. (Cited on page 192.)

Romero-Mujalli, D., F. Jeltsch, and R. Tiedemann. 2019. Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions. Regional Environmental Change 19:1–12. (Cited on pages 222 and 233.)

Rougemont, Q., A. Gaigher, E. Lasne, J. Côte, M. Coke, A.-L. Besnard, S. Launey, and G. Evanno. 2015. Low reproductive isolation and highly variable levels of gene flow reveal limited progress towards speciation between European river and brook lampreys. Journal of Evolutionary Biology 28:2248–2263. (Cited on pages 31, 141, 158, 160 and 193.)

Royle, N. J., P. T. Smiseth, and M. Kölliker, eds. 2012. The evolution of parental care. First edition ed. Oxford University Press, Oxford, United Kingdom. (Cited on page 12.)

Rudman, S. M., M. A. Barbour, K. Csilléry, P. Gienapp, F. Guillaume, N. G. Hairston Jr, A. P. Hendry, J. R. Lasky, M. Rafajlović, K. Räsänen, P. S. Schmidt, O. Seehausen, N. O. Therkildsen, M. M. Turcotte, and J. M. Levine. 2018. What genomic data can reveal about eco-evolutionary dynamics. Nature Ecology & Evolution 2:9–15. Publisher: Nature Publishing Group. (Cited on page 245.)

Rundle, H. D., and P. Nosil. 2005. Ecological speciation: Ecological speciation. Ecology Letters 8:336–352. (Cited on page 141.)

Salewski, V. 2003. Satellite species in lampreys: a worldwide trend for ecological speciation in sympatry?: sympatric speciation in lampreys. Journal of Fish Biology 63:267–279. (Cited on pages 30 and 140.)

Sandlund, O. T., K. Gunnarsson, P. M. Jónasson, B. Jonsson, T. Lindem, K. P. Magnússon, H. J. Malmquist, H. Sigurjónsdóttir, S. Skúlason, S. S. Snorrason, P. M. Jonasson, K. P. Magnusson, H. Sigurjonsdottir, and S. Skulason. 1992. The Arctic Charr Salvelinus alpinus in Thingvallavatn. Oikos 64:305. (Cited on page 139.)

Sandströ, O., I. Abrahamsson, J. Andersson, and M. Vetemaa. 1997. Temperature effects on spawning and egg development in Eurasian perch. Journal of Fish Biology 51:1015–1024. (Cited on page 24.)

Scheiner, S. M. 2013. The ecological literature, an ideafree distribution. Ecology Letters 16:1421–1423. (Cited on page 182.)

Schluter, D., and T. Price. 1993. Honesty, perception and population divergence in sexually selected traits. Proceedings of the Royal Society of London. Series B: Biological Sciences 253:117–122. (Cited on page 139.)

Schneider, J. M., and M. A. Elgar. 1998. Spiders hedge genetic bets. Trends in Ecology & Evolution 13:218–219. Publisher: Elsevier. (Cited on page 6.)

Schoener, T. W. 2011. The Newest Synthesis: Understanding the Interplay of Evolutionary and Ecological Dynamics. Science 331:426–429. Publisher: American Association for the Advancement of Science. (Cited on page 222.)

Scott, A. M., Z. Zhang, L. Jia, K. Li, Q. Zhang, T. Dexheimer, E. Ellsworth, J. Ren, Y.-W. Chung-Davidson, Y. Zu, R. R. Neubig, and W. Li. 2019. Spermine in semen of male sea lamprey acts as a sex pheromone. PLOS Biology 17:e3000332. (Cited on pages 73 and 194.)

Seagle, H. H., and J. W. Nagel. 1982. Life Cycle and Fecundity of the American Brook Lamprey, Lampetra appendix, in Tennessee. Copeia 1982:362–366. Publisher: American Society of Ichthyologists and Herpetologists (ASIH), Allen Press. (Cited on page 35.)

Shuker, D. M. 2010. Sexual selection: endless forms or tangled bank? Animal Behaviour 79:e11–e17. (Cited on page 5.)

Shuker, D. M., and C. Kvarnemo. 2021. The definition of sexual selection. Behavioral Ecology 32:781–794. (Cited on pages 1, 3, 7, 9 and 47.)

Shuster, S. M. 2009. Sexual selection and mating systems. Proceedings of the National Academy of Sciences 106:10009–10016. (Cited on pages 3, 4 and 20.)

Shuster, S. M., and M. J. Wade. 2003. Mating Systems and Strategies. Princeton University Press. (Cited on pages 12 and 95.)

Siepielski, A. M., J. D. DiBattista, and S. M. Carlson. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. Ecology Letters 12:1261–1276. (Cited on pages 18 and 47.)

Silva, S., A. Gooderham, M. Forty, B. Morland, and M. C. Lucas. 2015. *Egg drift and hatching success in European river lamprey* Lampetra fluviatilis: *is egg deposition in gravel vital to spawning success?*: EGG DRIFT AND HATCHING SUCCESS IN EUROPEAN RIVER LAMPREY. Aquatic Conservation: Marine and Freshwater Ecosystems 25:534–543. (Cited on pages 206, 207 and 215.)

Silver, G. S., C. W. Luzier, and T. A. Whitesel. 2009. Detection and Longevity of Uncured and Cured Visible Implant Elastomer Tags in Larval Pacific Lampreys. North American Journal of Fisheries Management 29:1496–1501. (Cited on pages 52, 98 and 145.)

Simmons, L. W., and D. J. Emlen. 2006. Evolutionary trade-off between weapons and testes. Proceedings of the National Academy of Sciences 103:16346–16351. Publisher: Proceedings of the National Academy of Sciences. (Cited on page 198.)

Simmons, L. W., and J. L. Fitzpatrick. 2012. Sperm wars and the evolution of male fertility. REPRODUCTION 144:519–534. (Cited on page 8.)

Sims, D. W., V. J. Wearmouth, M. J. Genner, A. J. Southward, and S. J. Hawkins. 2004. Low-temperature-driven early spawning migration of a temperate marine fish. Journal of Animal Ecology 73:333–341. (Cited on page 96.)

Sjoberg, K. 1977. Locomotor activity of river lamprey Lampetra fluviatilis (L.) during the spawning season. Hydrobiologia 55:265–270. (Cited on pages 52, 99 and 209.)

Skulason, S., and T. B. Smith. 1995. Resource polymorphisms in vertebrates. Trends in Ecology & Evolution 10:366–370. (Cited on page 139.)

Slatkin, M. 1978. Spatial patterns in the distributions of polygenic characters. Journal of Theoretical Biology 70:213–228. (Cited on page 226.)

Smallegange, I. M., and T. Coulson. 2013. Towards a general, population-level understanding of eco-evolutionary change. Trends in Ecology & Evolution 28:143–148. (Cited on page 226.)

Smith, S. J., and J. E. Marsden. 2009. Factors Affecting Sea Lamprey Egg Survival. North American Journal of Fisheries Management 29:859–868. (Cited on pages 206, 207 and 215.)

Sorensen, P. W., J. M. Fine, V. Dvornikovs, C. S. Jeffrey, F. Shao, J. Wang, L. A. Vrieze, K. R. Anderson, and T. R. Hoye. 2005. Mixture of new sulfated steroids functions as a migratory pheromone in the sea lamprey. Nature Chemical Biology 1:324–328. (Cited on page 37.)

Soularue, J.-P., and A. Kremer. 2014. Evolutionary responses of tree phenology to the combined effects of assortative mating, gene flow and divergent selection. Heredity 113:485–494. Publisher: Nature Publishing Group. (Cited on pages 230, 240 and 241.)

Stacey, N. E. 1984. Control of the timing of ovulation by exogenous and endogenous factors. Fish reproduction : Strategies and tactics pages 207–222. (Cited on page 24.)

Sterba, G. 1962. Die Neunaugen (Petromyzonidae). ISBN: 9783510410156 Publisher: Schweizerbart'sche Verlagsbuchhandlung. (Cited on page 34.)

Stiver, K. A., and S. H. Alonzo. 2009. Parental and Mating Effort: Is There Necessarily a Trade-Off? Ethology 115:1101–1126. (Cited on page 26.)

Stockley, P., M. J. G. Gage, G. A. Parker, and A. P. Møller. 1997*a*. Sperm Competition in Fishes: The Evolution of Testis Size and Ejaculate Characteristics. The American Naturalist 149:933–954. Publisher: The University of Chicago Press. (Cited on page 187.)

Stockley, P., J. B. Searle, D. W. MacDonald, and C. S. Jones. 1997*b*. Female multiple mating behaviour in the common shrew as a strategy to reduce inbreeding. Proceedings of the Royal Society of London. Series B: Biological Sciences 254:173–179. Publisher: Royal Society. (Cited on page 6.)

Sutherland, W. J. 1985. Chance can produce a sex difference in variance in mating success and explain Bateman's data. Animal Behaviour 33:1349–1352. (Cited on page 13.)

Taborsky, M. 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *In* Advances in the Study of Behavior. Academic Press. Google-Books-ID: E_UQtKg8V7cC. (Cited on page 158.)

———. 1998. Sperm competition in fish: 'bourgeois' males and parasitic spawning. Trends in Ecology & Evolution 13:222–227. (Cited on page 141.)

———. 2008. Alternative reproductive tactics in fish. Cambridge University Press. (Cited on pages 158 and 159.)

Taborsky, M., and H. J. Brockmann. 2010. Alternative reproductive tactics and life history phenotypes. Pages 537–586 *in* P. Kappeler, ed. Animal Behaviour: Evolution and Mechanisms. Springer, Berlin, Heidelberg. (Cited on pages 174 and 195.)

Takayama, M. 2002. Spawning activities and physical characteristics of the spawning ground of Lethenteron reissneri at the headstream of the Himekawa River, central Japan. Ichthyological Research 49:165–170. (Cited on page 35.)

Tentelier, C., J.-C. Aymes, B. Spitz, and J. Rives. 2016. Using proximity loggers to describe the sexual network of a freshwater fish. Environmental Biology of Fishes 99:621–631. (Cited on page 74.)

terHorst, C. P., P. C. Zee, K. D. Heath, T. E. Miller, A. I. Pastore, S. Patel, S. J. Schreiber, M. J. Wade, and M. R. Walsh. 2018. Evolution in a Community Context: Trait Responses to Multiple Species Interactions. The American Naturalist 191:368–380. (Cited on page 242.)

Thiele, J. C., W. Kurth, and V. Grimm. 2014. Facilitating Parameter Estimation and Sensitivity Analysis of Agent-Based Models: A Cookbook Using NetLogo and R. Journal of Artificial Societies and Social Simulation 17:11. (Cited on page 245.)

Tieleman, B. I., H. J. Van Noordwijk, and J. B. Williams. 2008. Nest site selection in a hot desert: trade-off between microclimate and predation risk? The Condor 110:116–124. (Cited on page 216.)

Travis, J. M. J., K. Mustin, K. A. Bartoń, T. G. Benton, J. Clobert, M. M. Delgado, C. Dytham, T. Hovestadt, S. C. F. Palmer, H. Van Dyck, and D. Bonte. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods in Ecology and Evolution 3:628–641. (Cited on page 234.)

Travis, J. M. J., H. S. Smith, and S. M. W. Ranwala. 2010. Towards a mechanistic understanding of dispersal evolution in plants: conservation implications. Diversity and Distributions 16:690–702. (Cited on pages 232 and 241.)

Trivers, R. L. 1974. Parent-Offspring Conflict. American Zoologist 14:249–264. (Cited on page 12.)

Tréhin, C., E. Rivot, L. Lamireau, L. Meslier, A.-L. Besnard, S. D. Gregory, and M. Nevoux. 2021. Growth during the first summer at sea modulates sex-specific maturation schedule in Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 78:659–669. (Cited on page 25.)

Tyler, F., X. A. Harrison, A. Bretman, T. Veen, R. Rodríguez-Muñoz, and T. Tregenza. 2013. Multiple post-mating barriers to hybridization in field crickets. Molecular Ecology 22:1640–1649. (Cited on page 192.)

Urban, M. C., A. Scarpa, J. M. J. Travis, and G. Bocedi. 2019. Maladapted Prey Subsidize Predators and Facilitate Range Expansion. The American Naturalist 194:590–612. Publisher: The University of Chicago Press. (Cited on page 232.)

Uy, J. A. C., G. L. Patricelli, and G. Borgia. 2001. Complex Mate Searching in the Satin Bowerbird Ptilonorhynchus violaceus. The American Naturalist 158:530–542. (Cited on page 178.)

van der Post, D. J., R. Verbrugge, and C. K. Hemelrijk. 2015. The Evolution of Different Forms of Sociality: Behavioral Mechanisms and Eco-Evolutionary Feedback. PLOS ONE 10:e0117027. Publisher: Public Library of Science. (Cited on pages 230, 232 and 239.)

Venables, W. N., and B. D. Ripley. 2002. Random and Mixed Effects. Pages 271–300 *in* W. N. Venables and B. D. Ripley, eds. Modern Applied Statistics with S, Statistics and Computing. Springer, New York, NY. (Cited on page 211.)

Via, S. 2001. Sympatric speciation in animals: the ugly duckling grows up. Trends in Ecology & Evolution 16:381–390. (Cited on page 139.)

Vladykov, V. D., and E. Kott. 1979. Satellite species among the holarctic lampreys (Petromyzonidae). Canadian Journal of Zoology 57:860–867. (Cited on pages 30 and 140.)

Wacker, S., T. Amundsen, E. Forsgren, and K. B. Mobley. 2014. Within-season variation in sexual selection in a fish with dynamic sex roles. Molecular Ecology 23:3587–3599. (Cited on pages 21 and 48.)

Wade, M. J. 1979. Sexual Selection and Variance in Reproductive Success. The American Naturalist 114:742–747. Publisher: The University of Chicago Press. (Cited on pages 13, 49, 54, 100 and 175.)

Wade, M. J., and S. J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. Animal Behaviour 28:446–461. (Cited on pages 13, 54 and 100.)

Wade, M. J., P. Bijma, E. D. Ellen, and W. Muir. 2010. Group selection and social evolution in domesticated animals. Evolutionary Applications 3:453–465. (Cited on page 223.)

Wagner, W. E. 1998. Measuring female mating preferences. Animal Behaviour 55:1029–1042. (Cited on page 172.)

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395. (Cited on page 94.)

Wang, H., N. Johnson, J. Bernardy, T. Hubert, and W. Li. 2013. Monitoring sea lamprey pheromones and their degradation using rapid stream-side extraction coupled with UPLC-MS/MS. Journal of Separation Science 36:1612–1620. (Cited on page 69.)

Wang, H.-Y., Y.-S. Chen, C.-C. Hsu, and S.-F. Shen. 2017. Fishing-induced changes in adult length are mediated by skipped-spawning. Ecological Applications 27:274–284. (Cited on page 244.)

Wang, H.-Y., and T. O. Höök. 2009. Eco-genetic model to explore fishing-induced ecological and evolutionary effects on growth and maturation schedules. Evolutionary Applications 2:438–455. (Cited on page 244.)

Ward, B. A., and S. Collins. 2022. Rapid evolution allows coexistence of highly divergent lineages within the same niche. Ecology Letters 25:1839–1853. (Cited on pages 232 and 243.)

Warren, D. R., J. M. Robinson, D. C. Josephson, D. R. Sheldon, and C. E. Kraft. 2012. Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (Salvelinus fontinalis). Global Change Biology 18:1804–1811. (Cited on page 25.)

Webb, B. W., and F. Nobilis. 1995. Long term water temperature trends in Austrian rivers. Hydrological Sciences Journal 40:83–96. (Cited on page 185.)

Webber, Q. M. R., and E. Vander Wal. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. Journal of Animal Ecology 87:113–127. (Cited on page 222.)

Weber, M. G., C. E. Wagner, R. J. Best, L. J. Harmon, and B. Matthews. 2017. Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution. Trends in Ecology & Evolution 32:291–304. (Cited on pages 224, 242 and 243.)

Wedekind, C., and C. Küng. 2010. Shift of Spawning Season and Effects of Climate Warming on Developmental Stages of a Grayling (Salmonidae). Conservation Biology 24:1418–1423. (Cited on page 94.)

Weir, L. K., J. W. Grant, and J. A. Hutchings. 2011. The Influence of Operational Sex Ratio on the Intensity of Competition for Mates. The American Naturalist 177:167–176. (Cited on page 11.)

Werner, E. E., and B. R. Anholt. 1993. Ecological Consequences of the Trade-Off between Growth and Mortality Rates Mediated by Foraging Activity. The American Naturalist 142:242–272. (Cited on page 139.)

Whitford, M., and A. P. Klimley. 2019. An overview of behavioral, physiological, and environmental sensors used in animal biotelemetry and biologging studies. Animal Biotelemetry 7:26. (Cited on page 74.)

Wiklund, C., and T. Fagerström. 1977. Why do males emerge before females? Oecologia 31:153–158. (Cited on page 122.)

Wilensky, U. 1999. NetLogo: Center for Connected Learning and Computer-Based Modeling. (Cited on page 101.)

Williams, C. T., H. E. Chmura, C. K. Deal, and K. Wilsterman. 2022. Sex-Differences in Phenology: A Tinbergian Perspective. Integrative and Comparative Biology 62:980–997. (Cited on page 95.)

Williams, G. C. 1966. Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist 100:687–690. Publisher: The University of Chicago Press. (Cited on page 9.)

Wittenberger, J. 1983. Tactics of mate choice. Pages 435–447 *in* Mate choice, p. bateson ed. Cambridge University Press. (Cited on page 178.)

Yamazaki, C., and I. Koizumi. 2017. High frequency of mating without egg release in highly promiscuous nonparasitic lamprey Lethenteron kessleri. Journal of Ethology 35:237–243. (Cited on pages 33, 51, 193, 197 and 199.)

Yamazaki, Y., and A. Goto. 2000. Breeding season and nesting assemblages in two forms oflethenteron reissneri, with reference to reproductive isolating mechanisms. Ichthyological Research 47:271–276. (Cited on pages 39 and 140.)

Yamazaki, Y., S. Konno, and A. Goto. 2001. Interspecific differences in egg size and fecundity among Japanese lampreys. Fisheries Science 67:375–377. (Cited on pages 30 and 157.)

Yamazaki, Y., H. Sugiyama, and A. Goto. 1998. Mature dwarf males and females of the arctic lamprey,Lethenteron japonicum. Ichthyological Research 45:404–408. (Cited on pages 32, 38, 140, 141 and 144.)

Yamazaki, Y., R. Yokoyama, T. Nagai, and A. Goto. 2011. Formation of a fluvial non-parasitic population of Lethenteron camtschaticum as the first step in petromyzontid speciation. Journal of Fish Biology 79:2043–2059. (Cited on pages 31 and 143.)

Yang, E., K. Lee, J.-m. Ha, W. Kim, H.-K. Song, I. Hwang, S.-i. Lee, and P. G. Jablonski. 2018. Affordable method of video recording for ecologists and citizen-science participants. Journal of Ecology and Environment 42:11. (Cited on page 74.)

Yasui, Y. 1997. A "Good-Sperm" Model Can Explain the Evolution of Costly Multiple Mating by Females. The American Naturalist 149:573–584. (Cited on page 6.)

———. 1998. The 'genetic benefits' of female multiple mating reconsidered. Trends in Ecology & Evolution 13. (Cited on pages 6 and 110.)

———. 2001. Female multiple mating as a genetic bet-hedging strategy when mate choice criteria are unreliable: Female multiple mating as genetic bet-hedging. Ecological Research 16:605–616. (Cited on page 72.)

Yazawa, Y. 1998. Annual change of lamprey's catch at the lower stream of Ishikari River near Ebetsu city. Tech. rep., Reports of the Taisetsuzan Institute of Science, Japan. (Cited on page 184.)

Yeates, S. E., S. E. Diamond, S. Einum, B. C. Emerson, W. V. Holt, and M. J. G. Gage. 2013. Cryptic choice of conspecific sperm controlled by the impact of ovarian fluid on sperm swimming behavior. Evolution 67:3523–3536. (Cited on page 192.)

Yorke, M. A., and D. B. McMillan. 1979. Nature and cellular origin of the adhesive coats of the lamprey egg (Petromyzon marinus). Journal of Morphology 162:313–325. (Cited on page 207.)

Zanandrea, S. 1959. Speciation among Lampreys. Nature 184:380–380. (Cited on pages 30 and 140.)

Zuk, M., F. Garcia-Gonzalez, M. E. Herberstein, and L. W. Simmons. 2014. Model Systems, Taxonomic Bias, and Sexual Selection: Beyond *Drosophila*. Annual Review of Entomology 59:321–338. (Cited on page 183.)

# Abstract

Spatial and temporal variations in the social environment are predicted to modulate the pattern of inter-sexual interactions within populations through changes in the operational sex ratio and phenotypic composition. Research exploring how the social environment plays a key role in shaping variation in sexual selection usually compares spatially isolated populations or the same populations between breeding seasons. However, small changes in demographics can happen during a breeding season and may also alter selection. Moreover, studies mostly focus on single-species populations with similar life histories, limiting the generalisation of the role of environmental complexity on sexual selection. Driven by this context, this thesis aims to further our understanding of three broad questions (1) How do changes in social context throughout a breeding season influence sexual selection? (2) How do different levels of reproductive synchrony within and between sexes affect sexual selection? and (3) Can the intra-specific process of sexual selection lead to interspecific sexual isolation in sympatric species with synchronized breeding events? To achieve this, I used lampreys as a biological model, as they constitute a highly polygynandrous system in which the duration of individual mating activity is short relative to the length of the breeding season. By developing a model that decomposes the effect of individual traits on the two processes leading to mating success (i.e. number of mating attempts, probability of successful mating), I first showed that the advantage conferred by body size depends on the competitive environment faced by individuals during a breeding season, and their timing of activity (1). Through an experiment study and an Agent-Based-Model, we then highlighted that the level of synchrony within and between sexes modifies the strength and direction of sexual selection, inducing a potential adaptative response in individuals' reproductive timing (2). Finally, I show that considering the complexity of the social environment, e.g. by incorporating the effect of conspecifics with distinct life histories, may explain the emergence of alternative mating strategies through sexual selection such as sneaking in lampreys and shed light on the potential mechanism behind sympatric speciation (3). Overall, this thesis illustrates the role that variation in competitive structure may play on how sexual selection operates both within and between populations and advocates that the complexity and dynamics of the social environment should be more often considered when studying mating system dynamics.

**Keywords:** sexual selection, social environment, lampreys

# Résumé

Les variations spatiales et temporelles de l'environnement social sont supposées moduler le schéma des interactions inter-sexuelles au sein des populations par le biais de changements dans le sex-ratio opérationnel et dans la composition phénotypique. Les recherches explorant la manière dont l'environnement social joue un rôle clé dans la variation de la sélection sexuelle comparent généralement des populations isolées dans l'espace ou des mêmes populations entre des saisons de reproduction successives. Cependant, des changements démographiques peuvent survenir au sein même d'une saison de reproduction et ainsi modifier la sélection à plus petite échelle. De plus, les études se concentrent principalement sur des populations monospécifiques avec des histoires de vie similaires, ce qui limite la généralisation du rôle de la complexité de l'environnement sur la sélection sexuelle. Dans ce contexte, cette thèse visait à approfondir notre compréhension de trois questions majeures (1) comment les changements du contexte social au cours d'une saison de reproduction influencent-ils la sélection sexuelle ? (2) comment les différents niveaux de synchronie reproductive entre et parmi les sexes affectent-ils la sélection sexuelle ? et (3) le processus intraspécifique de sélection sexuelle peut-il conduire à un isolement sexuel interspécifique chez les espèces sympatriques dont les événements de reproduction sont synchronisés ? Pour ce faire, j'ai utilisé les lamproies comme modèle biologique, car elles constituent un système hautement polygynandre dans lequel la durée de l'activité d'accouplement individuelle est courte par rapport à la durée de la saison de reproduction. En développant un modèle qui décompose l'effet des traits individuels sur les deux processus menant au succès de l'accouplement (c'est-à-dire le nombre de tentatives d'accouplement et la probabilité d'accouplement réussi), j'ai d'abord montré que l'avantage conféré par la taille corporelle dépend de l'environnement compétitif auquel les individus sont confrontés pendant la saison de reproduction, et de leur timing d'activité (1). Par le biais d'une étude expérimentale et d'un modèle à base d'agents, j'ai ensuite mis en évidence que le degré de synchronie entre et parmi les sexes modifie la force et la direction de la sélection sexuelle, induisant une réponse adaptative potentielle dans le timing reproductif des individus (2). Enfin, je montre que la prise en compte de la complexité de l'environnement social, par exemple en incorporant l'effet des congénères ayant des histoires de vie distinctes, peut expliquer l'émergence de stratégies d'accouplement alternatives par la sélection sexuelle, telles que le sneaking chez les lamproies, et mettre en lumière le mécanisme potentiel de la spéciation sympatrique (3). Dans l'ensemble, cette thèse illustre le rôle que la variation de la structure compétitive peut jouer sur la manière dont la sélection sexuelle opère à la fois au sein des populations et entre elles, et préconise que la complexité et la dynamique de l'environnement social soient plus souvent prises en compte dans l'étude des dynamiques des systèmes d'appariement.

**Mots clés:** sélection sexuelle, environnement social, lamproies